

Is a restricted niche the explanation for species vulnerability? Insights from a large field survey of Astragalus tragacantha L. (Fabaceae)

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1 Baumberger T, Baumel A, Dumas PJ, Ugo J, Keller L, Dumas E, Tatoni T, Miché L, Mirleau P, Laffont-2 Schwob I, Affre L 2021 Is a restricted niche the explanation for species vulnerability? Insights from a 3 large field survey of Astragalus tragacantha L. (Fabaceae). Flora 283:151902, doi: 4 10.1016/j.flora.2021.151902 5 6 Running Title: Ecological niche of Astragalus tragacantha 7 8 Title: Is a restricted niche the explanation for species vulnerability? Insights from a large field 9 survey of Astragalus tragacantha L. (Fabaceae) 10 Authors: Teddy Baumberger¹, Alex Baumel^{1*}, Pierre-Jean Dumas¹, Julien Ugo², Laureen Keller³, 11 12 Estelle Dumas¹, Thierry Tatoni¹, Lucie Miché¹, Pascal Mirleau¹, Isabelle Laffont-Schwob⁴, Laurence 13 Affre¹ 14 ¹ Aix Marseille Univ, Avignon Université, CNRS, IRD, IMBE, Marseille, France 15 ² Conservatoire Botanique National Méditerranéen de Porquerolles, 34 avenue Gambetta, 83400 16 Hyères 17 ³ Parc National des Calanques, 141 avenue du Prado, Bât. A, 13008 Marseille 18 ⁴ Aix Marseille Univ, IRD, LPED, UMR 151, Marseille, France 19 *Corresponding author: <u>alex.baumel@imbe.fr</u> 20 Aix Marseille Univ, Avignon Université, CNRS, IRD, IMBE, 52 avenue Escadrille N. Niemen, 13013 21 Marseille, France 22 23 Abstract 24 Understanding the environmental drivers of the realized niche of rare plant species is crucial for 25 conservation programs. We have examined the ecological niche of Astragalus tragacantha L.. This 26 rare plant is the main component of the relict west-Mediterranean phrygana, a plant community 27 impacted by urbanization and landscape degradation which are major threats for biodiversity of 28 Mediterranean littoral. During our field work in Provence (southern France), we studied habitat 29 characteristics, floristic composition and carried out an exhaustive population census. The census 30 revealed less than five thousand individuals, a strong habitat fragmentation and a high ratio of foliar 31 necrosis. Niche analyses were conducted considering either all individuals or separated size stages. 32 Analyses based on all individuals did not support the hypothesis that a too narrow niche by itself 33 explains the vulnerability of A. tragacantha. However, niche modelling revealed differences among 34 size stages supporting a restricted regeneration niche and a wider ecological range in the past. Our

- 35 comprehensive field survey underlines a worrying situation for *A. tragacantha* and sets a baseline for
- 36 conservation program.
- 37
- 38 Key words: biodiversity conservation, demography, ecological niche, joint species distribution model,
- 39 outlying mean index, rare plants, vulnerability

40 **1. Introduction**

Rare plant specialists are often weak competitors that found refuge in harsh environments
where they can be locally abundant (Youssef et al., 2011; Boulangeat et al., 2012). However,
compared to widespread species, they are expected to be more vulnerable to environmental
changes due to a restricted niche and/or less ability to disperse (Brown, 1984; Hanski et al., 1993;
Gaston, 1994). Knowing the drivers of vulnerability of rare plant species remain a challenging issue
for conservationists who aim to preserve and strengthen their natural populations (Heywood, 2014;
Scheele et al., 2017; Pogorzelec et al., 2020).

48 At the Pleistocene-Holocene transition (11,700 years before present), plant species of 49 northern Mediterranean lowlands steppes experienced a dramatic reduction of their habitat due to 50 forest expansion (Suc et al., 2018; Allen et al., 2020; Mendoza-Fernández et al., 2021). These plant 51 species have survived in long lasting opened habitats that formed azonal refugia such as rocky 52 outcrops, infertile soils, seashore and dry escarpments used for livestock grazing. Land use changes in 53 relation to human activities constitute now a major threat for this rare biodiversity adapted to harsh 54 stressful habitats (Mendoza-Fernández et al., 2014). Even when they are red listed, direct 55 disturbance caused by human activities may compromise the persistence of rare species (Gauthier et 56 al., 2019). Such a scenario is a perfect illustration of the situation of rare plants in coastal Provence 57 (South East France). First 52% of the most suitable areas for rare plant species disappeared with 58 urbanization (Doxa et al., 2017), then touristic frequentation, overcrowding and various pollutions 59 caused severe degradations of coastline habitats with some irreversible consequences (Small and 60 Nicholls, 2003; Lotze et al., 2006; Schoeman et al., 2008; Youssef et al., 2009; Fenu et al., 2013; Affre 61 et al., 2015). For these reasons, rare plants that have found refuge in Mediterranean coastline 62 habitats are becoming increasingly vulnerable and some of them are on the verge of extinction 63 (Abdel Samad et al., 2020).

64 Astragalus tragacantha L., (1753) (Fabaceae) is a rare thorny cushion plant species belonging 65 to the circum-Mediterranean Astragalus L. sect. Tragacantha DC. (Fabaceae). This lineage took its origin from the Near East probably during the Pliocene (5.3 to 2.6 million years before present) and 66 67 its diversification occurred during the Pleistocene (2.6 million years before present) after a wide 68 expansion across the Mediterranean regions followed by geographical isolation in coastal and 69 mountainous habitats (Hardion et al., 2010; Hardion et al., 2016). The closest relatives of A. 70 tragacantha are vulnerable, narrow endemics living in Corsica and Sardinia requiring high 71 conservation priorities (Cogoni et al., 2014; Sau et al., 2014; Sau et al., 2015; Orsenigo et al., 2018; 72 Fenu et al., 2019). With a distribution highly fragmented on capes and islands of south-eastern 73 France, north-eastern Spain and south-eastern Portugal (Valsecchi, 1994), A. tragacantha is one of 74 the key foundation plant species of the relict west-Mediterranean phrygana plant community

75 (Astragalo massiliensis-Plantaginetum subulatae Molinier, 1934; European Corine biotope code 76 H5410; Davies et al., 2004; European Commission, 2013). Strictly protected in France, it is among the 77 5% of 3,282 plant species deserving the highest priority of conservation in Provence (Le Berre et al., 78 2017, 2019). Urbanization is the cause of disappearance of at least four known populations, its 79 remnant habitats were degraded and polluted (Laffont-Schwob et al., 2011; Salducci et al., 2019) and 80 regular field investigations since 2005 revealed a worrying situation with high individual mortality 81 and low regeneration (L. Affre and P.J. Dumas, unpublished data). Thus, the local stakeholder in 82 charge with the conservation of the main populations of A. tragacantha, i.e. the Calanques National Park, has recently launched a LIFE Habitats Calangues project (LIFE16 NAT / FR / 000593, 2017-2022) 83 for the large-scale restoration of degraded coastal habitats. This project included A. tragacantha of 84 85 which highly visible cushions are a symbol of conservation.

86 In the perspective of conservation actions such as reintroduction or population 87 reinforcement, we examine the realized niche of A. tragacantha in Provence coastline habitats. We 88 focus our field work on habitat characteristics, floristic survey and perform an exhaustive 89 demographic census. Particularly, we decipher the habitat drivers of A. tragacantha demographic 90 density. Although population density is a good estimator of population viability, in long living 91 perennial plants such as A. tragacantha it is recommended to use population structure, i.e. the 92 distribution of age or size stage related to the age (Kienberg and Becker, 2017). We therefore base 93 our analyses on total density and densities of different size stages of A. tragacantha. After the 94 population assessment of A. tragacantha in Provence, we delineate its realized ecological niche with 95 the Outlying Mean Index (OMI; Dolédec et al., 2000) multivariate method and estimated the effects 96 of environmental gradients on A. tragacantha populations with the Generalized Joint Attribute 97 Modelling method (GJAM; Clark et al., 2017).

98

99 2. Material and methods

100 **2.1. Study sites**

101 The studied sites are including the entire French range of A. tragacantha, which is situated in 102 Provence on the Mediterranean shoreline from 5.29°E; 43.29°N to 5.88°E; 43.04°N (Fig. 1). More 103 precisely, the SILENE database (Delauge et al., 2013) records the occurrences of A. tragacantha in the 104 Bouches-du-Rhône and Var counties in the vicinity or inside five cities: Marseille, la Ciotat, Saint-Cyr, 105 Six-Fours-les-plages and La Seyne-sur-mer (Fig. 1). Near Marseille, the western occurrences, from 106 5.29°E to 5.40°E longitudes, are in an area now included in the Calangues National Park, created in 107 April 2012. These sites occur on compact limestone in continental or insular shoreline. The other 108 populations occur from 5.60°E to 5.70°E longitudes, on different substrates: dolomitic (Cap Canaille 109 near the city of La Ciotat), siliceous conglomerates (Bec de l'Aigle close to the city of La Ciotat), or

- sandy soils (city of Saint-Cyr). The eastern populations, from 5.80°E to 5.88°E longitudes, are mainly
- 111 present on phyllite cliffs (cities of Six-Fours-les-plages and La Seyne-sur-mer). The extent of
- 112 occurrences was split in 7 sectors and then in 32 subsectors (according to the toponymy) to
- 113 summarize demographic data (Table 1).



114

115 **Fig. 1:** Study area in Provence that encompass all French populations of *Astragalus tragacantha* L.,

116 1753. The black dots on the map are indicating all *A. tragacantha* occurrences detected by our survey

117 in 2019. Pictures: Calanques habitats and *A. tragacantha* cushions, Marseille, France.

118

119 **2.2.** Astragalus tragacantha demography

120 The field campaign occurred during winters 2018-2019 across all 32 subsectors listed in the 121 Table 1. For each of them, all individuals were counted recording their GPS coordinates (Lambert 93), 122 mean diameter (averaging two perpendicular diameters) and foliar necrosis ratio (percentage). GPS 123 coordinates were adjusted using satellite orthophotos in the field, hence the precision of individual 124 spatial position is assumed to be close to 1 m. The populations of A. tragacantha were described 125 based on individual size stages and foliar necrosis, used as proxies of regeneration and health, 126 respectively. Foliar necrosis is possibly due to the conjunction of water deficit stress and of sea-127 sprays polluted by maritime traffic and submarine outfall of discharges of wastewater (Barbour, 128 1978; Affre et al., 2015; Robert-Peillard et al., 2015). Five size stages were defined based on the 129 mean diameter classes: inferior to 10 cm; between 10 and 50 cm; between 51 and 100 cm; between 130 101 and 200 cm; and superior to 200 cm. Four classes of foliar necrosis were considered: inferior to

10%; between 10 and 50%; more than 50%; and dead individual (i.e, 100%). A grid of 100 m² squares
 (QGIS Development Team, 2020) was used to calculate the Area Of Occupancy (AOO) of the species.

- 133 Within each square of the grid, spatial requests in QGIS software (QGIS Development Team, 2020)
- 134 were performed to count the total number of individuals, then the number of individuals within each
- 135 of the size stages and necrosis classes. Each square was used as a unit sample to summarize
- demographic data and assess densities within the *A. tragacantha* distribution. To assess the isolation
- 137 of individual within sector we performed spatial analysis using QGIS software to compute mean,
- 138 minimum and maximum distances between individuals.
- 139

140 **2.3.** Environmental factors and floristic surveys

Ecological data are composed of the floristic and environmental relevés obtained from a recent study (Pouget et al., 2016) and those acquired for this study during spring 2019. The 499 relevés, situated within 2 km from seashore, encompass the ecological gradient from rocky shoreline to littoral scrublands. Among them, 162 are occupied by *A. tragacantha*.

145 For each of the 499 relevés, the following environmental variables were recorded within a 146 surface of 100 m²: elevation above sea level (meters), distance from the seashore (meters), slope 147 (degree), exposure (index from 0 to 4 corresponding to north exposure to south exposure, i.e. 0 for 148 north, 1 north-east and north-west, 2 for east and west, 3 for south-east and south-west, and 4 for 149 south), estimated cover rate of rocky substrate type such as rock (rocky outcrops), block i.e. $\emptyset > 20$ 150 cm, stone i.e. $\emptyset < 20$ cm, estimated cover rate of bare soil, and estimated cover rate of herbaceous 151 and woody plants. The vegetation and environmental cover variables were estimated on the basis of 152 a semi-quantitative mode using 6 cover classes (0: cover = 0%, 1: 0% < cover < 10%, 2: 10% ≤ cover < 153 25%, 3: $25\% \le \text{cover} < 50\%$, 4: $50\% \le \text{cover} < 75\%$, 5: $\text{cover} \ge 75\%$). To analyze co-occurring plant 154 communities with A. tragacantha, all plant species within the 100 m² plots were inventoried.

155

156 **2.4. Niche analyses**

157 To provide a comparative framework in niche analysis, we searched for plant species 158 significantly associated to A. tragacantha (hereafter called "companion species"). To define this 159 subset of companion species, we defined two groups of relevés according to the presence and absence of A. tragacantha and used the "multipatt" function of the indicspecies packages in R 160 161 software which is based on specificity and fidelity criteria (De Caceres and Legendre, 2009). A strong 162 value close to 1 indicates a strong association between A. tragacantha and the focal species (e.g. it is 163 present and abundant only when A. tragacantha is present). To design a manageable subset for 164 analyses, we selected the plant species having an indicator value superior or equal to 0.5.

166 **2.4.1. Outlying Mean Index multivariate method (OMI)**

167 Our first approach was based on a multivariate ordination method that uses environmental 168 and species assemblage data to correlate the occurrence of many species with ecological factors. 169 Dolédec et al. (2000) demonstrated that OMI is suited for finding the most structuring environmental 170 gradients in species distributions. The ordination diagrams of OMI analysis from the niche() function 171 of the ade4 package in R software (Dray and Dufour, 2007) are based on the table of normalized 172 environmental variables and the floristic table. In the OMI scatterplot, the distance of the centroid of 173 a species to the origin of the diagram is an estimate of the environmental marginality of this species. 174 A species with a high marginality is constrained by a narrower environmental requirement compared 175 to other species, *i.e.* it has a more specialized niche in the context of the analysis. The OMI releases 176 also the species tolerance, which is a measurement of the species niche breadth. Marginality and 177 tolerance are correlated when common species have the broader niche breadth, but the residual 178 tolerance is not correlated to marginality (Dolédec et al., 2000). Niche parameters, marginality and 179 residual tolerance values, were computed with the niche.params() function (R ade4) and compared 180 between A. tragacantha, its companion species, species common in the study area and to mean 181 values computed for all the species. To illustrate the ordination diagrams of OMI by A. tragacantha total density (number of individuals counted in each 100 m² plots) we used the coordinates of each 182 183 relevé along the OMI axes to form a scatterplot of circles with diameter proportional to A. 184 tragacantha density with the R function "point". Spearman correlations between environmental 185 variables and OMI axes were plotted as a heatmap (R cor function and ggcorrplot function; 186 Kassambara, 2016) for inferences of the main ecological gradient revealed by OMI.

187

188 2.4.2. Generalized Joint Attribute Modelling method (GJAM)

189 Our second approach of niche modelling was based on GJAM method developed by Clark et 190 al. (2017). We used it to quantitatively estimate the sensitivity and response of A. tragacantha size 191 stage densities to the main ecological gradients. We achieved a pilot analysis to control that 192 congruent inferences were obtained while using either the eleven environmental variables or the 193 OMI axis, which allowed to choose the OMI axes as predictor variables for GJAM. The response 194 variables were the presence/absence of all plant species present in at least 25 relevés (*i.e.* 5% of the 195 data) and A. tragacantha densities. Two GJAM models were fitted with the main OMI axis as 196 predictors: (i) A. tragacantha density of all living individuals (hereafter named "total density") as first 197 model and (ii) the five size stage densities (0-10 cm, 11-50 cm, 51-100 cm, 101-200 cm, only living 198 individuals) as second model. GJAM was performed with the following model parameters: linear 199 terms, non-informative prior for the coefficients and covariance matrix, 10,000 iterations with a 200 burn-in of 2,500 iterations. The response variables concerning A. tragacantha were coded as "DA"

- 201 (discrete counts) and the floristic data as "PA" (presence/absence). Astragalus tragacantha was
- 202 removed from the list of plant species involved in the analysis. We controlled the convergence of the
- 203 model and the model fitting to data by using the outputs of GJAM. We used build-in gjamplot
- 204 functions to produce the matrix of beta coefficients and a clustering of the response variables based
- 205 on sensitivity. Sensitivity to environmental predictors were displayed with boxplots. Beta coefficients
- were summarized in a table to show the response of *A. tragacantha* to ecological gradients.
- 207 Scripts and data of our analyses are deposed in DRYAD database (doi:10.5061/dryad.bzkh1898p). We
- used the following packages: ade4 (Dray and Dufour, 2007), adegenet (Jombart, 2008), labdsv
- 209 (Roberts, 2013), gjam (Clark et al., 2017), and ggcorrplot (Kassambara, 2016).

Table 1: Population sizes and densities of Astragalus tragacantha in Provence by sectors and sub-sectors based on the 1,571 squares of 100 m².

Sector	Sub-sector	Total number of individuals	Percentage of total number of individuals	Minimum density (individual/100 m²)	Maximum density (individual/100 m²)	Mean proportion of individuals smaller than 10cm (%)	Mean density (individual/100 m ²)	Number of occupied 100 m ² squares	Area of occupancy (number of squares x 100 m ²)
County of Bouches-du-Rhône		4,349	88.41%	1	34	4.6	2.73	1,401	14.01 ha
	Total	2,252	45.78%	1	34	6.8	3.36	669	6.69 ha
	Calanque de Callelongue	104	2.11%	1	13	4.8	4.52	23	0.23 ha
	Calanque de la Mounine	28	0.57%	1	5	0	2.33	12	0.12 ha
	Calanque de Marseilleveyre	307	6.24%	1	13	4.9	2.49	123	1.23 ha
	Calanque des Queyrons	3	0.06%	3	3	33.3	3.00	1	0.01 ha
	Calanque des trous	227	4.61%	1	27	15.4	3.66	62	0.62 ha
	Cap Croisette - la Maronnaise	409	8.31%	1	14	9.3	2.73	150	1.5 ha
Calanques littoral	Escalette	186	3.78%	1	14	0.5	3.88	48	0.48 ha
area (Marseille)	La Poulidette	15	0.3%	1	5	6.7	3.75	4	0.04 ha
	Maïre	11	0.22%	1	2	0	1.10	10	0.1 ha
	Mauvais pas	53	1.08%	1	5	0	1.93	27	0.27 ha
	Mont Rose	738	15%	1	34	4.6	4.92	150	1.5 ha
	Parking des Goudes	88	1.79%	1	12	11.4	2.32	38	0.38 ha
	Samena	10	0.2%	1	2	0	1.00	8	0.08 ha
	Sormiou Cap Redon	73	1.48%	1	16	16.4	3.17	23	0.23 ha
	Marseille – Pointe Carinade	3	0.06%	1	1	0	3.00	1	0.01 ha
	Total	8	0.16%	1	3	0	1.50	6	0.06 ha
Calangues inland area	La Cayolle	2	0.04%	1	1	0	1.00	2	0.02 ha
(Marseille)	Sablières Aniarre	2	0.04%	1	1	0	1.00	2	0.02 ha
(Luminy	4	0.08%	1	3	0	2 00	2	0.02 ha
	Editinity		0.0070		0	Ŭ	2.00	2	0.02 110
La Ciotat	Bec de l'Aigle	173	3.52%	1	15	9.8	2.75	63	0.36 ha
	Total	1,054	21.43%	1	18	1	2.85	370	3.7 ha
Pomègues (Frioul	Fort Pomègues	133	2.7%	1	8	0	1.82	73	0.73 ha
archipelago)	Port de Pomègues	124	2.52%	1	18	0	3.18	39	0.39 ha
	Sémaphore de Pomègues	797	16.2%	1	18	1.4	3.09	258	2.58 ha
	Total	859	17.46%	1	22	3.6	2.94	292	2.92 ha
	Calangue de Morgiret	662	13.46%	1	22	4.7	3.39	195	1.95 ha
Ratonneau (Frioul	Calangue du Berger	35	0.71%	1	9	0	3.50	10	0.1 ha
archipelago)	Hôpital Caroline	42	0.85%	1	4	0	1.83	23	0.23 ha
	Pointe Brigantin	83	1 69%	1	12	0	1 89	44	0 44 ha
	Port de Banc - Fort de Ratonne	37	0.75%	1	5	õ	1.85	20	0.2 ha
-									
County of Var		570	11.59%	1	17	0	1.78	170	1.7 ha
Six-Fours-les-plages	Cap Nàgro	1	0.02%	1	1	0	1.00	1	0.01 ba
	Cap Negle	I	0.02 /6	I	I	0	1.00	I	0.01 11a
	Total	569	11 57%	1	17	0.9	2 56	169	1.69 ha
	Amphitria	/31	8 76%		17	0.7	2.00	101	1.00 ha
		401	0.70%	1	5	0.7	2.31	5	0.05 ba
Cap Sicié		13	0.20%	1	5	1.1	2.00	5	0.05 ha
·	Grande pointe des Jonquiers	105	2.13%	1	6	1	1.88	56	0.56 ha
	La Verne	19	0.39%	1	8	0	3.17	6	0.06 ha
	Plage de la Fosse	1	0.02%	1	1	0	1.00	1	0.01 ha
I otal in France		4,919	100%	1	34	4.5	2.5	1,571	15.71 ha

213 3. Results

214 **3.1.** Population assessment of *Astragalus tragacantha* in Provence

215 The 4,919 individuals of A. tragacantha counted in southern France are distributed only in a 216 total Area Of Occupancy (AOO) of 15.71 ha. The density estimates and AOOs are disparate among 217 and within sectors (Table 1). 45.8% of individuals are in the "Calangues littoral" sector and 25.1% on Frioul archipelago ("Pomègues" and "Ratonneau") indicating that the areas in the vicinity of 218 219 Marseille encompass ca 70% of the Provence total number of individuals. Remarkably, 88.4% of the 220 individuals of *A. tragacantha* live inside the Calangues National Park ("Bouches-du-Rhône" county) 221 and only 11.6% elsewhere ("Var" county). A high variance is observed at the 100 m² plot level ranging 222 from 1 to 34 individuals. The maximum density is heterogeneous within sectors, as for instance, 223 "Calanques littoral" sector where maximum densities varies from 2 to 27 ind./100 m². Sectors 224 holding the higher number of plants such as "Calanques littoral", "Pomègues" and "Ratonneau" show the lower populations isolation, whereas sectors "Six-fours-les-plages" and "Cap Sicié", holding a 225 226 very low number of plants show the highest population isolation (Table S1 in sup. mat.). Within the 227 Calanques National Park the "Calanques inland" area is characterized by three isolated occurrences 228 accounting for a total of 8 individuals.

229

230 Table 2: Proportion of crossed classes of the mean individual diameter and mean individual foliar

231 necrosis rate calculated for the 4,919 individuals of Astragalus tragacantha counted i	n Provence
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	Mean diameter								
Foliar necrosis rate	Inferior to 10cm	Between 10 and	Between 10 and Between 51 and		Superior to 200				
		50 cm	100 cm	and 200 cm	cm				
Inferior to 10%	3.8%	14.4%	11.9%	3.1%	0.5%				
Between 10 and 50% 0.5%		14%	19.7%	8.3%	1.8%				
Superior to 50%	0%	4.8%	6.1%	3.9%	1%				
Dead (i.e. 100%)	0.1%	3.1%	2.5%	0.6%	0%				
% of living plants	4.3%	33.2%	37.7%	15.3%	3.3%				

232

Among the 4,919 individuals, 4,614 are alive (e.g. with necrosis ratio inferior to 100%) and 37.7% present a mean diameter between 50 and 100 cm which is the most abundant size stage (Erreur ! Source du renvoi introuvable.). Overall, the mean proportion of individuals inferior to 10 cm in size is 4.3% but more than half of subsectors (51.5%) have no small individuals. The highest

- 237 numbers of small individuals are observed in the "Calanques littoral" sector (especially "Escalette",
- 238 "Goudes", and "Cap Redon" subsectors) where the proportion vary from 11 to 16%.
- The foliar necrosis is high, most individuals (66.3%) present a foliar necrosis superior to 10%
- 240 (Table 2, Fig. 2) and 22% have a foliar necrosis superior to 50% of the cushion.
- 241



242

- 243 **Fig. 2:** Proportion of the individual foliar necrosis rate for each size stage of the 4,919 Astragalus
- 244 *tragacantha* individuals in Provence (see also Table 2).
- 245
- 246

247 **3.2.** The realized niche and environmental drivers of demography

248 The indicator species analysis reveals a significative value (p value $\leq 1\%$) for 20 plant species 249 in presence of A. tragacantha and 15 in absence (Table S2 in sup. mat.). In presence of A. 250 tragacantha, only six species have an indicator value superior or equal to 0.5 with a specificity 251 ranging from 0.68 to 0.72 and a fidelity ranging from 0.45 to 0.76. In a decreasing order of indicator value, these companion plant species of A. tragacantha are Catapodium marinum (L.) C.E. Hubbard, 252 253 Valantia muralis L., Limonium pseudominutum Erben, Lotus cytisoides L., Crithmum maritimum L., 254 and Camphorosma monspeliaca L. On the opposite, some species which are common in Provence 255 shrublands are almost never found with A. tragacantha such as shrubs or small trees as Erica 256 multiflora L., Quercus coccifera L., Rhamnus alaternus L., but also small chamaephytes such as 257 Globularia alypum L. or Thymus vulgaris L. 258 The OMI analysis sets the realized niche of A. tragacantha in a multivariate space built by the 259 main ecological gradients shaping plant communities (Fig. 3). The first four OMI axes account for 85% 260 of the total inertia. The correlation among OMI axes and habitat variables is shown in the heatmap of 261 Spearman Rho correlations (Fig. S1 in sup. mat.). The first OMI axis (53% of inertia) opposes woody 262 vegetation, increasing with elevation, to biotopes close to the shoreline. The second OMI axis (14% of 263 inertia) associates facing north sites with herbaceous cover. The third OMI axis (10% of inertia) 264 opposes rock cover to herbaceous cover and litter cover. The fourth OMI axis (8% of inertia) opposes 265 opened places with high bare soil and stone covers to places occupied by woody vegetation. On 266 diagram defined by the two main ecological gradients (OMI axes 1 and 2), the density of A.

tragacantha is higher on the right part (Fig. 3). These sites are situated in opened littoral biotopes.



Fig. 3: Multivariate analysis of the realized niche of *Astragalus tragacantha* in Provence shown by
diagram of the Outlying Mean Index (OMI) method. Arrows correspond to environmental variables,
black dots are relevés without *A. tragacantha*, grey circles are relevés with *A. tragacantha*, the
diameter being proportional to the number of individuals within the relevé. Triangles indicate plots
where *A. tragacantha* disappeared between 2007 and 2019.

275

276 Analyses of niche parameters show that over all plant species, the mean standardized marginality is 31 with a 95% confidence interval between 28 and 38. The mean residual tolerance is 277 278 57 with a 95% confidence interval between 54 and 60. As expected, the plant species being common 279 in the study area and in Provence littoral have lower marginality and higher residual tolerance : e.g. 280 Brachypodium retusum (Pers.) P.Beauv. (marginality = 2.1, residual tolerance = 78), Erica multiflora 281 (marginality =9.8, residual tolerance =71), Lobularia maritima (L.) Desv. (marginality =1.8, residual 282 tolerance = 87), Matthiola incana (L.) R. Br. (marginality =7.7, residual tolerance =87), Pinus halepensis Miller (marginality = 9, residual tolerance = 75), or Pistacia lentiscus L. (marginality = 5.8, 283 284 residual tolerance =77). Astragalus tragacantha and its seven companion plant species have a mean 285 marginality of 9, and a mean residual tolerance of 80. Astragalus tragacantha alone shows a mean 286 marginality of 8 and a mean residual tolerance of 82. Thus, in the study area, A. tragacantha and its 287 companion plant species have similar niche parameters indicating a low marginality and high 288 tolerance that do not support a restricted amplitude of the realized niche. 289 GJAM modelling method quantitatively estimated the sensitivity and response of A. 290 tragacantha demography to the main ecological gradients (OMI axes). For the two GJAM models,

291 analyzing the total density of A. tragacantha or the density of the five size stages, the response 292 matrix was reduced to height dimensions. The models well converge, and the environmental 293 predictors and response variables are well predicted (Fig. S2 in sup. mat.). Model sensitivities and 294 responses to ecological gradients (Fig. S3 in sup. mat. and Table 3) were different among the total 295 density and the different size stages of A. tragacantha. The A. tragacantha total density is mostly 296 determined by the first and fourth ecological gradients, OMI_1 and OMI_4 ("All stages", Table 3). 297 This result indicates that A. tragacantha total density is increasing when elevation and wood cover 298 are decreasing as well as when bare soil is increasing. The second ecological gradient, OMI 2, 299 opposing south facing to north facing places has also a small but significant effect indicating that A. 300 tragacantha is responding positively to north facing, such places having also higher herbaceous cover 301 (Fig. 3). Similar effects are observed for the most populated stages, the D50 (33% of the counts) and 302 D100 size stage (38% of the counts). The main differences are observed for the D10 and the D200 303 and Dsup 200 size stages which are not sensitive to the second and fourth OMI axis. The only 304 significant response of the last size stage (Dsup200) is for the third axis indicating a preference of the 305 biggest individuals for places with high herbaceous and litter cover rather than rocky outcrops. By 306 comparison to other size stages, the smallest individuals have the most important responses to the 307 first and third OMI axes indicating their preference for opened places near the sea, with a low wood 308 cover and with herbaceous rather than rock cover.

309

Table 3: Significative positive or negative responses of *Astragalus tragacantha* population

parameters to ecological gradients estimated by GJAM. "All stages" indicates that all individuals were
 considered whereas "D0-10" to "Dsup200" indicate that individuals were organized as size stages

according to the mean individual diameter (cm) from the smallest to the biggest individuals. Dead

314 individuals were removed.

Ecological	from	to						
gradient	negative pole	positive pole	All stages	D10	D50	D100	D200	Dsup200
OMI_1	high elevation,	lowland,						
	wood	close to sea	4.1	0.54	0.35	0.42	0.22	ns
OMI_2	south facing	North facing	1.8	ns	0.15	0.252	ns	ns
OMI_3	rocky places	herb	ns*	0.42	ns	0.27	0.25	0.29
OMI_4	bare soil, stones	wood	-5.4	ns	-0.18	-0.49	ns	ns

315 **ns= non significative value*

316

The differences among size stages appeared also clearly when they are clustered with the other species based on their responses to ecological gradients (Fig. S4 in sup. mat.). The first three stages (D10 to D100) are grouped together into one of the three main clusters. In this group, we 320 observed the companion plant species of *A. tragacantha* (previous results) such as *Camphorosma*

321 monspeliaca, Plantago subulata L., Limonium pseudominutum, Catapodium marinum, Valantia

322 *muralis* and *Lotus cytisoides*. Yet, these three stages did not share the same companions. The first

323 stage (D10) is separated from the stages D50 and D100 and the last stages, D200 and Dsup200 are

324 clustered together in association with a different community composed of *Euphorbia pithyusa* L.,

325 Plantago lagopus L., Lagurus ovatus L., or Lobularia maritima (Fig. S4).

326

327 4. Discussion

328 4.1. A dangerous demographic situation

329 In southern France, Astragalus tragacantha is reaching 4,919 individuals distributed in seven 330 sectors. It is worth noting that all these sectors are situated within or in the vicinity of cities in a 331 context of more than one century of urbanization and land uses changes. We observed a great 332 heterogeneity of abundance within A. tragacantha distribution. In fact, at the western part of the 333 range 84.7% of the individuals are concentrated in the "Calanques littoral" area and on the Frioul 334 archipelago (Pomègues and Ratonneau islands) representing a 10 km radius area. The "Cap Sicié" 335 population, which represents 11% of all individuals, is more than 50 km away from these main areas 336 on the east side of the range (Fig. 1, Table 1). All other sectors present few individuals, weak 337 densities and are distant from each other in several tens kilometers, especially for the eastern 338 populations.

339 Such situation of spatial fragmentation and unbalanced population raises questions on the 340 persistence of especially small and isolated populations (Ouborg et al., 2006; Frankham et al., 2014). 341 Theoretical models predict that any kind of stochasticity (demographic, genetic, environmental) will 342 exponentially increase the extinction risk of small and isolated popultions (Ovaskainen and Meerson, 343 2010). Schurr et al. (2019) have shown the existence of both inbreeding and outbreeding depression 344 within and among the A. tragacantha populations and observed that different predominant 345 pollinators are confined in different sites: Anthophora plumipes Pallas (1772) in the "Cap Croisette" 346 sub-sector, Eucera caspica Morawitz (1873) on Frioul archipelago, and Bombus terrestris L. (1758) in 347 the sector of "Calanque des Trous". This interaction with pollinators being restricted at a fine scale 348 may worsen the impact of population fragmentation. Their results suggest that fragmentation is 349 already impacting A. tragacantha population fitness even in the sites where the abundance of A. 350 tragacantha is the highest.

At first glance, the low frequency of smallest and biggest individuals (4.3% and 3.3%), with most intermediate sizes individuals (Table 2), suggests a stable population type by comparison to the demography of *Astragalus exscapus* L., an endangered steppe grassland species (Kienberg and Becker, 2017). However, by contrast to *A. exscapus*, seedlings and plantlets were very rarely

355 observed during 15 years of a regular field survey (L. Affre pers. com). This is also in contrast with the 356 observation of larger amount of seedling and plantlets in populations of Astragalus angustifolius 357 Lam. on Mount Lebanon which lives on deeper soils and is a close relative of A. tragacantha (A. 358 Baumel pers. com.). Moreover, by comparison to previous field campaigns (Affre et al., 2015; Pouget 359 et al., 2016), this new updated survey shows that A. tragacantha has not colonized any new habitats, 360 even within the subsectors near living individuals. The habitat requirements represent important 361 drivers of A. tragacantha density but dispersal to new areas is certainly also a crucial factor. Survey of 362 dispersal for A. exscapus revealed a very low dispersal potential leading to the clumping of 363 individuals (Becker, 2010), a spatial pattern observed for A. tragacantha. Although our study does 364 not estimate dispersal, we showed that A. tragacantha has similar niche marginality and tolerance 365 than its companion plant species who are more abundant, suggesting a disequilibrium between 366 probability of local extinction and recolonization for A. tragacantha. This is also supported by the 367 OMI analyses showing the existence of several suitable sites where A. tragacantha is absent. Most of 368 these sites are close to occurrences and could be reachable if a dispersal agent was present.

A final point of concern is that only the small individuals have low ratio of necrosis. Above 10 cm of diameter, all size stages show a necrosis rate superior to 10% of their cushion. We counted also 305 individuals having a 100% foliar necrosis ratio and which are probably dead. Representing 6.2% of the total number of individuals they suggest that mortality rate is strong. Such important foliar necrosis rate was not observed in closely related species of *A. tragacantha* living on deeper soils (A. Baumel com. pers.). Deciphering between polluted sea sprays and water stress deficit as causes for foliar necrosis is an important issue that deserves an *adhoc* study.

376

4.2. Is population vulnerability caused by a restricted niche breadth?

The ecological niche analyses show that habitat openness is required for *A. tragacantha* individuals that avoid competition from woody plant species. South facing places with high rock areas are less suitable than more north facing situations with more soil and herbaceous cover. These results indicate that drought is likely to also limit the expansion of the species. Is this enough to explain the vulnerability of the *A. tragacantha* populations? In fact, the similar niche parameters between *A. tragacantha* and its companion plant species, which are less vulnerable and more common, do not support the hypothesis of a range limited by the realized niche.

On the other hand, GJAM models revealed different responses to ecological gradients among the different size stages. Postulating that small individuals are more representative of the last regeneration event than the bigger ones, we can hypothesize that regeneration is higher in opened places near the sea, with a low wood cover and with herbaceous rather than rock cover. The smallest individuals, which are also the one having lowest foliar necrosis rate, are associated to an original

plant community indicating that the regeneration niche is more restricted than the current realized
niche. Soil depth is important for germination (Bullied et al., 2012) and studies on *Astragalus* species
underline the importance of seed dispersal toward bare soil areas for recruitment (Becker, 2010;
Baer and Maron, 2019, 2020). Indeed, sufficiently deep soil allowing water retention is required for
the seed emergence whereas once taller adult individuals develop their root system, soil depth
become less crucial for their survival, especially under Mediterranean climate (Padilla and Pugnaire,
2007).

397 Therefore, regeneration of A. tragacantha is subject to a dual constraint caused by the 398 requirement of open habitat and low competition from woody plants on the one hand, and low rock 399 cover to allow seed germination on the other. The fact that these conditions are limited within the 400 realized niche suggests that the habitat of A. tragacantha has changed. In the past, the strong grazing 401 pressure by cattle on woody plant regeneration (Romey et al., 2015) may have been favorable to A. 402 tragacantha and the abandon of pastoral activities contributed to current fragmentation. In the OMI 403 analysis, the scattered occurrences on the left part of the diagram (Fig. 3) are related to the less 404 suitable places where woody vegetation develops. In these environments, the disappearance of A. 405 tragacantha from relevés (corresponding to triangles in Fig. 3) indicates that local extinction 406 occurred in less than 20 years. In association with historical occurrences, these extinction of patches 407 of A. tragacantha far from the coastline (currently in woods), are insights indicating a wider realized 408 niche breadth in the past. These results highlights that extinction debt (Tilman et al., 1994; Hanski 409 and Ovaskainen, 2002) is probably a reality for A. tragacantha. In the same study area, Martín-410 Queller et al. (2017) analyzed the impact of fragmentation on plant communities and revealed that it 411 was higher for perennial plants and higher in islands, suggesting as here that extinction debt is likely 412 in Provence for several plant species, including A. tragacantha. Our results and inferences are 413 consistent with the ecological characteristics of declining species (Scheele et al., 2017).

414

415 **5. Conclusion**

416 The results of this study do not support the hypothesis that a too narrow niche by itself explains the 417 vulnerability of A. tragacantha. However, niche modelling by GJAM supports a restricted 418 regeneration niche, a wider niche in the past and that ecological constraints on dispersal and 419 recruitment are important drivers of A. tragacantha's vulnerability. The high foliar necrosis rate 420 revealed here is also of concern and calls for monitoring at the individual level. In this context, our 421 study constitutes the basis of a long-term demographic survey of A. tragacantha and the essential 422 prerequisites to guide the conservation of its populations. Conservation actions should aim to (i) 423 increase abundance and (ii) expand current realized niche. Reinforcement of A. tragacantha populations and (re)introduction in favorable habitats are therefore needed. 424

425

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432	
433	Supplementary materials
434	Data sets and R scripts were deposed in DRYAD data base and are available at the URL:
435	doi:10.5061/dryad.bzkh1898p
436	Supplementary materials can be found in the online version and contain tables and figures
437	completing results.
438	• Table S1: Synthesis of distances between individuals for all seven sectors.
439	• Table S2 : Specificity, Fidelity and Indicator species values for taxa in presence or absence of
440	A. tragacantha. Only taxa with p values inferior or equal to 1% were kept
441	• Fig. S1: Spearman Rho correlations among environmental variables and the OMI axes
442	gradients identified by the Outlying Mean Index method and used here to design the main
443	ecological gradients structuring plant communities in the range area of Astragalus
444	tragacantha. The variables are elevation above sea level, distance to the sea, slope orientation,
445	and covers of woody plants, herbaceous plants, rock, block, stone, bare soil and litter,
446	respectively.
447	• Fig. S2 : Environmental and response variables prediction by GJAM model.
448	• Fig. S3: GJAM analysis of sensitivity of Astragalus tragacantha total density ("all stages") and
449	size stages to ecological gradients obtained by OMI. Plant size increased from D10 to Dsup200
450	• Fig. S4: Cluster of species and Astragalus tragacantha size stages based on response to
451	ecological gradients (eta coefficients of GJAM model). This figure helps to find species having the
452	same model response than A. tragacantha.
453	
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632 **Figures** 633 Fig. 2: Study area in Provence that encompass all French populations of Astragalus tragacantha L., 634 1753. The black dots on the map are indicating all A. tragacantha occurrences detected by our survey 635 in 2019. Pictures: Calangues habitats and *A. tragacantha* cushions, Marseille, France. 636 637 Fig. 2: Proportion of the individual foliar necrosis rate for each size stage of the 4,919 Astragalus 638 tragacantha individuals in Provence (see also Table 2). 639 640 Fig. 3: Multivariate analysis of the realized niche of Astragalus tragacantha in Provence shown by 641 diagram of the Outlying Mean Index (OMI) method. Arrows correspond to environmental variables, black dots are relevés without A. tragacantha, grey circles are relevés with A. tragacantha, the 642 643 diameter being proportional to the number of individuals within the relevé. Triangles indicate plots where A. tragacantha disappeared between 2007 and 2019. 644 645 646 Tables 647 Table 1: Population sizes and densities of Astragalus tragacantha in Provence by sectors and sub-648 sectors based on the 1,571 squares of 100 m². 649 650 Table 2: Proportion of crossed classes of the mean individual diameter and mean individual foliar 651 necrosis rate calculated for the 4,919 individuals of Astragalus tragacantha counted in Provence. 652 653 Table 3: Significative positive or negative responses of Astragalus tragacantha population 654 parameters to ecological gradients estimated by GJAM. "All stages" indicates that all individuals were 655 considered whereas "D0-10" to "Dsup200" indicate that individuals were organized as size stages 656 according to the mean individual diameter (cm) from the smallest to the biggest individuals. Dead 657 individuals were removed. 658 659 660

662 Table 1

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Sector	Sub-sector	Total number of individuals	Percentage of total number of individuals	Minimum density (individual/100 m²)	Maximum density (individual/100 m²)	Mean proportion of individuals smaller than 10cm (%)	Mean density (individual/100 m²)	Number of occupied 100 m ² squares	Area of occupancy (number of squares x 100 m²)
County of Bouches-du-Rhône		4,349	88.41%	1	34	4.6	2.73	1,401	14.01 ha
	Total	2,252	45.78%	1	34	6.8	3.36	669	6.69 ha
	Calanque de Callelongue	104	2.11%	1	13	4.8	4.52	23	0.23 ha
	Calanque de la Mounine	28	0.57%	1	5	0	2.33	12	0.12 ha
	Calanque de Marseilleveyre	307	6.24%	1	13	4.9	2.49	123	1.23 ha
	Calanque des Queyrons	3	0.06%	3	3	33.3	3.00	1	0.01 ha
	Calanque des trous	227	4.61%	1	27	15.4	3.66	62	0.62 ha
	Cap Croisette - la Maronnaise	409	8.31%	1	14	9.3	2.73	150	1.5 ha
Calanques littoral	Escalette	186	3.78%	1	14	0.5	3.88	48	0.48 ha
area (Marseille)	La Poulidette	15	0.3%	1	5	6.7	3.75	4	0.04 ha
	Maïre	11	0.22%	1	2	0	1.10	10	0.1 ha
	Mauvais pas	53	1.08%	1	5	0	1.93	27	0.27 ha
	Mont Rose	738	15%	1	34	4.6	4.92	150	1.5 ha
	Parking des Goudes	88	1.79%	1	12	11.4	2.32	38	0.38 ha
	Samena	10	0.2%	1	2	0	1.00	8	0.08 ha
	Sormiou Cap Redon	73	1.48%	1	16	16.4	3.17	23	0.23 ha
	Marseille – Pointe Carinade	3	0.06%	1	1	0	3.00	1	0.01 ha
	Total	8	0.16%	1	3	0	1.50	6	0.06 ha
Calangues inland area	La Cayolle	2	0.04%	1	1	0	1.00	2	0.02 ha
(Marseille)	Sablières Aniarre	2	0.04%	1	1	0	1.00	2	0.02 ha
	Luminy	4	0.08%	1	3	0	2 00	2	0.02 ha
	Lonniy		0.0070	·	0	Ū	2.00	-	0102 114
La Ciotat	Bec de l'Aigle	173	3.52%	1	15	9.8	2.75	63	0.36 ha
-	5								
-	Total	1,054	21.43%	1	18	1	2.85	370	3.7 ha
Pomèques (Frioul	Fort Pomègues	133	2.7%	1	8	0	1.82	73	0.73 ha
archipelago)	Port de Pomègues	124	2.52%	1	18	0	3.18	39	0.39 ha
	Sémanhore de Pomèques	797	16.2%	1	18	14	3.09	258	2.58 ha
	Comphere de l'oméguée	101	10.270		10	1.4	0.00	200	2.00 114
	Total	859	17.46%	1	22	3.6	2.94	292	2.92 ha
	Calangue de Morgiret	662	13.46%	1	22	4.7	3 39	195	1 95 ba
Botoppogu (Erioul	Calanque de Morgiret	35	0.71%	1	0		3.50	10	0.1 ha
Ratonneau (Filoui		30	0.7178	1	9	0	3.30	10	0.111a
archipelago)	Ropital Caroline	42	0.85%	1	4	0	1.03	23	0.23 ha
	Pointe Brigantin	83	1.69%	1	12	0	1.89	44	0.44 na
	Port de Banc - Fort de Ratonne	37	0.75%	1	5	0	1.85	20	0.2 ha
County of Vor		E70	44 50%	4	47	•	4 70	470	176
County of Var		570	11.39%	1	17	Ų	1.70	170	1.7 ha
Six-Fours-les-plages	Ora Niliara		0.000/		4	0	4.00		0.04 h -
	Cap Negre	1	0.02%	1		0	1.00	1	0.01 ha
	Tatal	ECO	44 670/	4	47	0.0	0 EC	460	1.00 ha
		209	11.5/%	1	17	0.9	2.30	109	1.09 na
	Amphitria	431	8.76%	1	17	0.7	2.91	101	1.01 na
Can Siciá	Bau Rouge	13	0.26%	1	5	7.7	2.60	5	0.05 ha
Oup Cloic	Grande pointe des Jonquiers	105	2.13%	1	6	1	1.88	56	0.56 ha
	La Verne	19	0.39%	1	8	0	3.17	6	0.06 ha
	Plage de la Fosse	1	0.02%	1	1	0	1.00	1	0.01 ha
Total in France		4,919	100%	1	34	4.5	2.5	1,571	15.71 ha

665 Table 2

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	Mean diameter								
Foliar necrosis rate	Inferior to 10cm	Between 10 and	Between 51 and	Between 101	Superior to 200				
		50 cm	100 cm	and 200 cm	cm				
Inferior to 10%	3.8%	14.4%	11.9%	3.1%	0.5%				
Between 10 and 50%	0.5%	14%	19.7%	8.3%	1.8%				
Superior to 50%	0%	4.8%	6.1%	3.9%	1%				
Dead (i.e. 100%)	0.1%	3.1%	2.5%	0.6%	0%				
% of living plants	4.3%	33.2%	37.7%	15.3%	3.3%				

668 Table 3

Ecological gradient	from negative pole	to positive pole	All stages	D10	D50	D100	D200	Dsup200
OMI_1	high elevation,	lowland,						•
	wood	close to sea	4.1	0.54	0.35	0.42	0.22	ns
OMI_2	south facing	North facing	1.8	ns	0.15	0.252	ns	ns
OMI_3	rocky places	herb	ns*	0.42	ns	0.27	0.25	0.29
OMI_4	bare soil, stones	wood	-5.4	ns	-0.18	-0.49	ns	ns

669 **ns= non significative value*