1 Demographic vulnerability in cliff-dwelling *Sonchus*

2 species endemic to the western Mediterranean

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

19 *Pustulati*.

Abstract

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

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

Zusammenfassung

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

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

69 Entwicklung dieser Population negativ beeinflussen, wird der gegenwärtige

70 Klimawandel ihr Fortbestehen gefährden.

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Introduction

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

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

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

Material and methods

Plant species

The subgenus *Sonchus* section *Pustulati* includes three species: *Sonchus pustulatus*, *S. fragilis* and *S. masguindalii*. They are restricted to four non-overlapping small areas within the Baetic-Rifan complex biodiversity hotspot (western Mediterranean; Fig. 1, A-D), always occurring on low cliffs located on the coast or less than 20 km from the sea. Some herbarium specimens of *S. pustulatus* collected in the 19th century (e.g., herbarium COI) indicate that it was also present in rocky places on the oceanfront near Ghazaouet (Fig. 1, E, northwestern Algeria), but we were unable to visit this area and their presence 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. masguindalii*. 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. masguindalii*, 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.

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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 mutliplying 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^2; *Class-II*, (50–

198 200] cm^2; *Class-III*, (200–500] cm^2; *Class-IV*, (500–1000] cm^2; *Class-V*, (1000–

199 3000] cm^2; and *Class-VI*, >3000 cm^2. 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

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

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

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

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

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

262

Population dynamics and climate

264 In the CAB population, we tested the relationship between annual λ 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

Results

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%).

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Reproductive success

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

Population trends and viability of Spanish populations of *S. pustulatus*

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

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

332 rate of decline over the study period of 9.6% (λ_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 metereological 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

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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.

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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^2;

565   *Class-II*, (50–200] cm^2; *Class-III*, (200–500] cm^2; *Class-IV*, (500–1000] cm^2;

566   *Class-V*, (1000–3000] cm^2; and *Class-VI*, >3000 cm^2. Numbers above bars are

567   sampled individuals, and their percentage of the total estimated population size

568   is in brackets.

569

Table1

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^2)	Area of occupancy (m^2)	Nuclei	Population size	Reproductive plants	Density (plants/ 100 m^2)	Plots
Sonchus pustulatus - Spain, southeast				**6.7**	**3505**		**1058 (879*)**	**799**		
Aguadulce, Bco. San Antonio, 300m	ANT	36º50' / 2º34'	No/Yes		1972	2	707 (484*)	426	34	30
Almeria, Faro de San Telmo, 22m	TEL	36º49' / 2º29'	No/Yes		546	6	121 (112*)	104	22	18
Almeria, Bco. del Caballar, 100m	CAB	36º50' / 2º28'	No/Yes		987	3	230 (292*)	269	26	30
S. pustulatus - Morocco, western Rif				**242.9**	**15785**		**9991**	**8403**		
Oued Laud valley, 120m	LAUF	35º24' / 5º13'	No/No		1800	3	1062	945	46	25
Oued Laud valley, 153m	LAUL	35º21' / 5º11'	No/No		1038	2	540	427	42	25
Oued Laud valley, 150m	LAUO	35º18' / 5º14'	No/No		840	1	221	190	25	20
Oued Laud valley, 235m	TAL	35º15' / 5º13'	No/No		3008	5	1980	1643	64	30
Oued Al-Kannar gorge, 244m	KAN	35º13' / 5º02'	Yes/No		9100	1	6188	5198	72	25
S. fragilis - Morocco, northwestern Rif				**16.1**	**41336**		**33927**	**27409**		
Tetouan, Montes Ghorghiz, 550m	GHO1	35º32' / 5º23'	No/Yes		28912	2	26985	21858	92	30
Tetouan, Montes Ghorghiz, 550m	GHO2	35º32' / 5º22'	No/Yes		-	1	-	-	-	-
Tetouan, Montes Ghorghiz, 550m	GHO3	35º32' / 5º22'	No/Yes		2760	2	661	588	21	24
Tetouan, Montes Dersa, 275m	DER	35º36' / 5º25'	No/No		9664	1	6282	4963	47	15
S. masguindalii - Morocco, central Rif				**107.0**	**40001**		**42269**	**33281**		
Torres de Alcalá beach, sea level	TOR	35º10' / 4º20'	Yes/No		3568	1	6244	5495	90	10
Bades beach - Peñon de Vélez, s.l.	BAD1	35º10' / 4º18'	Yes/Yes		6038	2	6444	5542	106	26
Valley to Bades beach, 60 m	BAD2	35º10' / 4º17'	Yes/No		486	2	638	555	145	20
Boumahdi beach, s.l.	BOU	35º14' / 4º01'	Yes/No		16536	2	19513	14635	129	25
Cebadilla beach, Al-Hoceimas, s.l.	ALH	35º15' / 3º58'	Yes/No		1100	1	688	688	63	6
Quemado beach, Al-Hoceimas, s.l.	QUE	35º15' / 3º56'	No/No		10063	1	6708	4494	88	6
Sfiha beach, Al-hoceimas, s.l.	SFI	35º11' / 3º54'	No/Yes		2211	3	2035	1872	92	22

Table2

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 ± 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^2; *Class-II*: adults between (50–200] cm^2; *Class-III*: (200–500] cm^2; *Class-IV*: (500–1000] cm^2; and *Class-V&VI*: >1000 cm^2.

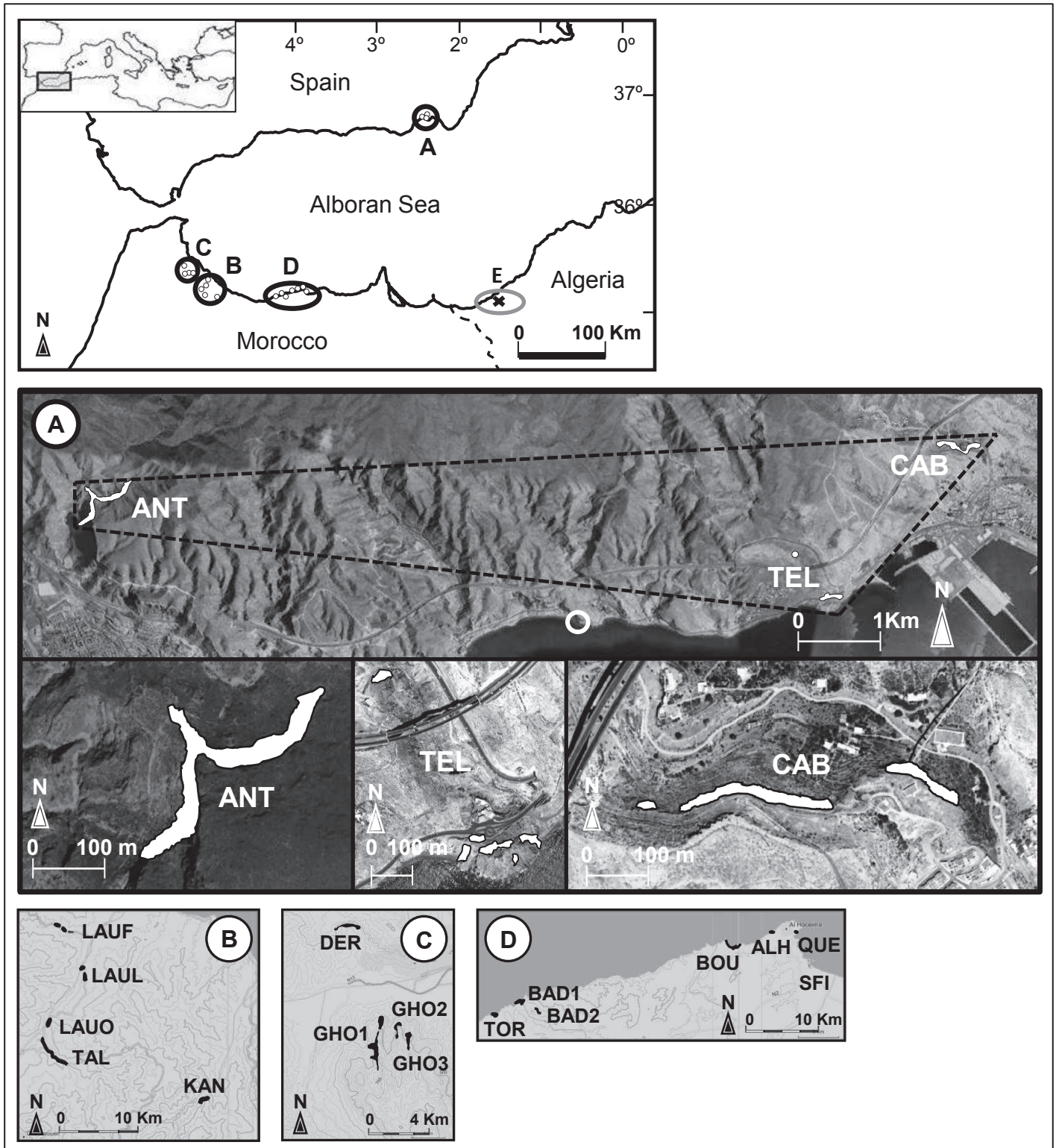|	*Class-S&J&I*	*Class-II*	*Class-III*	*Class-IV*	*Class-V&VI*
Class-S&J&I	0.500 ± 0.041	0.100 ± 0.027	0.050 ± 0.010	0.056 ± 0.011	0.069 ± 0.023
Class-II	0.189 ± 0.048	0.550 ± 0.035	0.183 ± 0.021	0.022 ± 0.022	0.015 ± 0.009
Class-III	0.047 ± 0.014	0.162 ± 0.010	0.584 ± 0.018	0.198 ± 0.036	0.026 ± 0.011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

Figure1_OnlyBlack&White

Figure2_Color
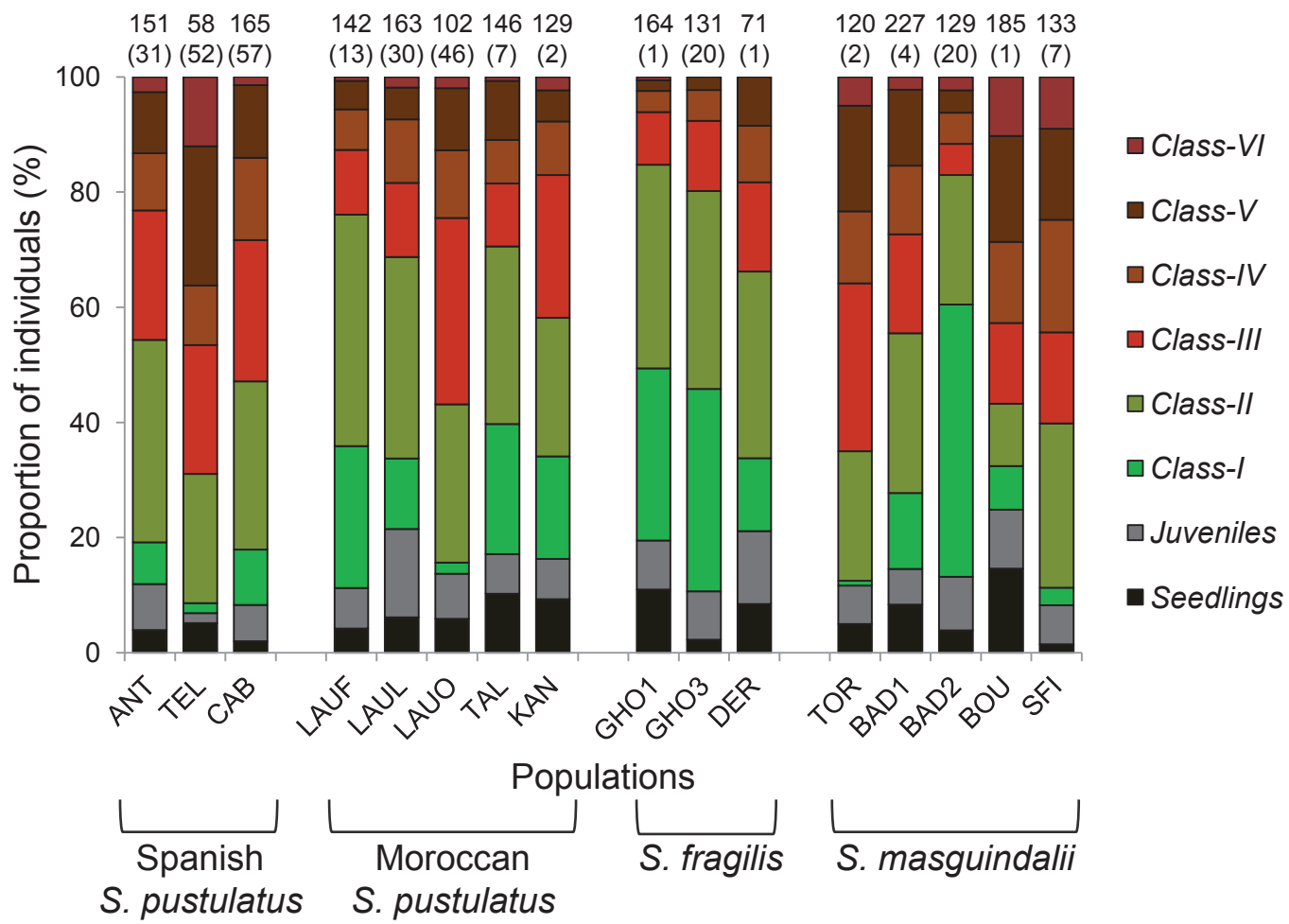
Figure2_Black&White
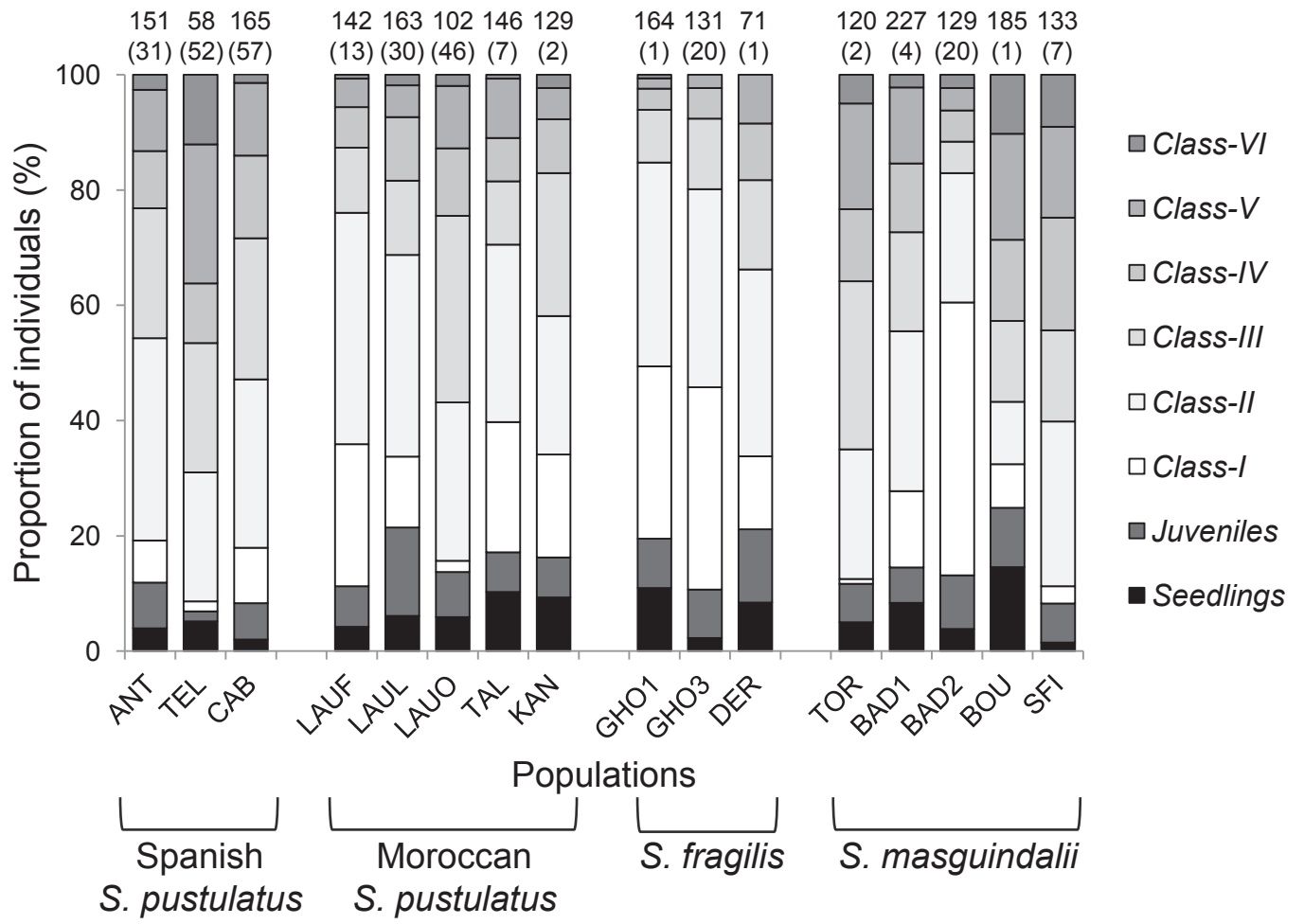
AppendixA

Click here to download Supplementary material: AppendixA.docx

AppendixA_Table3

AppendixA_Table4

AppendixA_Figure3_Caption

AppendixA_Figure3_OnlyColor