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Running header: SPECIALIZATION AS A RESPONSE TO COMPETITION

**Local habitat specialization as an evolutionary response to interspecific competition
between two sympatric shrews**

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Interspecific competition affects population dynamics, distribution ranges, and evolution of competing species. The competitive exclusion principle states that ecologically similar species cannot coexist unless they exhibit niche segregation. Herein, we assess whether niche segregation allows the coexistence of *Crocidura russula* and *C. suaveolens* in southwestern

23 Iberia and whether segregation is the result of current (ecological effect) or past (evolutionary
24 effect) competition. We performed an annual live-trapping cycle in the two main habitats of
25 the Odiel Marshes Natural Reserve (OMNR), the tidal marsh and the Mediterranean forest,
26 both in syntopic (i.e., where both species co-occur) and allotopic (where only one of the two
27 species occurs) sites within this Reserve. We modeled the presence/absence of each species in
28 both habitats and sites by generalized linear mixed models. The coexistence of both species
29 was favored by spatial and temporal niche segregation. *Crocidura suaveolens* was restricted
30 to tidal marsh and did not occupy Mediterranean forest, even when *C. russula* was absent. We
31 interpret this to be the result of competition in the past triggering an evolutionary response in
32 *C. suaveolens* towards its specialization in tidal marsh. Moreover, the specialist *C. suaveolens*
33 currently is outcompeting *C. russula* in tidal marshes, reversing the dominance pattern
34 observed elsewhere. The degree of co-occurrence between both species in syntopic sites was
35 low, as they showed inverse dynamics of seasonal abundances. Interspecific competition
36 leading to habitat specialization favors the coexistence of these ecologically similar species.

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38 Key words: coexistence, *Crocidura*, ecologically similar species, evolutionary response,
39 habitat specialization, habitat use, interspecific competition, niche segregation

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42 La competencia interespecífica afecta a la dinámica poblacional, los rangos de distribución y
43 la evolución de las especies competidoras. El principio de exclusión competitiva establece
44 que las especies ecológicamente similares no pueden coexistir a menos que segreguen sus
45 nichos. Aquí, evaluamos si el mecanismo que permite la coexistencia entre *C. russula* y *C.*
46 *suaveolens* en el suroeste de Iberia es la segregación de nicho y si esta es el resultado de la
47 competencia interespecífica actual (efecto ecológico) o pasada (efecto evolutivo). Realizamos

48 un ciclo anual de trampeos en vivo en los dos hábitats principales del Paraje Natural
49 Marismas del Odiel (OMNR), la marisma mareal y el bosque mediterráneo, tanto en sitios
50 sintópicos (es decir, donde coexisten ambas especies) como alotópicos (donde solo una de las
51 dos especies ocurre) dentro de este Paraje. Modelamos la presencia / ausencia de cada especie
52 en ambos hábitats y sitios mediante modelos mixtos lineales generalizados. La coexistencia
53 de ambas especies está favorecida por segregación espacial y temporal de nicho. *Crocidura*
54 *suaveolens* está restringida a marisma mareal y no ocupa bosque mediterráneo, incluso
55 cuando *C. russula* está ausente. Nuestra interpretación es que la competencia en el pasado
56 desencadenó una respuesta evolutiva en *C. suaveolens* hacia su especialización en marisma
57 mareal. Además, el especialista *C. suaveolens* está en la actualidad excluyendo
58 competitivamente a *C. russula* en las marismas mareales, un patrón de dominancia opuesto al
59 observado en otros lugares. El grado de coexistencia en los sitios sintópicos es bajo, porque
60 las dos especies muestran dinámicas inversas de abundancias estacionales. Este estudio
61 ejemplifica cómo la competencia interespecífica puede desencadenar una respuesta evolutiva
62 que conduce a la especialización del hábitat, y cómo esta especialización favorece la
63 coexistencia de especies ecológicamente similares.

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65 Palabras clave: coexistencia, *Crocidura*, especies ecológicamente similares, respuesta
66 evolutiva, especialización de hábitat, uso de hábitat, competencia interespecífica, segregación
67 de nicho.

68 Species coexist in communities that often include species ecologically very similar to each
69 other and that apparently use the same resources (Leibold and McPeck 2006; Ruokolainen
70 and Hanski 2016; Staples et al. 2016). However, the coexistence of ecologically similar
71 species may involve strong competition when resources are limited, causing species to suffer

72 a reduction in fertility, growth, or survivorship as a result of resource exploitation (Sarà et al.
73 2005; Wauters et al. 2005) or interference (Berger and Gese 2007; Geraldi 2015). This
74 competition affects the population dynamics, distributional ranges, and evolution of the
75 competing species (Montgomery et al. 2015; Drury et al. 2018; Neves et al. 2019).

76 The competitive exclusion principle states that two ecologically similar species cannot
77 coexist when resources are limiting unless they exhibit niche segregation (Gause 1934;
78 Hardin 1960). According to this principle, when the competitive relationship between species
79 is highly asymmetric, with one of the species being competitively superior, competition
80 eventually leads to extirpation of the inferior competitor (Yackulic 2017). However,
81 competing species can coexist by using available resources differently (i.e., through niche
82 segregation) because this causes a relaxation of competition pressure (MacArthur and Levins
83 1967). Thus, niche segregation may arise as an ecological effect of interspecific competition,
84 by which the inferior competitor is relegated to a reduced niche (realized niche) where
85 competition is avoided (Begon et al. 2006; Reif et al. 2018). In the absence of the superior
86 competitor, the inferior competitor should expand its niche as a result of competitive release.
87 Conversely, the niche of the inferior competitor could remain unchanged in the absence of the
88 superior competitor as a consequence, not of current but of past interspecific competition
89 (Connell 1980). Competition in the past may have triggered an evolutionary response in the
90 inferior competitor towards a fixed contraction or shift of its previous fundamental niche
91 (Futuyma and Moreno 1988; Mason et al. 2008). However, we must be cautious in invoking
92 past competition as the driver of current niche differences (Connell 1980), as niche
93 differences may arise through processes other than interspecific competition (Begon et al.
94 2006). For example, niche differentiation could be a direct consequence of the adaptive

95 response of the species to different environmental conditions they experienced in allopatry
96 (e.g., Dufour et al. 2015; Wereszczuk and Zalewski 2015).

97 The greater white-toothed shrew (*Crocidura russula*) and the lesser white-toothed
98 shrew (*Crocidura suaveolens*) are two species of small mammals morphologically and
99 ecologically very similar to each other. Both shrews are extremely similar in their external
100 appearances (Biedma et al. 2019b), although they can be distinguished by a detailed analysis
101 of their coloring patterns and body measurements (described in Materials and Methods).
102 *Crocidura russula* often is slightly larger than *C. suaveolens* (Niethammer and Krapp 1990),
103 although in some populations ranges of size and mass are highly overlapping (Poitevin et al.
104 1986, 1987). Moreover, both species are generalist insectivores and feed on the same large
105 variety of prey. The diet of *C. russula* is based on invertebrates such as insects, isopods,
106 molluscs, and annelids, although it occasionally preys on small vertebrates (Bever 1983;
107 Aulagnier et al. 2009; Brahmi et al. 2012). Similarly, *C. suaveolens* bases its diet mainly on
108 invertebrates such as insects, arachnids, isopods, and myriapods (Burda and Bauerová 1985;
109 Bauerova 1988), and occasionally on molluscs, amphipods, annelids, and small vertebrates
110 (Pernetta 1973; Mienis 1996; Rey 2007). Both species are described as habitat generalists.
111 *Crocidura russula* is an abundant and widespread species in North Africa and southwestern
112 Europe, occurring in all habitat types (Ramalhinho et al. 1999; Aulagnier et al. 2016), from
113 highly anthropized habitats, such as urban areas, gardens, and crops, to habitats with high
114 vegetation coverage, such as grasslands, shrublands, and forests. It has been recorded between
115 sea level and 2,000 m of elevation, from the marshes (Poitevin et al. 1987; Biedma et al.
116 2019b) to the Boreo-supalpine forests of the Mediterranean mountains (López-Fuster 2007;
117 Torre et al. 2014). *Crocidura suaveolens* occurs in the Palearctic where it lives in many
118 different habitats (Palomo et al. 2016), from moist deciduous and steppe forests of central

119 Europe (Libois et al. 1999) to semidesert areas and dry Mediterranean scrublands of the
120 Middle East (Mienis 1996; Haim et al. 1997). This species is able to live from sea level to
121 2,500 m, and from marshes (Poitevin et al. 1987; Cagnin et al. 1998; Biedma et al. 2019b) to
122 subalpine meadows (Meylan and Hausser 1974; Bauerova 1988). Shrews of the genus
123 *Crocidura* usually reach annual maximum abundance in autumn-winter when the breeding
124 season ends in Mediterranean climates, and individuals from different generations co-occur
125 (Poitevin et al. 1987; Genoud and Vogel 1990; Mortelliti and Boitani 2009; Torre et al. 2018).

126 Due to these great similarities between *C. russula* and *C. suaveolens*, some kind of
127 segregation in their ecological niches should be expected when living in sympatry. In
128 southwestern Europe numerous studies have reported highly asymmetric competition between
129 these species, with *C. russula* being the dominant species, managing to displace *C. suaveolens*
130 from large areas (Niethammer 1979; Cosson et al. 1996; Kraft 2000; Biedma et al. 2018).
131 Furthermore, the fossil record (e.g., Ruiz-Bustos et al. 1984; Montoya et al. 2001; Barroso
132 Ruiz and Desclaux 2006) indicates that the distribution of *C. suaveolens* in southwestern
133 Europe was much more extensive before the arrival of *C. russula* in the late Pleistocene than
134 at present (Brändli et al. 2005; Cosson et al. 2005; Biedma et al. 2018). These lines of
135 evidence indicate that both the present and past relationship between these two *Crocidura*
136 species is dominated by competition. However, *C. russula* and *C. suaveolens* occur in
137 sympatry in some regions of southwestern Europe (Libois et al. 1999; Ramalhinho et al.
138 1999), although the mechanisms that allow their coexistence remaining poorly understood.
139 Available evidence points to habitat segregation as an important coexistence mechanism.
140 Poitevin et al. (1987) found that, in areas of sympatry in southern France, *C. russula* was
141 abundant in all habitat types, whereas *C. suaveolens* was relegated to the most humid and

142 forested habitats, but in Corsica, where *C. russula* was absent, *C. suaveolens* occupied a wider
143 range of habitats.

144 A similar situation seems to occur in the Gulf of Cádiz, southwestern Iberia. Here, *C.*
145 *russula* is abundant and widespread and occupies all habitat types, whereas *C. suaveolens* is a
146 rare species present only in tidal marshes located at the mouths of some rivers of the region
147 (Biedma et al. 2019b). These marshes are thus the only areas of sympatry for both species in
148 the Gulf of Cádiz. However, within these marshes there are sites of syntopy (i.e., sites
149 occupied by both species) and allotopy (i.e., sites where only one species occurs). The two
150 species are syntopic only on the edge of the marshes, whereas in the interior of the marshes
151 only *C. suaveolens* was found (Biedma et al. 2019b). The interior of the marshes are
152 dominated by marsh habitats but, sometimes, there are also patches of forest. Therefore, the
153 interior of the marshes provides a great opportunity to test whether *C. suaveolens* expands its
154 realized habitat-niche when *C. russula* is absent, and thus whether past competition has
155 caused a stable reduction of the fundamental niche of *C. suaveolens* in this region.

156 The aim of this study is to assess whether niche segregation allows the coexistence of
157 *C. russula* and *C. suaveolens* in the marshes of the Gulf of Cádiz, and whether such niche
158 segregation is the result of current (ecological effect) or past (evolutionary effect)
159 interspecific competition. We specifically focused on the differences in habitat use, because
160 habitat use determines access to resources, and hence could directly influence the
161 reproductive success and survival of species (Powell and Mitchell 2012; Dufour et al.
162 2015). We also explored whether these species have different dynamics of seasonal
163 abundances, as competing species can coincide spatially as long as they access resources at
164 different times (temporal dimension of the niche; Albrecht and Gotelli 2001). Given previous
165 knowledge of the competitive relationship between these species, we expected that the

166 coexistence of *C. russula* and *C. suaveolens* would be facilitated by spatial niche segregation
167 associated with differentiated habitat-use patterns, by temporal niche segregation determined
168 by asynchronous variation of their seasonal abundances, or both. Furthermore, if niche
169 segregation were driven by current interspecific competition, then *C. suaveolens*, the
170 supposed inferior competitor, should shift its habitat use patterns in sites of allotopy with
171 respect to sites of syntopy with *C. russula*. By contrast, if niche segregation were the result of
172 an evolutionary response to past competition, then *C. suaveolens* should not shift its habitat-
173 use patterns between allotopic and syntopic sites.

174 MATERIALS AND METHODS

175 *Study area.*---The study was conducted in the Odiel Marshes Nature Reserve (29S
176 679633 4121992; hereafter OMNR), a marsh area located at the Odiel River mouth, on the
177 coast of the Gulf of Cádiz, southwestern Iberia (Fig. 1). OMNR was declared a Biosphere
178 Reserve in 1983 by UNESCO and it is one of the most extensive (7,185 ha) and diverse
179 marshes of the Iberian Peninsula (Nieva et al. 2005). The climate is Mediterranean oceanic
180 subhumid and is strongly influenced by the Atlantic Ocean (Gómez-Zotano et al. 2015).
181 Summer is hot and dry; the autumn and winter seasons are mild and concentrate the bulk of
182 the rainfall, whereas spring has intermediate characteristics. Mean annual rainfall ranges from
183 500 to 900 mm.

184 The two main habitats of OMNR are tidal marsh and Mediterranean forest. Most of
185 OMNR is formed by tidal marsh, but in the periphery and in some islands in the interior of
186 this Reserve there are extensive patches of Mediterranean forest (Fig. 1). Mediterranean forest
187 patches in the interior islands are completely surrounded by tidal marsh. The tidal marsh and
188 the Mediterranean forest are considered of community interest by the Habitats Directive
189 (Directive 92/43/CEE). Tidal marshes of OMNR are characterized by a high coverage of

190 seagrass and a rather homogeneous structure. Some of the most representative plant
191 associations are: *Puccinellio ibericae-Sarcocornietum perennis*, whose dominant species are
192 *Spartina maritima* and *Sarcocornia perennis*; *Cistancho phelypaeae-Sarcocornietum*
193 *fruticosae*, which is characterized by the presence of *Sarcocornia fruticosa* and *Halimione*
194 *portulacoides*; and *Inulo crithmoidis-Arthrocnemetum macrostachyi* and *Polygono*
195 *equisetiformis-Limoniastrum monopetali*, with *Arthrocnemum macrostachyum* and
196 *Limoniastrum monopetalum* being the most representative species, respectively.
197 Unfortunately, many areas of OMNR are invaded by the South American neophyte *Spartina*
198 *densiflora*, which can become the most abundant species in some tidal marsh associations
199 mentioned, displacing native vegetation. Mediterranean forests of OMNR are dominated
200 mainly by *Pinus pinea* and the *Osyrio quadripartitae-Juniperetum turbinatae* association,
201 with *Juniperus turbinata*, *Olea europaea* and *Quercus coccifera* trees, and *Pistacia lentiscus*,
202 *Phillyrea angustifolia* and *Myrtus communis* shrub species. Other common shrub species are
203 *Cistus* spp., *Halimimum* spp., gorses *Ulex* spp., *Stauracanthus genistoides*, and rosemary
204 *Rosmarinus officinalis*.

205 *Identification criteria.*--- *Crocidura suaveolens* and *C. russula* are two
206 morphologically similar species. However, there are morphological criteria based on color
207 patterns and biometric data that allow both species to be identified and distinguished
208 (Aulagnier et al. 2009). In the Gulf of Cádiz populations, we selected, based on accumulated
209 experience, a set of morphological criteria that allow the unequivocal identification of both
210 species. These criteria have been genetically validated in our previous studies (Biedma et al
211 2018; Biedma et al 2019a). Both species have slightly different coat colorations in the Gulf of
212 Cádiz (Supplementary Data SD1). The back coat of *C. suaveolens* is dark gray (topcoat) and
213 brown (undercoat), whereas the belly coat is somewhat lighter with whitish and yellowish

214 tones. In this species, the back-belly delimitation is not very marked. In addition, the lateral
215 areas of the snout, lower jaw, legs, ears, and tail are dark gray like the back coat. *Crocidura*
216 *russula* has a light gray (topcoat) and brown (undercoat) coat on the back, while the belly coat
217 is whitish. The back-belly delimitation for *C. russula* is much more evident than in *C.*
218 *suaveolens*. In addition, *C. russula* has pink tones that are easily appreciated in the lateral
219 areas of the snout, lower jaw, legs, ears, and tail.

220 *Shrew sampling*.---A complete annual live-trapping cycle, from spring 2013 to spring
221 2014 (both seasons included), was performed. Shrews were sampled with Trip trap live traps
222 (Trixie Heimtierbedarf, Tarp, Germany) baited with *Tenebrio molitor* (yellow mealworms)
223 larvae. Sampling was conducted in the Mediterranean forest and the tidal marsh of OMNR,
224 and in two study sites, on OMNR edge and in the Saltés Island, an island located in OMNR
225 interior (Fig. 1). One trapping session was performed per season. In each season, 11 trapping
226 lines were established (Table 1 and Fig. 1): four in Mediterranean forest (two on OMNR edge
227 and two on OMNR interior) and seven in tidal marsh (two on OMNR edge and five on
228 OMNR interior). The number of trapping points set by trapping line ranged between seven
229 and 15 (Table 1). Trapping points were set at 50-m intervals along the trapping lines. The
230 geographical location (latitude–longitude) of the trapping points was the same in all seasons.
231 Three traps were set in each trapping point to increase the capture probability of shrews and
232 minimize saturation by other small mammals. In each season, traps were active for four and
233 three consecutive nights in Mediterranean forest and tidal marsh, respectively. In the
234 Mediterranean forest, traps were active one night more because a low capture rate was
235 obtained in a previous test. All captured individuals were weighed and measured, and sex was
236 determined. Individuals were marked by ear-clipping and immediately released. Our study
237 followed ASM guidelines (Sikes et al. 2016) and was performed with official permit from the

238 competent environmental authority (Junta de Andalucía) and with a positive evaluation of the
239 bioethics committee of the University of Huelva.

240 *Estimation of prey availability.*---To estimate prey availability in the two main habitats
241 of OMNR, arthropod sampling was carried out simultaneously with the shrew trapping. Three
242 arthropod pitfall traps (diameter: 7.5 cm, height: 11.7 cm; Siewers et al. 2014) were set in
243 each shrew-trapping line. Arthropods were preserved in ethanol (96%) and subsequently
244 identified to Order using standard determination keys (Barrientos 1988). All captured
245 individuals were counted and measured (total length) with a precision of 0.5 mm. Total
246 Arthropoda Dry Mass (mg) was estimated using allometric equations. For non-crustacean
247 arthropods we used equations of Hódar (1996), whereas for *Isopoda* we used the equation for
248 *Tylos ponticus* (Dias et al. 2005), and for *Amphipoda* the equation for *Orchestia gammarellus*
249 (Dias and Sprung 2003). Malacostraca Dry Mass (mg) was also estimated and considered as
250 an explanatory variable in subsequent analyses, as Malacostraca crustaceans (*Isopoda* and
251 *Amphipoda*) represented a significant proportion (36%) of the total arthropods dry mass and,
252 specially, of the total arthropods dry mass sampled in tidal marsh habitats (62%). Averaged
253 seasonal values of Arthropoda Dry Mass and Malacostraca Dry Mass were calculated for each
254 shrew trapping line and assigned to all trapping points for shrews set on the same trapping
255 line.

256 *Presence–absence modeling for C. suaveolens and C. russula.*---Presence–absence of
257 *Crocidura* species at each trapping point was predicted based on a small set of explanatory
258 variables (Supplementary Data SD2): Habitat (Mediterranean forest or tidal marsh), Location
259 (OMNR edge or OMNR interior), Season, and prey availability (Arthropoda Dry Mass and
260 Malacostraca Dry Mass). We considered that a *Crocidura* species was present at a trapping
261 point if it was captured at least once in the season. Correlations between continuous variables

262 were computed through Pearson's correlation coefficients and correlations between
263 categorical and continuous variables were computed using generalized linear models (GLMs).
264 These preliminary analyses revealed a high correlation between Arthropoda Dry Mass and
265 Malacostraca Dry Mass ($r = 0.51$), and between Arthropoda Dry Mass and Season ($P =$
266 0.0098), so these pairs of variables were never included in the same model.

267 Candidate model equations were constructed with each of the explanatory variables
268 defined and with all possible combinations. Candidate model equations were fitted using
269 generalized linear mixed models (GLMM) in SAS v. 9.3 (procedure GLIMMIX; SAS
270 Institute Inc. 2012) with a binomial distribution and logit link function. Models were fitted for
271 each *Crocidura* species separately. The identification code of trapping points nested in the
272 trapping line was modelled as a random factor. We selected the most supported model by use
273 of protocols based on the Akaike information criterion (AIC), and we considered as plausible
274 all models with $\Delta AIC < 2$ (Burnham et al. 2011).

275 *Co-occurrence.*---Sometimes spatial niche segregation only can be determined at a
276 fine scale (Firth and Crowe 2010), thus we used the coefficient of Jaccard (Krebs 1999) to
277 estimate the degree of co-occurrence between *C. russula* (*Cr*) and *C. suaveolens* (*Cs*) in sites
278 of syntopy in OMNR:

$$279 \quad J = \frac{TPCr1Cs1}{(TPCr1Cs1) + (TPCr1Cs0) + (TPCr0Cs1)}$$

280 where $TPCr1Cs1$ was the number of trapping points where both species were captured
281 together during the same season, $TPCr1Cs0$ was the number of trapping points where only *C.*
282 *russula* was captured, and $TPCr0Cs1$ was the number of trapping points where only *C.*
283 *suaveolens* was captured. The coefficient of Jaccard varies from 0 (the two species are never
284 captured together), through 0.5 (independence), to 1 (the two species are always captured

285 together). To test significance, observations of all seasons were bootstrapped (10,000
286 replicates), and the observed value of the coefficient of Jaccard was considered significant if
287 the 95% confidence interval of the bootstrap distribution did not include 0.5.

288 RESULTS

289 A total of 355 individuals of *C. suaveolens* and 44 individuals of *C. russula* were
290 captured throughout the annual trapping cycle in OMNR (Table 2), using a trapping effort of
291 6,459 trap-nights (3,264 trap-nights in Mediterranean forest and 3,195 trap-nights in tidal
292 marsh). The mean body mass for *C. suaveolens* was 7.8 ± 1.33 g ($n = 265$ individuals; range =
293 3.9 - 11 g) and 6.7 ± 1.02 g ($n = 40$ individuals; range = 4.7 – 8.4 g) for *C. russula*. The mean
294 body masses of both species were significantly different ($t_{303} = -4.76$, $P < 0.001$). Practically
295 all *C. russula* (42 individuals) were captured on OMNR edge, both in Mediterranean forest
296 and in tidal marsh, although its capture rate was twice as high in tidal marsh as in
297 Mediterranean forest (Table 2). *Crocidura russula* was practically absent on OMNR interior,
298 where only two individuals of this species were captured in tidal marsh (Table 2). Overall
299 capture rate of *C. russula* on OMNR edge was moderate, whereas on OMNR interior its
300 capture rate was practically null (17.5 and 0.5 individuals per 100 trapping points,
301 respectively; Fig. 2). Overall capture rate of *C. russula* was similar in Mediterranean forest
302 and tidal marsh (6.3 and 7.6, respectively; Fig. 2). *Crocidura suaveolens* was present both on
303 the edge and in the interior of OMNR, but all 355 individuals of *C. suaveolens* were captured
304 in tidal marsh and none in Mediterranean forest (Table 2). Overall capture rate of *C.*
305 *suaveolens* on OMNR interior was twice as high as on OMNR edge (70.8 and 33.7
306 individuals per 100 trapping points, respectively; Fig. 2), and its capture rate in tidal marsh
307 was high (100 individuals per 100 trapping points; Fig. 2).

308 As *C. russula* was mostly found on OMNR edge (95.4% of the captures), and *C.*
309 *suaveolens* only in tidal marsh habitat (100% of the captures), the variable Location could not
310 be used to model the presence of *C. russula*, and the variable Habitat could not be used to
311 model the presence of *C. suaveolens*. In these instances, a low or null number of presences in
312 one of the two levels of these variables caused the models to not converge. For *C. russula*, the
313 best model included as predictors Season and Habitat (Supplementary Data SD3). A second
314 model including only Season as a predictor also was supported ($\Delta AIC < 2$). The probability of
315 capture of *C. russula* was higher in spring and lower in autumn, and higher in tidal marsh than
316 in Mediterranean forest (Fig. 3). Arthropoda Dry Mass had a low positive effect on the
317 probability of capture of *C. russula*. For *C. suaveolens* the best model included Season,
318 Location, and Malacostraca Dry Mass as predictors (Supplementary Data SD3). The
319 probability of capture of *C. suaveolens* was highest in autumn and lowest in spring, greater on
320 OMNR interior than on OMNR edge (Fig. 3), and it was positively related to the availability
321 of Malacostraca Dry Mass (Fig. 4).

322 In sites of syntopy (i.e., in tidal marsh of OMNR edge), the degree of co-occurrence
323 between *C. russula* and *C. suaveolens* was very low. Both species were captured at the same
324 trapping points during the same season on only four occasions of 100 possible (Table 3). The
325 value of the Jaccard coefficient obtained was very close to zero $J = 0.07$ (0.02–0.14; 95%
326 confidence interval) and significant.

327 DISCUSSION

328 Our results confirm that *C. russula* and *C. suaveolens* in OMNR demonstrated both
329 spatial and temporal niche segregation. As expected for a habitat generalist species, *C. russula*
330 was present in the two habitats of OMNR (Table 2, Fig. 2). However, contrary to
331 expectations, *C. suaveolens* was found only in tidal marsh and was never captured in

332 Mediterranean forest (Table 2, Fig. 2). The capture rates of both species in OMNR also were
333 different from what was expected. In Western Europe, *C. suaveolens* is much less abundant
334 than *C. russula* when sympatric (Libois et al. 1999); however, the capture rate of *C.*
335 *suaveolens* in OMNR was eight times higher than the capture rate of *C. russula* (56.6 and 7.0
336 individuals captured by 100 trapping points, respectively; Table 2). Therefore, the marshes of
337 the Gulf of Cádiz are, along with some coastal areas of southern France (Poitevin et al. 1987),
338 the only known places where *C. suaveolens* is more abundant than *C. russula* when
339 sympatric.

340 In OMNR, *C. suaveolens* did not occupy the Mediterranean forest even when *C.*
341 *russula* was absent (i.e., the Mediterranean forest of OMNR interior, on the Saltés Island;
342 Table 2, Fig. 1). We expected that if niche segregation was a consequence of current
343 competition between the species, in the absence of the hypothetical superior competitor (i.e.,
344 *C. russula*), the inferior competitor (i.e., *C. suaveolens*) would expand its habitat niche.
345 However, *C. suaveolens* did not expand its habitat niche in the absence of *C. russula*,
346 indicating that the niche filled by *C. suaveolens* is restricted, but not by current competition
347 with *C. russula*. Thus, Mediterranean forest does not seem to be part of the fundamental niche
348 of *C. suaveolens* in the Gulf of Cádiz. The Mediterranean forest patches of OMNR are well
349 preserved, having a high structural complexity and diverse invertebrate communities
350 (Supplementary Data SD4), so low habitat quality cannot explain the absence of *C.*
351 *suaveolens* in Mediterranean forest. Nor it can be argued that *C. suaveolens* is not a typical
352 species of the Mediterranean forest. In high-elevation areas of the central and northwestern
353 Iberian Peninsula, *C. suaveolens* and *C. russula* co-occur in Mediterranean forest (Biedma et
354 al. 2018), and it is a common habitat for *C. suaveolens* in other parts of its range where *C.*
355 *russula* is absent, such as Corsica, Italy, and Israel (Poitevin et al. 1987; Haim et al. 1997;

356 Cagnin et al. 1998; Mortelliti and Boitani 2009). Therefore, one possibility is that the
357 restriction of the habitat use observed for *C. suaveolens* in the Gulf of Cádiz may have arisen
358 as an evolutionary response of this species to past competition with *C. russula*. Based on the
359 fossil record (Ruiz-Bustos et al. 1984; Montoya et al. 2001; Barroso Ruiz and Desclaux
360 2006), the distribution of *C. suaveolens* in southwestern Europe was wider than at present,
361 and that its range reduction coincides with the arrival of *C. russula* in the late Pleistocene
362 (Brändli et al. 2005; Cosson et al. 2005; Biedma et al. 2018). So, competition with the newly
363 arrived species may be the cause of contraction of the *C. suaveolens* range. Recently we
364 reported how the phylogeography of *C. suaveolens* in Iberia has been shaped by competition
365 with *C. russula* (Biedma et al. 2018). Thus, in most of the habitats of the Gulf of Cádiz, the
366 competitive superiority of *C. russula* would have caused the extirpation of *C. suaveolens*.
367 However, individuals of *C. suaveolens* inhabiting tidal marshes could have escaped from the
368 competition exerted by *C. russula*. Maybe in this exceptionally humid habitat, *C. suaveolens*
369 has some competitive advantage (in fertility, growth, or survivorship) over *C. russula*, a more
370 thermophilic species (Torre et al. 2014; Torre et al. 2018) that reaches its optimum in a dry
371 Mediterranean climate (López-Fuster 2007; Aulagnier et al. 2016). The tidal marsh is a
372 habitat subjected to periodic flooding where the predominant prey are Malacostraca
373 crustaceans (62%, Supplementary Data SD4), which are infrequent prey for these two shrew
374 species (Bauerova 1988; Brahmi et al. 2012). In this sense, the behavioral and ecological
375 plasticity of *C. suaveolens* (Pernetta 1973) could favor its survival in these habitats compared
376 to *C. russula*. Presence of *C. suaveolens* in OMNR was influenced by availability of
377 Malacostraca Dry Mass (Fig. 4). Natural selection may have generated specific adaptations
378 to tidal marshes in *C. suaveolens*, apparently associated with a loss of capacity to live in other
379 habitats, resulting in a habitat specialization that ultimately favored the stable coexistence of
380 both species in the region (Begon et al. 2006).

381 We are aware of the difficulty in proving that past competition has been the ultimate
382 driver of observed niche differences. As Connell (1980:137) warned, we must be cautious and
383 not attribute all observed niche differences to the “ghost of past competition”. An alternative
384 hypothesis to explain the current situation in OMNR is that the specialization of *C.*
385 *suaveolens* could be due to optimal habitat selection (Wereszczuk and Zalewski 2015).
386 Besides the population in OMNR herein described, populations of *C. suaveolens* in the
387 Channel Islands also are known to feed mainly on marine organisms in the tidal zone
388 (Pernetta 1973). It is thus possible that the adaptation of *C. suaveolens* to feeding on marine
389 organisms could have occurred long before the appearance of *C. russula* in the Gulf of Cádiz,
390 and that this may have given the species a competitive advantage over *C. russula* in marshes,
391 where marine organisms, e.g., Malacostraca, are abundant. Perhaps those same, or other
392 subsequent adaptations to tidal marsh, reduced the ability of the species to occupy the
393 Mediterranean forest. When *C. russula* appeared on the Iberian Peninsula, it could
394 outcompete *C. suaveolens* in most habitats except marshes, due to adaptations that *C.*
395 *suaveolens* acquired in the absence of competition with *C. russula*.

396 The two hypotheses are possible explanations of this current ecological situation in OMNR.
397 However, temporal coincidence between range reduction and genetic isolation of *C.*
398 *suaveolens* populations in the Iberian Peninsula, with the arrival of *C. russula* to the
399 Peninsula, invites us to think that competition between these species may have acted as a
400 major driver of the observed niche segregation.

401 Only two *C. russula* were captured on the Saltés Island (OMNR interior; Table 2, Fig.
402 1), possibly because a large amount of fill material was brought in to build an access road. It
403 is likely that Saltés Island is inaccessible for this species because of the surrounding water
404 channels. Nevertheless, access to this island is not a problem for *C. suaveolens* or for other

405 species of the small mammal community captured in this study, such as *Mus spretus* and
406 *Suncus etruscus*, or previously cited by us, such as *Rattus norvegicus* (Biedma et al. 2019b).
407 An alternative explanation is that *C. suaveolens* is preventing the establishment of *C. russula*
408 on islands of OMNR interior. This supposes that, unlike what is usually described in other
409 Mediterranean areas (Libois et al. 1999), the competitive dominant species in tidal marsh is
410 not *C. russula*, but *C. suaveolens*. This is plausible because habitat specialists usually are the
411 dominant species in interspecific competitive relationships in their specific habitats, being
412 able to displace more generalist competitors (Morris 1996; Büchi and Vuilleumier 2014).
413 Therefore, the absence of both *Crocidura* species in the Mediterranean forest in the Saltés
414 Island can be explained by *C. suaveolens* not being able to inhabit them because of its
415 specialization in the tidal marsh, and *C. russula* not colonizing these forests because they are
416 completely surrounded by tidal marsh, where *C. suaveolens* is dominant and acts as a
417 biological barrier for *C. russula*. The competitive superiority of *C. suaveolens* in tidal marsh
418 habitats of OMNR also can be supported by the report of *C. russula* being abundant in other
419 tidal marshes of the Gulf of Cádiz (Biedma et al. 2019b) and southwestern Europe where *C.*
420 *suaveolens* is absent (Marques et al. 2015; van der Ende et al. 2017). *Crocidura russula* only
421 seems to be scarce or absent in tidal marshes occupied by *C. suaveolens*.

422 The habitat segregation patterns reported herein are consistent with those described for
423 many other similar shrews. For example, habitat segregation often allows the coexistence of
424 the water shrews *Neomys fodiens* and *N. anomalus* (Rychlik 1997; Keckel et al. 2014), and
425 also has been described among a wide variety of shrews of the genus *Sorex* (Hawes 1977;
426 Neet and Hausser 1990; Ford et al. 2001). Regarding the temporal dimension of the niche, *C.*
427 *suaveolens* had patterns of seasonal abundances concordant with those described for the genus
428 *Crocidura* in Mediterranean areas (Poitevin et al. 1987; Genoud and Vogel 1990; Mortelliti

429 and Boitani 2009), whereas *C. russula* showed patterns of seasonal abundances inverse to
430 these (Fig. 3). The unusual patterns of seasonal abundances in *C. russula* do not seem to be
431 explained by prey availability, as the season of maximum abundance of *C. russula* (spring;
432 Fig. 3) did not correspond with the season of maximum prey availability (summer in
433 Mediterranean forest and autumn in tidal marsh; Supplementary Data SD4). Moreover, in
434 other Mediterranean habitats of Iberia where *C. suaveolens* is absent, *C. russula* shows
435 seasonal abundance patterns concordant with those described for the genus in Mediterranean
436 areas (Torre et al. 2018). Interspecific competition may explain these unusual patterns of *C.*
437 *russula* in OMNR. *Crocidura russula* (the subordinate generalist species) may have reached
438 its maximum abundance in spring-summer because the abundance of *C. suaveolens* (the
439 dominant specialist species) was somewhat lower in these seasons (Fig. 3). Conversely, the
440 high abundance of *C. suaveolens* in autumn-winter would cause a low abundance of *C.*
441 *russula*. The coexistence of both species in OMNR edge is favored because *C. russula*
442 segregates from *C. suaveolens* both spatially, by occupying the Mediterranean forest adjacent
443 to the tidal marsh, and temporally, by using the tidal marsh in different seasons.

444 In conclusion, the coexistence of *C. russula* and *C. suaveolens* in the marshes of the
445 Gulf of Cádiz appears to be facilitated by spatial and temporal niche segregation. This niche
446 segregation is the result of two competitive processes that have acted at different times.
447 Interspecific competition in the past likely triggered an evolutionary response in *C.*
448 *suaveolens* that caused this species to specialize in tidal marsh. The habitat specialization of
449 *C. suaveolens* may have favored its coexistence with *C. russula* by reversing the competitive
450 relationship between these species. Current interspecific competition, in which the
451 competitively dominant specialist is *C. suaveolens*, is likely driving an ecological response of

452 *C. russula* consisting of the exclusion of tidal marsh from its realized niche in the Gulf of
453 Cádiz.

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462 SUPPLEMENTARY DATA

463 **Supplementary Data SD1.**---Individuals of the lesser white-toothed shrew (*C. suaveolens*,
464 above) and the greater white-toothed shrew (*C. russula*, below) captured in Odiel Marshes
465 Nature Reserve, Gulf of Cádiz, southwestern Iberia. Note the different colorations of the coat,
466 sides of the snout, ears and legs in the two species.

467 **Supplementary Data SD2.**---Explanatory variables used to model the capture probability of
468 *Crocidura* shrews in Odiel Marshes Nature Reserve (OMNR), Gulf of Cádiz, southwestern
469 Iberia. Trapping was performed from spring 2013 to spring 2014 (both seasons included).

470 **Supplementary Data SD3.**---Variables affecting the capture probability of *Crocidura russula*
471 and *Crocidura suaveolens* in Odiel Marshes Natural Reserve, Gulf of Cádiz, southwestern
472 Iberia. Trapping was performed from spring 2013 to spring 2014 (both seasons included).
473 Models are ranked by AIC values. Δ AIC is the difference of a given AIC value compared to

474 the smallest AIC value. The supported models ($\Delta AIC < 2$) are shown in bold. AIC weights
475 (wAIC) indicate the relative support of each model.

476 **Supplementary Data SD4**.---Prey availability by Habitat and Season in Odiel Marshes
477 Natural Reserve, Gulf of Cádiz, southwestern Iberia (29S 679633 4121992). One arthropod
478 trapping session was performed per season from spring 2013 to spring 2014 (both seasons
479 included). Prey are shown grouped by Class. For the Insecta Class, the main Orders identified
480 are also shown. For each Class, the average number of individuals caught per trap and the
481 average dry mass per trap (in parentheses) are shown. *n* is the number of arthropod traps used
482 in each season.

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FIGURE LEGENDS

698 **Fig. 1.**— **Map** of the study area showing the locations of the trapping lines on the edge (a)
 699 and on the interior (Saltés Island, b) of Odiel Marshes Natural Reserve (OMNR), Gulf of
 700 Cádiz, southwestern Iberia. The tidal marsh habitat is shown with a dotted fill pattern and the
 701 Mediterranean forest habitat in dark gray. Other habitat types (mainly crops) are shown in
 702 white. Urban and industrial areas are shown with a squared fill pattern. The salt water is
 703 shown in light gray. Trapping lines set in Mediterranean forest habitat (black stars) and tidal
 704 marsh habitat (black squares) are also shown. Trapping was performed from spring 2013 to
 705 spring 2014 (both seasons included).

706 **Fig. 2.**— Overall capture rates of *Crocidura russula* (*Cr*) and *Crocidura suaveolens* (*Cs*) by
 707 Location and Habitat in Odiel Marshes Natural Reserve (OMNR), Gulf of Cádiz,
 708 southwestern Iberia. Trapping was performed from spring 2013 to spring 2014 (both seasons
 709 included). Capture rates are shown as the number of individuals captured by 100 trapping
 710 points (TP). See also Table 2 for detailed capture rates by Location and Habitat.

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712 **Fig. 3.**— Capture probabilities of *C. suaveolens* and *C. russula* depending on Season (above),
 713 capture probability of *Crocidura suaveolens* depending on Location (below left), and of
 714 *Crocidura russula* depending on Habitat (below right) in Odiel Marshes Natural Reserve
 715 (OMNR), Gulf of Cádiz, southwestern Iberia. Trapping was performed from spring 2013 to
 716 spring 2014 (both seasons included). Captures probabilities are shown as $\text{lsmean} (\pm 95\%$
 717 $\text{confidence interval})$. The variable Habitat was not included in the models of *C. suaveolens*
 718 because the capture probability of this species in the Mediterranean forest was zero. The

719 variable *Location* was not included in the models of *C. russula* because the capture
720 probability of this species on OMNR interior was virtually zero.

721 **Fig. 4.**— Capture probability of *Crocidura suaveolens* depending on the availability of
722 Malacostraca Dry Mass in Odiel Marshes Natural Reserve (OMNR), Gulf of Cádiz,
723 southwestern Iberia. One trapping session was performed per season from spring 2013 to
724 spring 2014 (both seasons included). Only the model results for Season with the minimum
725 (Spring 2013) and maximum (Autumn 2013) capture probabilities are shown. The location on
726 OMNR edge is represented with continuous lines and the location on OMNR interior with
727 discontinuous lines.

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735 **TABLES**

736 **Table 1.**— Number of trapping lines (TL) and trapping points (TP) set by Location, Habitat,
 737 and Season in Odiel Marshes Natural Reserve (OMNR), Gulf of Cádiz, southwestern Iberia.
 738 One trapping session was performed per season from spring 2013 to spring 2014 (both
 739 seasons included).

		Spring	Summer	Autumn	Winter	Spring
Location	Habitat	2013	2013	2013	2014	2014
		TL/TP	TL/TP	TL/TP	TL/TP	TL/TP
OMNR edge	Med. Forest	2/20	2/30	2/30	2/30	2/30
	Tidal marsh	2/20	2/20	2/20	2/20	2/20
OMNR interior	Med. Forest	2/24	2/27	2/27	2/27	2/27
	Tidal marsh	5/51	5/51	5/51	5/51	5/51
Total		11/115	11/128	11/128	11/128	11/128

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750 **Table 2.**— Number of individuals of *Crocidura russula* (*nCr*) and *Crocidura suaveolens*
751 (*nCs*) captured, number of trapping points (TP) used, and capture rates of each species by
752 Location and Habitat in Odiel Marshes Natural Reserve (OMNR), Gulf of Cádiz,
753 southwestern Iberia. Trapping was performed from spring 2013 to spring 2014 (both seasons
754 included). Capture rates are shown as number of individuals captured by 100 trapping points.
755 Overall capture rates by Location and Habitat in OMNR for *C. russula* and *C. suaveolens* are
756 shown in Fig. 2.

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Location	Habitat	TP	<i>nCr</i>	(<i>nCr</i> /TP)100	<i>nCs</i>	(<i>nCs</i> /TP)100
OMNR edge	Med. Forest	140	17	12.1	0	0
	Tidal marsh	100	25	25	81	81
OMNR interior	Med. Forest	132	0	0	0	0
	Tidal marsh	255	2	0.8	274	107.5
Total		627	44	7.0	355	56.6

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772 **Table 3.**— Patterns of co-occurrence for *Crocidura russula* (*Cr*) and *Crocidura suaveolens*
773 (*Cs*) in tidal marsh habitats on the edge of Odiel Marshes Natural Reserve, Gulf of Cádiz,
774 southwestern Iberia. TPCr0Cs0, trapping points with no *Crocidura* species; TPCr0Cs1
775 trapping points with *Crocidura suaveolens* only; TPCr1Cs0 trapping points with *Crocidura*
776 *russula* only; TPCr1Cs1 trapping points with both species present. One trapping session was
777 performed per season from spring 2013 to spring 2014 (both seasons included)

778	Site	Spring	Summer	Autumn	Winter	Spring	All
779	occupation	2013	2013	2013	2013	2014	seasons
780	TPCr0Cs0	5	12	2	7	14	40
781	TPCr0Cs1	5	3	17	13	3	41
782	TPCr1Cs0	7	5	0	0	3	15
783	TPCr1Cs1	3	0	1	0	0	4
	Total	20	20	20	20	20	100

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