

1 **Demographic vulnerability in cliff-dwelling *Sonchus***  
2 **species endemic to the western Mediterranean**

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17

18 **Running title:** Demographic vulnerability in cliff-dwelling *Sonchus* sect.

19 *Pustulati.*

20 **Abstract**

21 Species of *Sonchus* section *Pustulati* (*Sonchus masquindalii*, *S. fragilis* and *S.*  
22 *pustulatus*) constitute a group of endemic cliff plants in the Mediterranean  
23 region, restricted to narrow non-overlapping areas within the Baetic-Rifan  
24 hotspot of plant species diversity. *S. pustulatus* occurs both in SE Spain and N  
25 Africa, whereas the other related species are exclusive to N Africa. We  
26 characterized all the extant populations of *Sonchus* species (section *Pustulati*)  
27 in 2008 by recording population size, demographic structure and reproductive  
28 success, and we estimated the population trends for the critically endangered  
29 Spanish *S. pustulatus* by repeating censuses in 2013. We also calculated the  
30 stochastic population growth rate ( $\lambda_S$ ) and modelled future viability (PVA) of one  
31 of the Spanish *S. pustulatus* populations by using matrix models derived from  
32 detailed demographic monitoring over a six-year period (2003–2008).

33 Population sizes ranged between 100-22000 reproductive individuals. In spite of  
34 differences in plant size, population protection and anthropogenic disturbance,  
35 the life history stage structure of all populations was similar and characterized  
36 by a low abundance of seedlings and juveniles, suggesting low recruitment. The  
37 population growth rate of Spanish *S. pustulatus* populations ranged between  
38 0.91 and 1.01, and the matrix model showed significant population decline ( $\lambda_S =$   
39 0.9042; 95% CI: 0.9041–0.9043). The PVA projected that this population would  
40 shrink to a few individuals in approximately forty years under present conditions.  
41 Since high temperatures and drought negatively affected the dynamics of this  
42 population, ongoing climatic change will jeopardize its future persistence.

43

## 44 **Zusammenfassung**

45 Die *Sonchus* -Arten der Sektion *Pustulati* (*Sonchus masquindalii*, *S. fragilis* and  
46 *S. pustulatus*) bilden eine Gruppe endemischer Felspflanzen in der  
47 Mittelmeerregion, die auf kleine, nicht überlappende Gebiete im Betikum/Rif-  
48 Hotspot der Pflanzendiversität beschränkt sind. *S. pustulatus* kommt sowohl in  
49 Südost-Spanien als auch Nordafrika vor, während die anderen Arten der  
50 Gruppe nur in Nordafrika auftreten. Wir beschrieben alle bestehenden  
51 Populationen der Sektion *Pustulati*, indem wir im Jahre 2008 Populationsgröße,  
52 demographische Struktur und Reproduktionserfolg erfassten, und wir  
53 bestimmten die Populationsentwicklung für die kritisch gefährdete spanische *S.*  
54 *pustulatus*, indem wir die Erhebungen 2013 wiederholten. Wir berechneten  
55 auch die stochastische Populationswachstumsrate ( $\lambda_S$ ) und modellierten die  
56 zukünftige Überlebenswahrscheinlichkeit (PVA) für eine der spanischen  
57 Populationen, auf der Basis von Matrix-Modellen für detaillierte  
58 demographische Erhebungen über einen sechsjährigen Zeitraum (2003-2008).

59 Die Populationsgrößen variierten zwischen 100 und 22000 reproduktiven  
60 Individuen. Trotz Unterschieden in der Pflanzengröße, im Schutzstatus und bei  
61 anthropogenen Störungen war die Altersstruktur in allen Populationen ähnlich  
62 und charakterisiert durch geringe Abundanzen von Sämlingen und  
63 Jungpflanzen, was auf geringe Rekrutierung hinweist. Die Wachstumsraten der  
64 spanischen *S. pustulatus*-Populationen rangierten zwischen 0.91 und 1.01, und  
65 das Matrix-Modell zeigte eine signifikante Populationsabnahme ( $\lambda_S = 0.9042$ ;  
66 95% CI: 0.9041-0.9043). Die PVA ergab, dass diese Population bei gleich  
67 bleibenden Bedingungen in ungefähr 40 Jahren auf wenige Individuen  
68 zusammenschrumpfen wird. Da hohe Temperaturen und Trockenheit die

69 Entwicklung dieser Population negativ beeinflussen, wird der gegenwärtige  
70 Klimawandel ihr Fortbestehen gefährden.

71

72 **Keywords:** Area of occupancy; Climatic trends; Population structure; PVA; Rare  
73 plants; *Sonchus* section *Pustulati*; Stochastic population growth rate.

## 74 **Introduction**

75 For the conservation of rare or endangered species, a demographic approach  
76 to species management is of critical importance (Schemske et al. 1994).  
77 Detailed demographic characterisation in terms of population number, size and  
78 structure across the distribution range of a species offers an accurate picture of  
79 its current conservation status. Population monitoring can reveal both temporal  
80 trends and the most critical life stages for the population growth rate (Horvitz &  
81 Schemske 1995), but this is more time and resource consuming, and is  
82 therefore often restricted to the most critically endangered species (Heywood &  
83 Iriondo 2003). The study of both the current status and the dynamics of  
84 populations are necessary to assess actual and potential threats and devise  
85 appropriate management strategies.

86 Long-term monitoring programmes are uncommon because of the need to  
87 maintain monitoring structures and funding in the long run. This becomes even  
88 more difficult in the case of cliff-dwelling species due to their difficult access.  
89 Consequently, our knowledge about the conservation and biology of cliff plants  
90 is greatly limited (Larsson, Matthes, & Kelly 2005), despite the fact that rocky  
91 habitats harbour many rare and endangered plants with narrow distributions;  
92 particularly in the Mediterranean region (Thompson 2005). Cliffs are highly  
93 fragmented, and offer very particular ecological environments that make life  
94 difficult, such as scarce microsite availability for plant establishment. However,  
95 competition in these habitats is also lower, and adapted organisms have a lower  
96 probability of suffering anthropogenic disturbances.

97 Although limited, studies on the populations and dynamics of cliff-dwelling  
98 plants suggest that local persistence is high (Lavergne, Thompson, Garnier, &  
99 Debussche 2004; Thompson 2005), they are extraordinarily long-lived (Larson  
100 et al. 2000; García, Guzman, & Goñi 2002), and their population sizes are  
101 unusually stable (Morris & Doak 1998; Picó & Riba 2002; García 2003).

102 In this study, we examine the demography of a small group of related plants  
103 that constitute the subgenus *Sonchus* section *Pustulati* (Asteraceae): *Sonchus*  
104 *pustulatus* Willk., *S. fragilis* Ball, and *S. masguindalii* Pau and Font Quer  
105 (Boulos 1973; Kim, Lee, & Mejías 2007). These narrow endemics are restricted  
106 to small areas of the western Mediterranean Basin (Boulos 1973) on both sides  
107 of the Alboran Sea (Fig. 1) and tend to be located on rocky cliffs at low altitudes.  
108 All three species are found in North Africa, where they are considered to be  
109 very rare (Fennane & Ibn Tadoo 1998). *S. pustulatus* also occurs in the SE  
110 Iberian Peninsula, where it is categorized as “critically endangered” (Cueto et al.  
111 2003). Phylogenetic and phylogeographic data suggest that these taxa are  
112 relicts of the late Tertiary period (Silva 2014). Their restricted and disjunct  
113 distribution seems to be related to old geological events of large biogeographic  
114 impact: the Messinian Salinity Crisis (during which North Africa and the Iberian  
115 Peninsula were connected by land), and the subsequent Zanclean reflooding of  
116 the Mediterranean basin (by which Africa and the Iberian Peninsula were  
117 separated).

118 The principal goal of this study was to assess the current conservation status  
119 and future risk of extinction for these cliff-dwelling species and their vulnerability  
120 to ongoing climate change. For that purpose, we undertook extensive fieldwork

121 to analyse the overall demographic situation of the clade, and modelled the  
122 dynamics of one of the Iberian populations in detail. We focused on the  
123 following specific objectives: (1) to accurately define the boundaries of the  
124 distribution range of the species after visiting all known populations and  
125 potentially suitable habitats; (2) to estimate extent of occurrence of each taxon,  
126 as well as area of occupancy, size, structure, and reproductive success of all  
127 extant populations; (3) to analyze temporal trends in the three Spanish  
128 populations of *S. pustulatus*, and to model the viability (PVA) of the *a priori* most  
129 endangered population by matrix models. Our results will help in assessing the  
130 conservation status and vulnerability of a group of cliff-dwelling species of high  
131 biogeographic and conservation value.

132

## 133 **Material and methods**

### 134 **Plant species**

135 The subgenus *Sonchus* section *Pustulati* includes three species: *Sonchus*  
136 *pustulatus*, *S. fragilis* and *S. masquindalii*. They are restricted to four non-  
137 overlapping small areas within the Baetic-Rifan complex biodiversity hotspot  
138 (western Mediterranean; Fig. 1, A-D), always occurring on low cliffs located on  
139 the coast or less than 20 km from the sea. Some herbarium specimens of *S.*  
140 *pustulatus* collected in the 19<sup>th</sup> century (e.g., herbarium COI) indicate that it was  
141 also present in rocky places on the oceanfront near Ghazaouet (Fig. 1, E,  
142 northwestern Algeria), but we were unable to visit this area and their presence  
143 at this site could therefore not be confirmed.

144 The *Sonchus* section *Pustulati* includes suffrutescent chamaephyte plants, with  
145 flower heads comprising approximately 30–120 florets in the case of *S.*  
146 *pustulatus* and *S. fragilis*, and 60–250 florets in *S. masquindalii*. They bloom in  
147 the spring and are visited by many species of Diptera and Coleoptera. The  
148 incidence of self-incompatibility that enforces outcrossing is high in *S.*  
149 *pustulatus* and *S. masquindalii*, and very low in *S. fragilis* (Silva 2014). Fruits  
150 are achenes with a short-lasting pappus, released during late spring and early  
151 summer.

152

### 153 **Distribution area, extent of occurrence and area of occupancy**

154 We conducted an intensive field work campaign from spring to early summer in  
155 2007 and 2008. We visited all the locations for each of the three species that we  
156 found recorded in different herbariums (BC, BM, COI, G, HUAL, MA, MPU,  
157 RNG and SEV) and bibliographic references (Boulos L. 1973; Deil & Galán de  
158 Mera 1996; Deil & Hammoumi 1997; Cueto et al. 2003; Mota et al. 2005), plus  
159 potentially suitable habitats nearby. Following the IUCN criteria (IUCN 2001),  
160 the extent of occurrence for each taxon was estimated as the area contained  
161 within the shortest continuous imaginary boundary which encompasses all the  
162 known sites in which the taxon is present, and the area of occupancy for each  
163 population as the area within the extent of occurrence that is occupied by the  
164 individuals. To measure the extent of occurrence, we used orthophotos  
165 (obtained from REDIAM 2008 for Spain), maps (GPS GARMIN, for Morocco)  
166 and AUTOCAD software (v.2006). The area of occupancy was measured by  
167 multiplying the population longitudinal ranges by the average distance between



168 the highest and lowest heights where individuals occurred (measured at the  
169 level of each sampling plot; see sampling design below).

170

## 171 **Population size and structure**

172 Population size was estimated by multiplying the area of occupancy by plant  
173 density. Density was obtained during May and June 2008 using a variable  
174 number of homogeneously distributed sampling plots (2×2 m), in which we  
175 recorded the number of individuals. In order to adapt the sampling strategy to  
176 the fragmented and clumped nature of cliff-dwelling plants and to their  
177 population sizes, the number of plots (6–30, mean 21.5; Table 1) and distances  
178 between plots varied. Sampling plots were placed along the cliffs at low (0–2 m  
179 from the cliff base), medium (2–4 m) and high (>4 m) transects. This plot  
180 sampling system was able to cover most of the spatial range of plant  
181 occurrence because either the cliffs were not too high or the individuals did not  
182 occur on the higher parts. When plants were inaccessible, we used binoculars  
183 to record the number of individuals. When populations occurred in a very  
184 narrow valley and plants grew on both wall sides (KAN and LAUF), plots were  
185 established in two parallel transects on each cliff. In order to test the accuracy  
186 of the plot-based method for estimating population size, all of the individuals in  
187 the three Spanish populations were also directly counted.

188 We also used the sampling plots to estimate population structure (proportion of  
189 plants in different life history stages) as most recorded individuals were  
190 sufficiently accessible to be classified into three categories: seedlings (less than  
191 1 year old, usually with cotyledons), juveniles (one or, rarely, two herbaceous

192 stems bearing mature leaves, no flowering stalks and no evidence of past  
193 flowering events), and adults (plants with lignification, well-developed leaves,  
194 and usually with one or more flowering stems). The two largest perpendicular  
195 axes were measured for each plant to calculate their elliptic surface, and  
196 individuals were then reclassified into one of the following size classes (see  
197 Appendix A: Fig. 3): *Seedlings*; *Juveniles*; *Class-I*, [0–50] cm<sup>2</sup>; *Class-II*, (50–  
198 200] cm<sup>2</sup>; *Class-III*, (200–500] cm<sup>2</sup>; *Class-IV*, (500–1000] cm<sup>2</sup>; *Class-V*, (1000–  
199 3000] cm<sup>2</sup>; and *Class-VI*, >3000 cm<sup>2</sup>. One Spanish population (CAB, Table 1)  
200 was monitored over six consecutive years (2003–2008), and the average  
201 demographic structure across years was used in this case.

202

### 203 **Reproductive success**

204 For each population, we estimated seed set (seed/ovule ratio) in 2008 from one  
205 to three mature non-dispersed flower heads in 20 randomly selected individuals.  
206 We performed one way ANOVA and Tamhane post hoc multiple comparisons  
207 tests to compare mean seed number per flower head among taxa, after  
208 checking for normality and homocedasticity. These statistical analyses were  
209 performed with SPSS software (SPSS for Windows, ver.15.0.1, 2006, Chicago:  
210 Inc.). For each population, we also counted the number of flower heads in all  
211 adults within the sampling plots.

212 The density of released seeds was considered an accurate estimation of pre-  
213 emergent population reproductive success (Wiens et al. 1987), and it was  
214 calculated from the number of flower heads per individual, seeds per flower

215 head, number of reproductive plants and area of occupancy. We also estimated  
216 the density of seedlings, juveniles and adults in the sampling plots.

217

### 218 **Population trends and viability analysis of Spanish *S. pustulatus***

219 Direct censuses performed in 2008 in the Spanish populations of *S. pustulatus*  
220 were repeated in 2013, and population growth rates were estimated as the 5th-  
221 root of the ratio between the number of plants in 2013 and 2008.

222 In the CAB population, a detailed individual-based monitoring study was  
223 performed from May 2003 to May 2008. All accessible individuals on the cliffs  
224 (approximately 75% of the total population) were mapped and their positions  
225 precisely recorded in the first year. During each census, we recorded individual  
226 persistence or death, estimated plant size as described above, but in this case  
227 adults were separated into generative (one or more flowering stems) and  
228 vegetative (just a few leaves with no evidence of flowering during the current  
229 year) (see Appendix A: Fig. 4). All new individuals appearing within the  
230 sampling area were also measured, mapped and incorporated into the  
231 monitoring study.

232

### 233 **Matrix analysis: Population growth rates and future viability**

234 Stage-based population projection matrix models were used to explore the  
235 demographic population trend of CAB under current conditions. Here, we  
236 grouped some of the size classes used to describe population structure in order  
237 to obtain a reasonable minimum sample size for each stage and thus to obtain

238 reliable estimates of vital rates. *Seedlings*, *Juveniles* and *Class-I* were joined in  
239 a single category (*Class-S&J&I*), as well as individuals of *Class-V* and *Class-VI*  
240 (*Class-V&VI*). We constructed a total of five 5×5 projection matrices for each  
241 pair of consecutive years (from 2003–2004 until 2007–2008) and used the  
242 standard procedure for measuring transition probabilities of the life-cycle graph  
243 (Caswell 2001). We calculated the dominant eigenvalue of each projection  
244 matrix, which represents the deterministic population growth rate ( $\lambda$ ) of the  
245 species present in a particular environment and at a particular time. We also  
246 calculated the stochastic population growth rate ( $\lambda_s$ ) and the 95% confidence  
247 interval for each population by simulating 50000 iterations where each matrix  
248 had the same probability of occurrence. These were calculated using the  
249 ‘Stoch\_log\_lam’ routine of Morris and Doak (2002). In addition, we calculated  
250 the conditional total life span of plants in this population (mean age at death,  
251 conditional on reaching a given stage) from the average matrix over years and  
252 the algorithm published by Cochran and Ellner (1992), which implies subtracting  
253 one year from the estimated life spans.

254 Finally, we estimated the probability of population extinction over the next 100  
255 years using the ‘simex’ routine of Morris and Doak (2002) with MATLAB R2010.  
256 For this population viability analysis (PVA), we used matrix sampling and ran  
257 2000 simulations with equal probabilities of occurrence for the five transition  
258 matrices. We set the quasi-extinction threshold to 10 plants, defined as the  
259 minimum population size considered being necessary to ensure successful  
260 crosses for this highly self-incompatible species that usually starts reproducing  
261 in its first year of life (Silva 2014).

262

## 263 **Population dynamics and climate**

264 In the CAB population, we tested the relationship between annual  $\lambda$  and  
265 meteorological variables by means of Pearson tests. We compiled the following  
266 monthly information from a weather station located 9 km from the population  
267 (Almeria Airport Weather Station): mean temperature, average of minimum and  
268 maximum temperatures and total precipitation. We also recorded the total  
269 number of days per year with rainfall or light precipitation. Climatic years (from  
270 September to the following August) were used for the analysis both including  
271 and excluding the Mediterranean dry and hot summer, which is stressful for  
272 most plants. We also tested the relationship between population growth rate  
273 and weather conditions in spring (March to June), during which plant growth is  
274 usually highest.

275

## 276 **Results**

### 277 **Demographic status**

278 A total of 19 populations were found during our extensive searches in 2008  
279 (Table 1, Fig. 1). *S. pustulatus* in its Spanish range showed the lowest extent of  
280 occurrence, the smallest population areas of occupancy and the smallest  
281 population sizes within the section *Pustulati* (Table 1). Furthermore, one  
282 population (Playa El Palmer; cited by Mota et al. 2005) was observed to be  
283 extinct suggesting a reduction in the extent of occurrence of Spanish *S.*  
284 *pustulatus* during the last few years (Fig. 1). Conversely, the Moroccan

285 populations of *S. pustulatus* were spread over larger areas. Regarding the  
286 African taxa, *S. fragilis* was restricted to very a small area but there was one  
287 exceptionally large population (GHO1). *S. masguindalii* was the taxon with the  
288 highest total number of plants and populations.

289 As expected for cliff habitats, perturbations were not especially prevalent.  
290 However, almost half of the populations were negatively affected by  
291 anthropogenic disturbances in some way (Table 1). A small area of the eastern  
292 end of the Spanish population CAB of *S. pustulatus* (approximately 20% of the  
293 area of occupancy) was being used for domestic waste disposal. We have  
294 recently (2013) detected numerous rock-climbing routes that cross the ANT  
295 population of *S. pustulatus*. Goat grazing has been observed in the Spanish  
296 populations ANT and TEL of *S. pustulatus*, as well as in populations GHO1,  
297 GHO2 and GHO3 of *S. fragilis*. Several individual groups of *S. masguindalii* on  
298 the low cliffs of population SFI occur in the vicinity of beach bars, whereas some  
299 groups in the BAD1 population of the same species are very close to small  
300 dwellings. The restoration of a lighthouse in the TEL population also appears to  
301 have resulted in the loss of some plants.

302 The stage structure of most populations was similar (Fig. 2). Adult plants were  
303 most frequent, particularly those of *Class-II*, followed by *Class-I* (in populations  
304 of *S. fragilis*) or *Class-III* (in the other species). The proportion of seedlings and  
305 juveniles was always below 15%. In the Spanish population of *S. pustulatus*  
306 (CAB), generative adults were clearly the most abundant plants (63.0–89.0%,  
307 depending on year), while vegetative adults only accounted for a small fraction  
308 of the population (3.2–26.1%).

309

## 310 **Reproductive success**

311 *S. masguindalii* produced significantly more seeds per flower head than the  
312 other species ( $F = 56.17$ ,  $P < 0.001$ ; Tamhane post hoc,  $P < 0.001$ ), which  
313 resulted in higher densities of released seeds (see Appendix A: Table 3). In the  
314 2008 census, the high density of released seeds (between 53–5742/m<sup>2</sup>)  
315 contrasted with the low density of seedlings, juveniles and adults (0–15/100 m<sup>2</sup>,  
316 0–12/100 m<sup>2</sup> and 19–130/100 m<sup>2</sup>, respectively; see Appendix A: Table 3). In the  
317 annually monitored CAB population of *S. pustulatus*, annual survival of  
318 seedlings was 0.13 ( $\pm 0.13$ ), with survival increasing considerably during the  
319 juvenile stage (0.71  $\pm$  0.07), and the adult stage (ranging from 0.77  $\pm$  0.06 to  
320 0.96  $\pm$  0.01, depending on size class).

321

## 322 **Population trends and viability of Spanish populations of *S.***

### 323 ***pustulatus***

324 The number of individuals in the CAB population dropped from 292 in 2008 to  
325 188 in 2013 ( $\lambda = 0.916$ ). A similar decline was estimated in TEL during the same  
326 period, as population size decreased from 112 to 94 individuals ( $\lambda = 0.966$ ). In  
327 contrast, the ANT population increased slightly, from 484 to 505 individuals ( $\lambda =$   
328 1.009).

329 Projected population growth rates calculated from matrix models for the CAB  
330 population in all five study years were less than 1 (ranging from 0.868 to 0.946;  
331 see also Table 2), and the stochastic lambda measure indicated a significant

332 rate of decline over the study period of 9.6% ( $\lambda_S = 0.9042$ ; 95% CI: 0.9041–  
333 0.9043). This negative trend is similar to the one based on counts, and it was  
334 only in part due to the contraction of the area of occupancy. The population  
335 viability analysis (PVA) projected a sharp decline of the population, with >99%  
336 probability of quasi-extinction (defined as  $N < 10$  individuals) during the next 100  
337 years. Should the present conditions persist, the population is projected to be  
338 reduced to only 10% of its current size (<30 individuals) in only 23 years. The  
339 conditional total life span of the largest class (average age at death for  
340 seedlings reaching that size class) was estimated to be 22 years. Therefore, *S.*  
341 *pustulatus* can be considered a long-lived plant.

342 Lambda was negatively correlated with monthly mean maximum temperature  
343 during the growing period (summer months excluded;  $r = -0.901$ ,  $p = 0.037$ ),  
344 and positively correlated with number of days with rainfall or light precipitation  
345 during the spring months ( $r = 0.896$ ,  $p = 0.040$ ). Lambda was not significantly  
346 correlated with any of the other meteorological variables ( $p > 0.05$ ).

347

## 348 **Discussion**

349 Our study compared demographic variables related to the rarity and  
350 vulnerability of a whole clade of three narrow endemic species of *Sonchus*  
351 section *Pustulati* in two continents. This clade occurred across a continuous  
352 area in the late Miocene-early Pliocene that is now separated into two regions  
353 by the Alboran Sea (Silva 2014).



354 The information gathered by this study serves to update the conservation status  
355 of the three taxa according to the categories and criteria of the IUCN Red List  
356 (IUCN 2012). The Spanish *S. pustulatus* moves from “critically endangered”  
357 (CR) to “endangered” (EN) but, based on the sharp decline projected for the  
358 CAB population, the species is predicted to revert to the CR category by the  
359 end of the century (see Appendix A: Conservation status). The remaining taxa  
360 are considered as “deficient data” until we have more information on changes in  
361 the extent of occurrence, area of distribution, size and/or number of populations  
362 (see Appendix A: Conservation status and Table 4).

363 Beyond their IUCN conservation status, we found that the demographic  
364 structure of most populations was similar, with adult plants being dominant and  
365 a low proportion of seedlings and juveniles. This is a typical demographic  
366 structure in rocky habitats (García et al. 2002; Larson et al. 2005), and is not  
367 necessarily evidence of “population senescence”. A combination of factors such  
368 as low seed germination and low seedling establishment in the few appropriate  
369 microsites available on cliffs, along with early reproductive onset (Silva 2014)  
370 and the longevity of individual plants (over 20 years for the largest individuals in  
371 the case of one Spanish population) may explain such a pattern.

372 Nevertheless, two of the three Spanish populations of *S. pustulatus* are in  
373 decline. The few existing studies on population dynamics of cliff-dwelling  
374 species suggest an unusual demographic stability and resilience of cliff plants  
375 (Pico & Riba 2002; García 2003) due to the much higher importance of the  
376 survival of existing individuals than recruitment of new ones for the maintenance  
377 of populations (Larson et al. 2000; García et al. 2008). High survival rates

378 translate into high individual longevity. However, our estimation of longevity in  
379 *S. pustulatus* is much lower than in other cliff-dwelling plants (45–324 years;  
380 Ehrlén & Lehtilä 2002, Forbis & Doak 2004; García, Picó, & Ehrlén 2008). This  
381 fact could be species-specific, but lifespan estimation from survival rates is also  
382 affected by the performance of the particular population. Lower lifespan may  
383 therefore be related to the lower performance of plants in a peripheral part of  
384 the geographical distribution of species of *Sonchus* section *Pustulati*, as found  
385 for *Silene ciliata* (Giménez-Benavides, Albert, Iriondo & Escudero 2011). In any  
386 case, the cliff-dwelling *Sonchus* studied, at least in the Baetic range, might be  
387 less resilient to global changes than generally assumed for plants of very stable  
388 habitats such as cliffs.

389 Due to the short distance between CAB and the other two populations, TEL and  
390 ANT (1.9 and 8.2 km, respectively), similar demographic trends were expected  
391 under the assumption of similar environmental factors acting in neighbouring  
392 populations (Buckley et al. 2010). However, this was not entirely the case, as  
393 TEL declined whereas ANT slightly increased. Differences in anthropogenic  
394 disturbances at small scales and/or different relationships between population  
395 dynamics and environmental factors may have promoted these divergent  
396 trends. *Sonchus* section *Pustulati* species have been considered a part of the  
397 pre-Mediterranean flora (Silva 2014) when a previously much wetter climatic  
398 period prevailed. The ANT population is located on high cliffs protected from the  
399 sun and with many points where water often oozes. Such conditions are  
400 presumably more similar to the typical habitats present during species  
401 diversification, suggesting that climatic refuges play a role in the persistence of  
402 old floristic elements including *Sonchus* section *Pustulati*.

403 Because we found a strong negative influence of spring drought and mean  
404 maximum temperature during the growing period on the growth rate of the  
405 Spanish CAB population of *S. pustulatus*, it can be expected that the increase in  
406 the number of days with no rainfall and drought periods predicted for the  
407 southern Spanish Mediterranean (Ruiz-Sinoga, Garcia-Marin, Gabarron-  
408 Galeote, & Martinez-Murillo 2012) as well as the global warming will negatively  
409 affect populations.

410 North Africa (Rif) represents the main distribution area for the *Pustulati* taxa  
411 (Fig. 1) and constitutes their most plausible centre of origin and diversification  
412 (Silva 2014). Although we do not know the dynamics of populations in Morocco,  
413 which prevents us from comparing them with the Spanish ones, we found that  
414 the latter tended to have the lowest extent of occurrence, area of occupancy,  
415 and population density and size. Although both the Spanish and Moroccan  
416 areas of *S. pustulatus* experience similar summers (dry and warm), the  
417 Moroccan area is at lower latitude and is considerably wetter, having up to three  
418 times higher annual rainfall than in the Spanish area (Hijmans, Cameron, Parra,  
419 Jones, & Jarvis 2005). Consequently, the peripheral position of the Spanish  
420 populations regarding the distribution of the *Pustulati* section as a whole, most  
421 probably at the limit of the optimal ecological amplitude (Silva 2014), might  
422 explain the demographic vulnerability of these populations to drought and high  
423 temperatures.

424 Even though all populations of *Pustulati* section occur in a relatively small area,  
425 have similar population structures, and experience similar limitations for  
426 recruitment due to conditions at their specific habitats, the larger Moroccan

427 populations do not appear to be as threatened as the Spanish ones. The  
428 evidences we present here of recent past extinctions and declining of  
429 populations suggest that the Spanish populations will be more sensitive to  
430 ongoing climate change.

431

## 432 **Acknowledgments**

433 Financial support for this research was provided by the Spanish Ministry of  
434 Science and Innovation (grants CGL2006–00817 and CGL2010-16512). The  
435 authors greatly appreciate the support in the field-work by the research group  
436 led by Prof. J.F. Mota from the University of Almeria and the assistance of R.  
437 Ajbilou from the University of Tetouan. We are also grateful to A.C. Brennan for  
438 the linguistic revision, and one referee for valuable comments to improve a  
439 preliminary version. J.L.S. was supported by a fellowship from the Spanish  
440 Ministry of Science and Innovation (BES–2007–17066) and a work contract  
441 from research grant CGL2010–16512. MBG was support by a national project  
442 during the writing of this study (CGL2010-21642).

443

## 444 **Appendix A. Supplementary data**

445 Supplementary data associated with this article can be found, in the online  
446 version, at XXXXX.

447

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553

## 554 **Figure captions**

555 **Fig. 1.** Overall geographical distribution of the *Sonchus* species (section  
556 *Pustulati*) and areas of occupancy of populations in the Spanish Baetic (A) and  
557 Moroccan Rifan ranges (B-C-D). A-B, *S. pustulatus*; C, *S. fragilis*; D, *S.*  
558 *masguindalii*. Algerian range (E), *S. pustulatus* is unconfirmed. In the Spanish  
559 area (A), the extent of occurrence is marked by a dashed line and an empty

560 white circle indicates the location of the extinguished population (Playa El  
561 Palmer).

562 **Fig. 2.** Composition of *Sonchus* section *Pustulati* populations based on life  
563 history stages and size classes. For abbreviation of population names see  
564 Table 1. Classes are: *Seedlings*; *Juveniles*; *Class-I*, adults between [0–50] cm<sup>2</sup>;  
565 *Class-II*, (50–200] cm<sup>2</sup>; *Class-III*, (200–500] cm<sup>2</sup>; *Class-IV*, (500–1000] cm<sup>2</sup>;  
566 *Class-V*, (1000–3000] cm<sup>2</sup>; and *Class-VI*, >3000 cm<sup>2</sup>. Numbers above bars are  
567 sampled individuals, and their percentage of the total estimated population size  
568 is in brackets.

569

**Table 1.** Populations of the taxa of *Sonchus* section *Pustulati*. Nuclei means groups of individuals spatially well delimited within a population. \* indicates direct counting of individuals. Plots refer to the number of sampling units used in the field for density and population size estimates.

Species, populations, altitude	Acronym	Coordinates (N/W)	Protected area/ Anthropogenic disturbance factor	Extent of occurrence (Km <sup>2</sup> )	Area of occupancy (m <sup>2</sup> )	Nuclei	Population size	Reproductive plants	Density (plants/ 100 m <sup>2</sup> )	Plots
<b><i>Sonchus pustulatus</i> - Spain, southeast</b>				<b>6.7</b>	<b>3505</b>		<b>1058 (879*)</b>	<b>799</b>		
Aguadulce, Bco. San Antonio, 300m	ANT	36°50' / 2°34'	No/Yes		1972	2	707 (484*)	426	34	30
Almeria, Faro de San Telmo, 22m	TEL	36°49' / 2°29'	No/Yes		546	6	121 (112*)	104	22	18
Almeria, Bco. del Caballar, 100m	CAB	36°50' / 2°28'	No/Yes		987	3	230 (292*)	269	26	30
<b><i>S. pustulatus</i> - Morocco, western Rif</b>				<b>242.9</b>	<b>15785</b>		<b>9991</b>	<b>8403</b>		
Oued Laud valley, 120m	LAUF	35°24' / 5°13'	No/No		1800	3	1062	945	46	25
Oued Laud valley, 153m	LAUL	35°21' / 5°11'	No/No		1038	2	540	427	42	25
Oued Laud valley, 150m	LAUO	35°18' / 5°14'	No/No		840	1	221	190	25	20
Oued Laud valley, 235m	TAL	35°15' / 5°13'	No/No		3008	5	1980	1643	64	30
Oued Al-Kannar gorge, 244m	KAN	35°13' / 5°02'	Yes/No		9100	1	6188	5198	72	25
<b><i>S. fragilis</i> - Morocco, northwestern Rif</b>				<b>16.1</b>	<b>41336</b>		<b>33927</b>	<b>27409</b>		
Tetouan, Montes Ghorghiz, 550m	GHO1	35°32' / 5°23'	No/Yes		28912	2	26985	21858	92	30
Tetouan, Montes Ghorghiz, 550m	GHO2	35°32' / 5°22'	No/Yes		-	1	-	-	-	-
Tetouan, Montes Ghorghiz, 550m	GHO3	35°32' / 5°22'	No/Yes		2760	2	661	588	21	24
Tetouan, Montes Dersa, 275m	DER	35°36' / 5°25'	No/No		9664	1	6282	4963	47	15
<b><i>S. masquindalii</i> - Morocco, central Rif</b>				<b>107.0</b>	<b>40001</b>		<b>42269</b>	<b>33281</b>		
Torres de Alcalá beach, sea level	TOR	35°10' / 4°20'	Yes/No		3568	1	6244	5495	90	10
Bades beach - Peñon de Vélez, s.l.	BAD1	35°10' / 4°18'	Yes/Yes		6038	2	6444	5542	106	26
Valley to Bades beach, 60 m	BAD2	35°10' / 4°17'	Yes/No		486	2	638	555	145	20
Boumahdi beach, s.l.	BOU	35°14' / 4°01'	Yes/No		16536	2	19513	14635	129	25
Cebadilla beach, Al-Hoceimas, s.l.	ALH	35°15' / 3°58'	Yes/No		1100	1	688	688	63	6
Quemado beach, Al-Hoceimas, s.l.	QUE	35°15' / 3°56'	No/No		10063	1	6708	4494	88	6
Sfiha beach, Al-hoceimas, s.l.	SFI	35°11' / 3°54'	No/Yes		2211	3	2035	1872	92	22

**Table 2.** Mean transition matrix corresponding to the CAB population of *S. pustulatus* over the 2003–2008 period. Column and row labels represent the first (origin) and second (destination) year, respectively, for the transition probabilities (mean  $\pm$  SE) between size categories. The transitions to categories of lower sizes denote size reduction. *Class-S&J&I*: seedlings, juveniles and adults between [0–50] cm<sup>2</sup>; *Class-II*: adults between (50–200] cm<sup>2</sup>; *Class-III*: (200–500] cm<sup>2</sup>; *Class-IV*: (500–1000] cm<sup>2</sup>; and *Class-V&VI*: >1000 cm<sup>2</sup>.

	<i>Class-S&amp;J&amp;I</i>	<i>Class-II</i>	<i>Class-III</i>	<i>Class-IV</i>	<i>Class-V&amp;VI</i>
<i>Class-S&amp;J&amp;I</i>	0.500 $\pm$ 0.041	0.100 $\pm$ 0.027	0.050 $\pm$ 0.010	0.056 $\pm$ 0.011	0.069 $\pm$ 0.023
<i>Class-II</i>	0.189 $\pm$ 0.048	0.550 $\pm$ 0.035	0.183 $\pm$ 0.021	0.022 $\pm$ 0.022	0.015 $\pm$ 0.009
<i>Class-III</i>	0.047 $\pm$ 0.014	0.162 $\pm$ 0.010	0.584 $\pm$ 0.018	0.198 $\pm$ 0.036	0.026 $\pm$ 0.011
<i>Class-IV</i>	0.011 $\pm$ 0.007	0.028 $\pm$ 0.010	0.095 $\pm$ 0.028	0.468 $\pm$ 0.041	0.195 $\pm$ 0.028
<i>Class-V&amp;VI</i>	0.006 $\pm$ 0.006	0.012 $\pm$ 0.008	0.025 $\pm$ 0.004	0.215 $\pm$ 0.033	0.682 $\pm$ 0.038

Figure1\_OnlyBlack&White

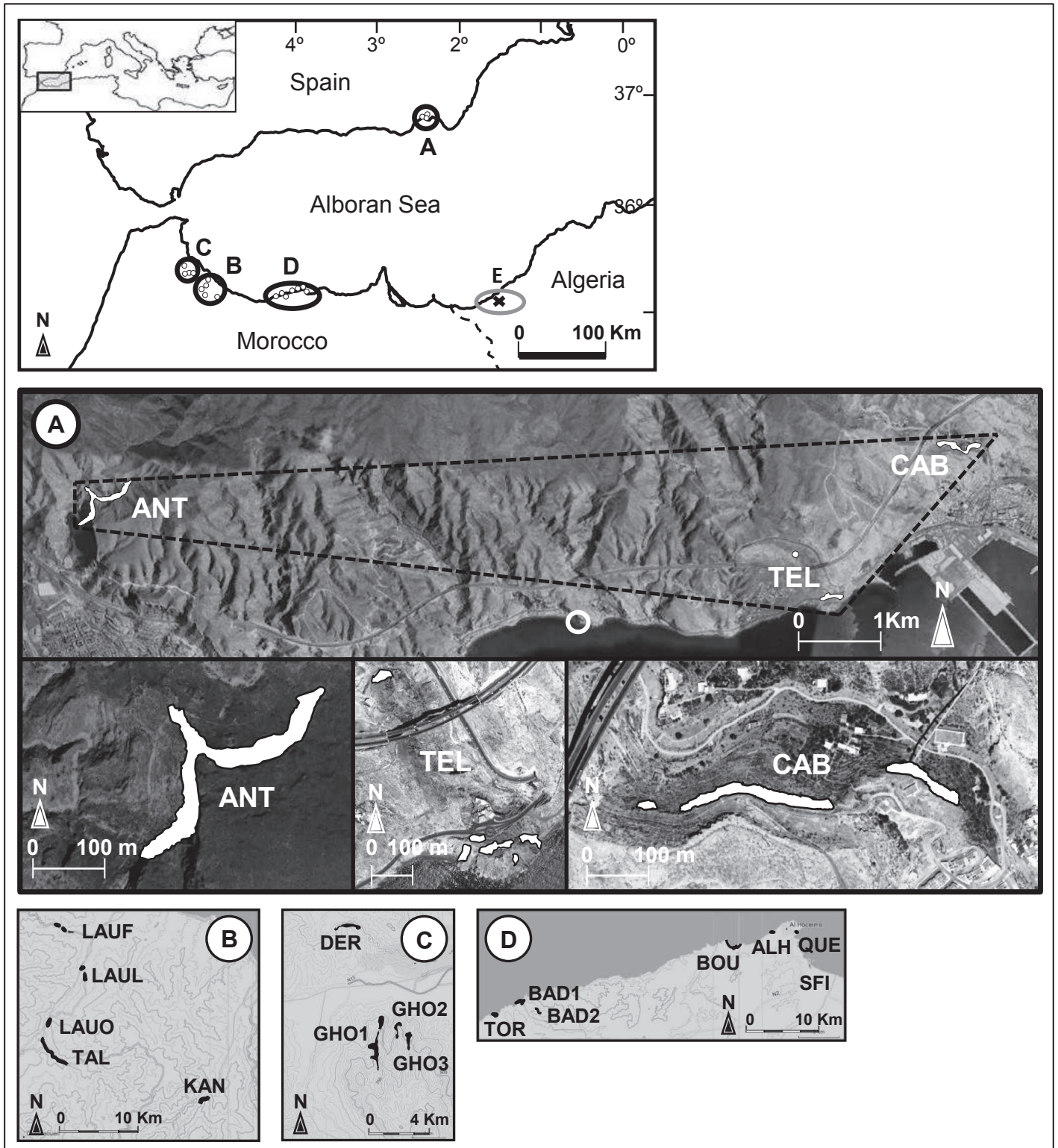


Figure2\_Color

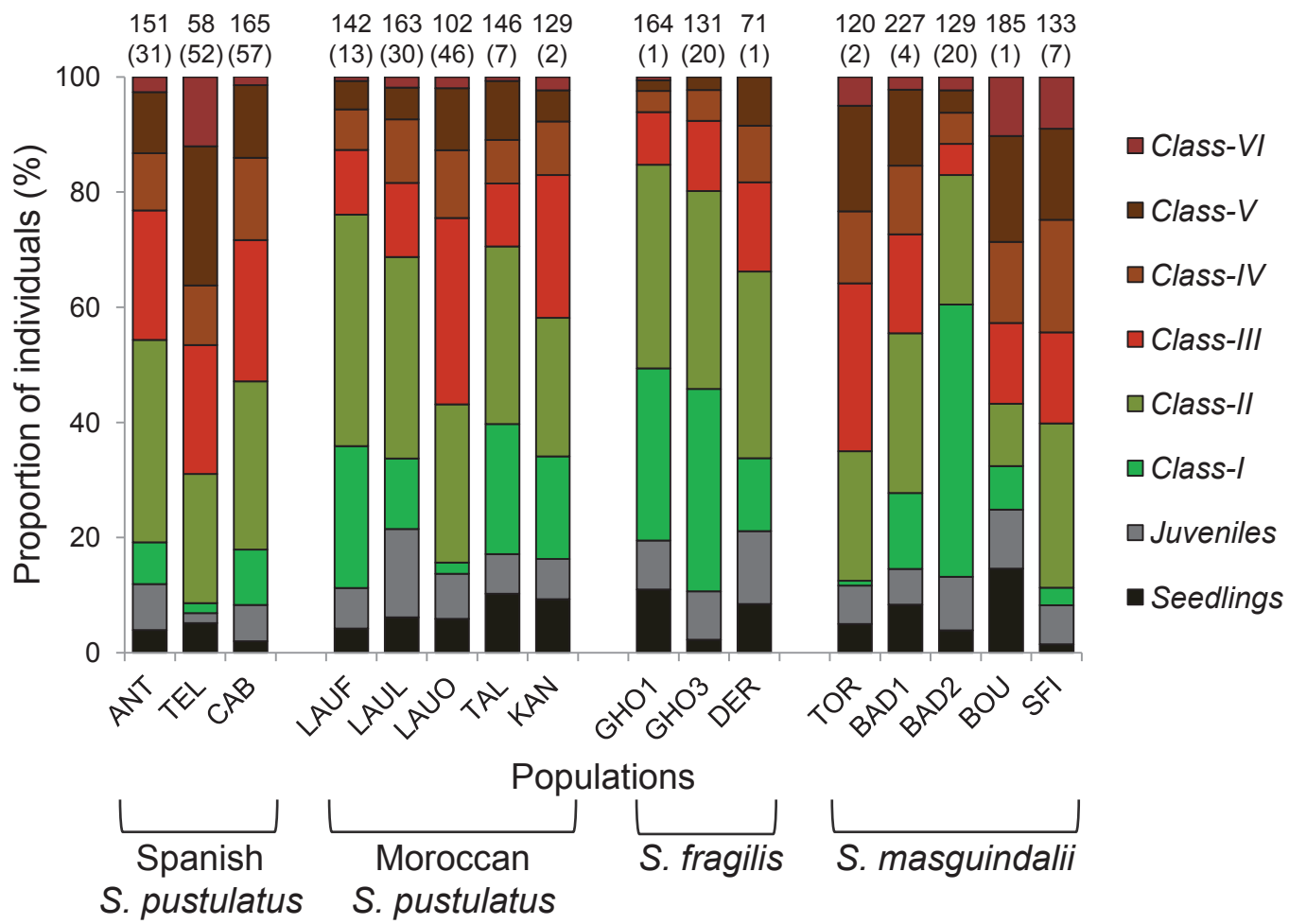
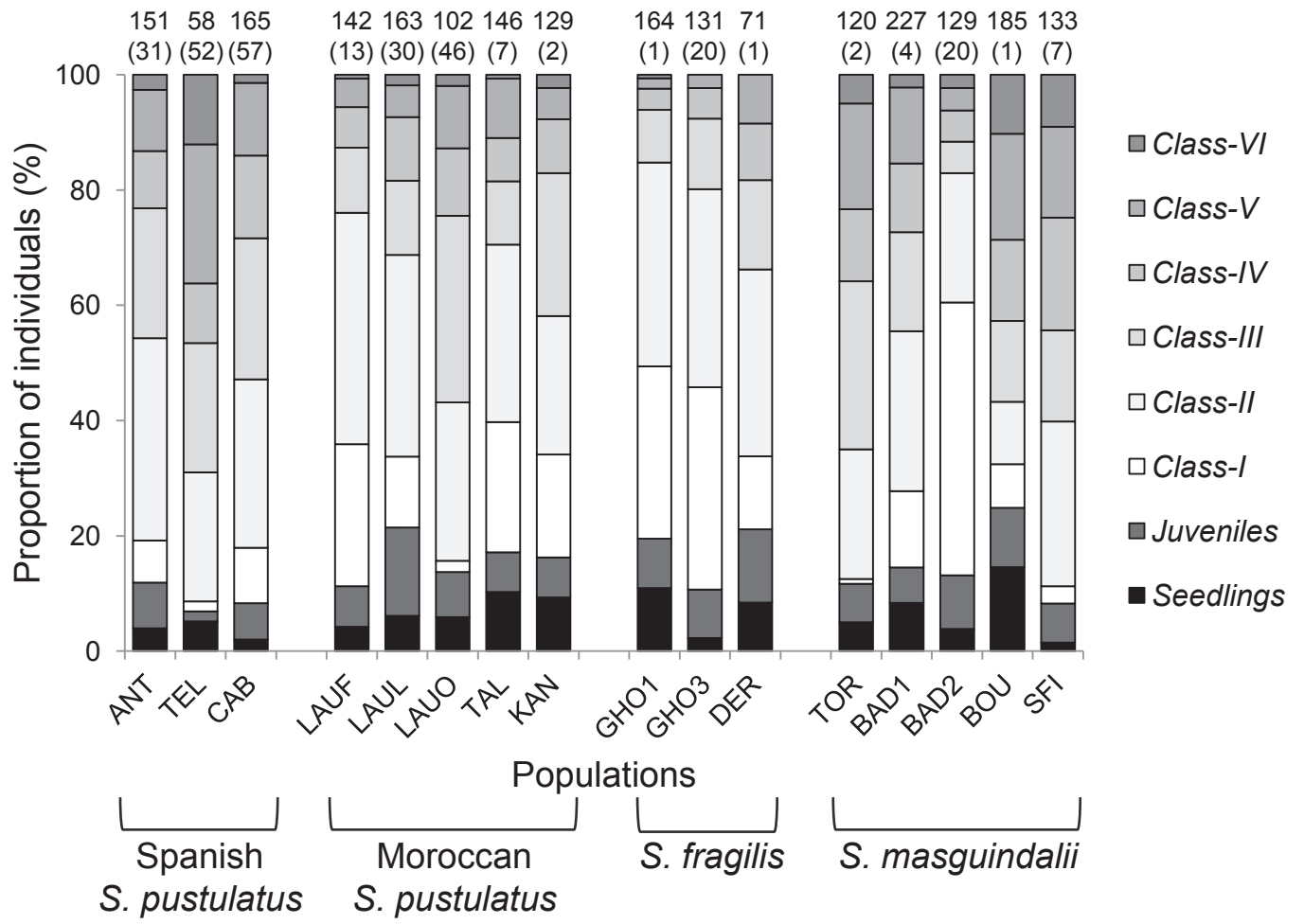


Figure2\_Black&White





## Appendix A

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**AppendixA\_Table3**

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**AppendixA\_Table4**

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