



HAL
open science

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

Teddy Baumberger, Alex Baumel, Pierre-Jean Dumas, Julien Ugo, Laureen Keller, Estelle Dumas, Thierry Taton, Lucie Miché, Pascal Mirleau, Isabelle Laffont-Schwob, et al.

► To cite this version:

Teddy Baumberger, Alex Baumel, Pierre-Jean Dumas, Julien Ugo, Laureen Keller, et al.. Is a restricted niche the explanation for species vulnerability? Insights from a large field survey of *Astragalus tragacantha* L. (Fabaceae). *Flora*, 2021, 283, pp.151902. 10.1016/j.flora.2021.151902 . hal-03573389

HAL Id: hal-03573389

<https://hal-amu.archives-ouvertes.fr/hal-03573389>

Submitted on 28 Mar 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Running Title: **Ecological niche of *Astragalus tragacantha***

2

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

5

6 Authors: Teddy Baumberger¹, Alex Baumel^{1*}, Pierre-Jean Dumas¹, Julien Ugo², Laureen Keller³,
7 Estelle Dumas¹, Thierry Tatoni¹, Lucie Miché¹, Pascal Mirleau¹, Isabelle Laffont-Schwob⁴, Laurence
8 Affre¹

9 ¹ Aix Marseille Univ, Avignon Université, CNRS, IRD, IMBE, Marseille, France

10 ² Conservatoire Botanique National Méditerranéen de Porquerolles, 34 avenue Gambetta, 83400
11 Hyères

12 ³ Parc National des Calanques, 141 avenue du Prado, Bât. A, 13008 Marseille

13 ⁴ Aix Marseille Univ, IRD, LPED, UMR 151, Marseille, France

14 *Corresponding author: alex.baumel@imbe.fr

15 Aix Marseille Univ, Avignon Université, CNRS, IRD, IMBE, 52 avenue Escadrille N. Niemen, 13013
16 Marseille, France

17

18 Abstract

19 Understanding the environmental drivers of the realized niche of rare plant species is crucial for
20 conservation programs. We have examined the ecological niche of *Astragalus tragacantha* L.. This
21 rare plant is the main component of the relict west-Mediterranean phrygana, a plant community
22 impacted by urbanization and landscape degradation which are major threats for biodiversity of
23 Mediterranean littoral. During our field work in Provence (southern France), we studied habitat
24 characteristics, floristic composition and carried out an exhaustive population census. The census
25 revealed less than five thousand individuals, a strong habitat fragmentation and a high ratio of foliar
26 necrosis. Niche analyses were conducted considering either all individuals or separated size stages.
27 Analyses based on all individuals did not support the hypothesis that a too narrow niche by itself
28 explains the vulnerability of *A. tragacantha*. However, niche modelling revealed differences among
29 size stages supporting a restricted regeneration niche and a wider ecological range in the past. Our
30 comprehensive field survey underlines a worrying situation for *A. tragacantha* and sets a baseline for
31 conservation program.

32

33 Key words: biodiversity conservation, demography, ecological niche, joint species distribution model,
34 outlying mean index, rare plants, vulnerability

35 1. Introduction

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

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

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

70 (*Astragalo massiliensis-Plantaginietum subulatae* Molinier, 1934; European Corine biotope code
71 H5410; Davies et al., 2004; European Commission, 2013). Strictly protected in France, it is among the
72 5% of 3,282 plant species deserving the highest priority of conservation in Provence (Le Berre et al.,
73 2017, 2019). Urbanization is the cause of disappearance of at least four known populations, its
74 remnant habitats were degraded and polluted (Laffont-Schwob et al., 2011; Salducci et al., 2019) and
75 regular field investigations since 2005 revealed a worrying situation with high individual mortality
76 and low regeneration (L. Affre and P.J. Dumas, unpublished data). Thus, the local stakeholder in
77 charge with the conservation of the main populations of *A. tragacantha*, i.e. the Calanques National
78 Park, has recently launched a LIFE Habitats Calanques project (LIFE16 NAT / FR / 000593, 2017-2022)
79 for the large-scale restoration of degraded coastal habitats. This project included *A. tragacantha* of
80 which highly visible cushions are a symbol of conservation.

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

93

94 **2. Material and methods**

95 **2.1. Study sites**

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

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



109
 110 **Fig. 1:** Study area in Provence that encompass all French populations of *Astragalus tragacantha* L.,
 111 1753. The black dots on the map are indicating all *A. tragacantha* occurrences detected by our survey
 112 in 2019. Pictures: Calanques habitats and *A. tragacantha* cushions, Marseille, France.

113
 114 **2.2. *Astragalus tragacantha* demography**

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

126 10%; between 10 and 50%; more than 50%; and dead individual (i.e., 100%). A grid of 100 m² squares
127 (QGIS Development Team, 2020) was used to calculate the Area Of Occupancy (AOO) of the species.
128 Within each square of the grid, spatial requests in QGIS software (QGIS Development Team, 2020)
129 were performed to count the total number of individuals, then the number of individuals within each
130 of the size stages and necrosis classes. Each square was used as a unit sample to summarize
131 demographic data and assess densities within the *A. tragacantha* distribution. To assess the isolation
132 of individual within sector we performed spatial analysis using QGIS software to compute mean,
133 minimum and maximum distances between individuals.

134

135 **2.3. Environmental factors and floristic surveys**

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

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

150

151 **2.4. Niche analyses**

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

160

161 **2.4.1. Outlying Mean Index multivariate method (OMI)**

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

182

183 **2.4.2. Generalized Joint Attribute Modelling method (GJAM)**

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

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

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 m ²)	Maximum density (individual/100 m ²)	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 Queyrans	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 area (Marseille)	Escalette	186	3.78%	1	14	0.5	3.88	48	0.48 ha
	La Poulidette	15	0.3%	1	5	6.7	3.75	4	0.04 ha
	Maire	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
Calanques inland area (Marseille)	La Cayolle	2	0.04%	1	1	0	1.00	2	0.02 ha
	Sablières Anjarre	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
La Ciotat	Bec de l'Aigle	173	3.52%	1	15	9.8	2.75	63	0.36 ha
Pomègues (Frioul archipelago)	Total	1,054	21.43%	1	18	1	2.85	370	3.7 ha
	Fort Pomègues	133	2.7%	1	8	0	1.82	73	0.73 ha
	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
Ratonneau (Frioul archipelago)	Total	859	17.46%	1	22	3.6	2.94	292	2.92 ha
	Calanque de Morgiret	662	13.46%	1	22	4.7	3.39	195	1.95 ha
	Calanque du Berger	35	0.71%	1	9	0	3.50	10	0.1 ha
	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	0	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 Nègre	1	0.02%	1	1	0	1.00	1	0.01 ha
Cap Sicié	Total	569	11.57%	1	17	0.9	2.56	169	1.69 ha
	Amphitria	431	8.76%	1	17	0.7	2.91	101	1.01 ha
	Bau Rouge	13	0.26%	1	5	7.7	2.60	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
Total in France		4,919	100%	1	34	4.5	2.5	1,571	15.71 ha

208 **3. Results**

209 **3.1. Population assessment of *Astragalus tragacantha* in Provence**

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

224

225 **Table 2:** Proportion of crossed classes of the mean individual diameter and mean individual foliar
 226 necrosis rate calculated for the 4,919 individuals of *Astragalus tragacantha* counted in Provence.

Foliar necrosis rate	Mean diameter				
	Inferior to 10cm	Between 10 and 50 cm	Between 51 and 100 cm	Between 101 and 200 cm	Superior to 200 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%

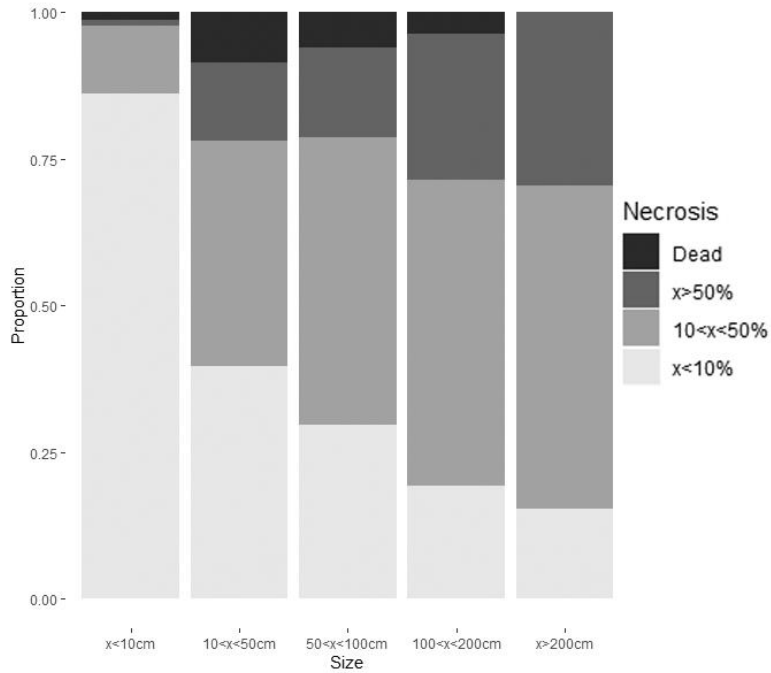
227

228 Among the 4,919 individuals, 4,614 are alive (e.g. with necrosis ratio inferior to 100%) and
 229 37.7% present a mean diameter between 50 and 100 cm which is the most abundant size stage
 230 (**Erreur ! Source du renvoi introuvable.**). Overall, the mean proportion of individuals inferior to 10
 231 cm in size is 4.3% but more than half of subsectors (51.5%) have no small individuals. The highest

232 numbers of small individuals are observed in the “Calanques littoral” sector (especially “Escalette”,
233 “Goudes”, and “Cap Redon” subsectors) where the proportion vary from 11 to 16%.

234 The foliar necrosis is high, most individuals (66.3%) present a foliar necrosis superior to 10%
235 (Table 2, Fig. 2) and 22% have a foliar necrosis superior to 50% of the cushion.

236



237

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

240

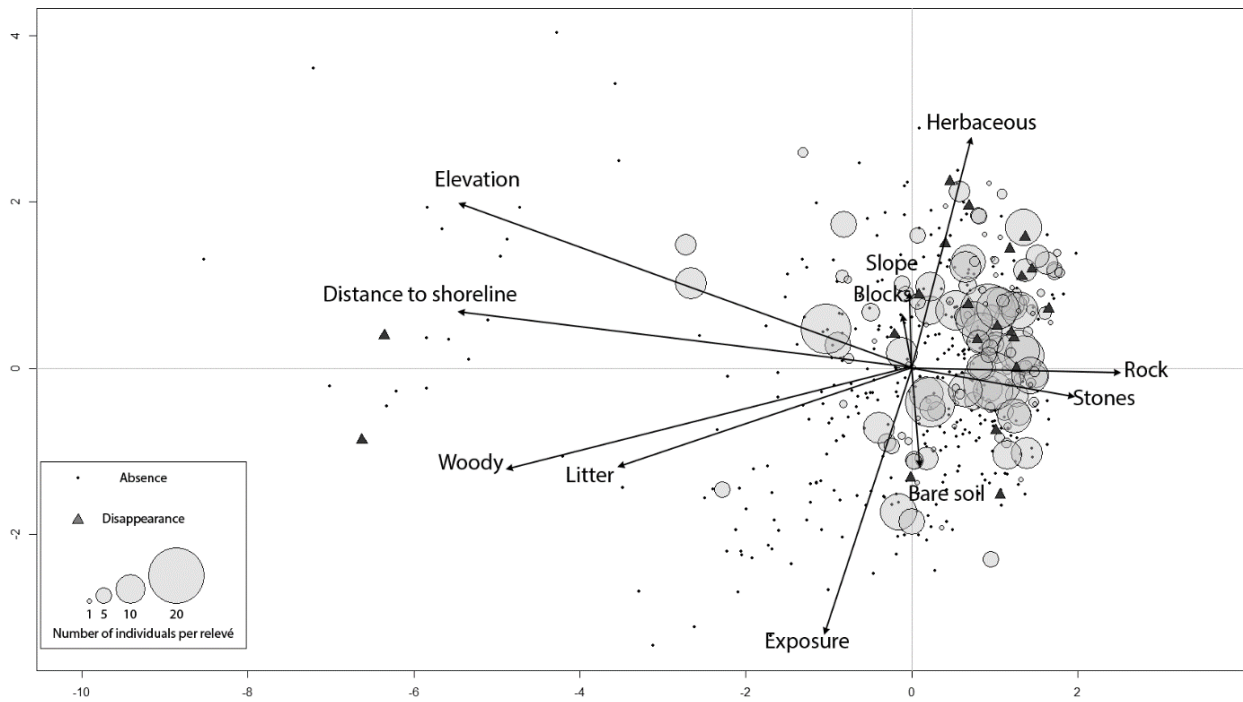
241

242 **3.2. The realized niche and environmental drivers of demography**

243 The indicator species analysis reveals a significative value (p value $\leq 1\%$) for 20 plant species
244 in presence of *A. tragacantha* and 15 in absence (Table S2 in sup. mat.). In presence of *A.*
245 *tragacantha*, only six species have an indicator value superior or equal to 0.5 with a specificity
246 ranging from 0.68 to 0.72 and a fidelity ranging from 0.45 to 0.76. In a decreasing order of indicator
247 value, these companion plant species of *A. tragacantha* are *Catapodium marinum* (L.) C.E. Hubbard,
248 *Valantia muralis* L., *Limonium pseudominutum* Erben, *Lotus cytisoides* L., *Crithmum maritimum* L.,
249 and *Camphorosma monspeliaca* L.. On the opposite, some species which are common in Provence
250 shrublands are almost never found with *A. tragacantha* such as shrubs or small trees as *Erica*
251 *multiflora* L., *Quercus coccifera* L., *Rhamnus alaternus* L., but also small chamaephytes such as
252 *Globularia alypum* L. or *Thymus vulgaris* L.

253 The OMI analysis sets the realized niche of *A. tragacantha* in a multivariate space built by the
254 main ecological gradients shaping plant communities (Fig. 3). The first four OMI axes account for 85%
255 of the total inertia. The correlation among OMI axes and habitat variables is shown in the heatmap of
256 Spearman Rho correlations (Fig. S1 in sup. mat.). The first OMI axis (53% of inertia) opposes woody
257 vegetation, increasing with elevation, to biotopes close to the shoreline. The second OMI axis (14% of
258 inertia) associates facing north sites with herbaceous cover. The third OMI axis (10% of inertia)
259 opposes rock cover to herbaceous cover and litter cover. The fourth OMI axis (8% of inertia) opposes
260 opened places with high bare soil and stone covers to places occupied by woody vegetation. On
261 diagram defined by the two main ecological gradients (OMI axes 1 and 2), the density of *A.*
262 *tragacantha* is higher on the right part (Fig. 3). These sites are situated in opened littoral biotopes.

263



264

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

270

271 Analyses of niche parameters show that over all plant species, the mean standardized
 272 marginality is 31 with a 95% confidence interval between 28 and 38. The mean residual tolerance is
 273 57 with a 95% confidence interval between 54 and 60. As expected, the plant species being common
 274 in the study area and in Provence littoral have lower marginality and higher residual tolerance : e.g.
 275 *Brachypodium retusum* (Pers.) P.Beauv. (marginality = 2.1, residual tolerance = 78), *Erica multiflora*
 276 (marginality =9.8, residual tolerance =71), *Lobularia maritima* (L.) Desv. (marginality =1.8, residual
 277 tolerance = 87), *Matthiola incana* (L.) R. Br. (marginality =7.7, residual tolerance =87), *Pinus*
 278 *halepensis* Miller (marginality = 9, residual tolerance = 75), or *Pistacia lentiscus* L. (marginality =5.8,
 279 residual tolerance =77). *Astragalus tragacantha* and its seven companion plant species have a mean
 280 marginality of 9, and a mean residual tolerance of 80. *Astragalus tragacantha* alone shows a mean
 281 marginality of 8 and a mean residual tolerance of 82. Thus, in the study area, *A. tragacantha* and its
 282 companion plant species have similar niche parameters indicating a low marginality and high
 283 tolerance that do not support a restricted amplitude of the realized niche.

284

285 GJAM modelling method quantitatively estimated the sensitivity and response of *A.*
tragacantha demography to the main ecological gradients (OMI axes). For the two GJAM models,

286 analyzing the total density of *A. tragacantha* or the density of the five size stages, the response
 287 matrix was reduced to height dimensions. The models well converge, and the environmental
 288 predictors and response variables are well predicted (Fig. S2 in sup. mat.). Model sensitivities and
 289 responses to ecological gradients (Fig. S3 in sup. mat. and Table 3) were different among the total
 290 density and the different size stages of *A. tragacantha*. The *A. tragacantha* total density is mostly
 291 determined by the first and fourth ecological gradients, OMI_1 and OMI_4 (“All stages”, Table 3).
 292 This result indicates that *A. tragacantha* total density is increasing when elevation and wood cover
 293 are decreasing as well as when bare soil is increasing. The second ecological gradient, OMI_2,
 294 opposing south facing to north facing places has also a small but significant effect indicating that *A.*
 295 *tragacantha* is responding positively to north facing, such places having also higher herbaceous cover
 296 (Fig. 3). Similar effects are observed for the most populated stages, the D50 (33% of the counts) and
 297 D100 size stage (38% of the counts). The main differences are observed for the D10 and the D200
 298 and Dsup 200 size stages which are not sensitive to the second and fourth OMI axis. The only
 299 significant response of the last size stage (Dsup200) is for the third axis indicating a preference of the
 300 biggest individuals for places with high herbaceous and litter cover rather than rocky outcrops. By
 301 comparison to other size stages, the smallest individuals have the most important responses to the
 302 first and third OMI axes indicating their preference for opened places near the sea, with a low wood
 303 cover and with herbaceous rather than rock cover.

304

305 **Table 3:** Significant positive or negative responses of *Astragalus tragacantha* population
 306 parameters to ecological gradients estimated by GJAM. “All stages” indicates that all individuals were
 307 considered whereas “D0-10” to “Dsup200” indicate that individuals were organized as size stages
 308 according to the mean individual diameter (cm) from the smallest to the biggest individuals. Dead
 309 individuals were removed.

Ecological gradient	from negative pole	to positive pole	All stages	D10	D50	D100	D200	Dsup200
OMI_1	high elevation, wood	lowland, 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

310 *ns= non significative value

311

312 The differences among size stages appeared also clearly when they are clustered with the
 313 other species based on their responses to ecological gradients (Fig. S4 in sup. mat.). The first three
 314 stages (D10 to D100) are grouped together into one of the three main clusters. In this group, we

315 observed the companion plant species of *A. tragacantha* (previous results) such as *Camphorosma*
316 *monspeliaca*, *Plantago subulata* L., *Limonium pseudominutum*, *Catapodium marinum*, *Valantia*
317 *muralis* and *Lotus cytisoides*. Yet, these three stages did not share the same companions. The first
318 stage (D10) is separated from the stages D50 and D100 and the last stages, D200 and Dsup200 are
319 clustered together in association with a different community composed of *Euphorbia pithyusa* L.,
320 *Plantago lagopus* L., *Lagurus ovatus* L., or *Lobularia maritima* (Fig. S4).

321

322 **4. Discussion**

323 **4.1. A dangerous demographic situation**

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

334 Such situation of spatial fragmentation and unbalanced population raises questions on the
335 persistence of especially small and isolated populations (Ouborg et al., 2006; Frankham et al., 2014).
336 Theoretical models predict that any kind of stochasticity (demographic, genetic, environmental) will
337 exponentially increase the extinction risk of small and isolated populations (Ovaskainen and Meerson,
338 2010). Schurr et al. (2019) have shown the existence of both inbreeding and outbreeding depression
339 within and among the *A. tragacantha* populations and observed that different predominant
340 pollinators are confined in different sites: *Anthophora plumipes* Pallas (1772) in the "Cap Croisette"
341 sub-sector, *Eucera caspica* Morawitz (1873) on Frioul archipelago, and *Bombus terrestris* L. (1758) in
342 the sector of "Calanque des Trous". This interaction with pollinators being restricted at a fine scale
343 may worsen the impact of population fragmentation. Their results suggest that fragmentation is
344 already impacting *A. tragacantha* population fitness even in the sites where the abundance of *A.*
345 *tragacantha* is the highest.

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

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

364 A final point of concern is that only the small individuals have low ratio of necrosis. Above 10
365 cm of diameter, all size stages show a necrosis rate superior to 10% of their cushion. We counted
366 also 305 individuals having a 100% foliar necrosis ratio and which are probably dead. Representing
367 6.2% of the total number of individuals they suggest that mortality rate is strong. Such important
368 foliar necrosis rate was not observed in closely related species of *A. tragacantha* living on deeper
369 soils (A. Baumel com. pers.). Deciphering between polluted sea sprays and water stress deficit as
370 causes for foliar necrosis is an important issue that deserves an *ad hoc* study.

371

372 **4.2. Is population vulnerability caused by a restricted niche breadth?**

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

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

385 plant community indicating that the regeneration niche is more restricted than the current realized
386 niche. Soil depth is important for germination (Bullied et al., 2012) and studies on *Astragalus* species
387 underline the importance of seed dispersal toward bare soil areas for recruitment (Becker, 2010;
388 Baer and Maron, 2019, 2020). Indeed, sufficiently deep soil allowing water retention is required for
389 the seed emergence whereas once taller adult individuals develop their root system, soil depth
390 become less crucial for their survival, especially under Mediterranean climate (Padilla and Pugnaire,
391 2007).

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

409

410 **5. Conclusion**

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

420

421 **Acknowledgements**

422 We thank the European Union for financial support of the LIFE Habitats Calanques project (LIFE16
423 NAT / FR / 000593, 2017-2022); the Regional Agency for the Environment - Regional Agency for the
424 Biodiversity (ARPE-ARB) Provence-Alpes-Côte-d'Azur for the coordination of the LIFE Habitats
425 Calanques project; the Departmental Council of Bouches-du-Rhône, the City of Marseille and the
426 Calanques National Park for field access, Daniel Pavon (IMBE) for its expertise on floristic taxonomy.

427

428 **Supplementary materials**

429 Data sets and R scripts were deposited in DRYAD data base and are available at the URL:

430 doi:10.5061/dryad.bzkh1898p

431 Supplementary materials can be found in the online version and contain tables and figures
432 completing results.

- 433 • **Table S1:** Synthesis of distances between individuals for all seven sectors.
- 434 • **Table S2:** Specificity, Fidelity and Indicator species values for taxa in presence or absence of
435 *A. tragacantha*. Only taxa with p values inferior or equal to 1% were kept
- 436 • **Fig. S1:** Spearman Rho correlations among environmental variables and the OMI axes
437 gradients identified by the Outlying Mean Index method and used here to design the main
438 ecological gradients structuring plant communities in the range area of *Astragalus*
439 *tragacantha*. The variables are elevation above sea level, distance to the sea, slope orientation,
440 and covers of woody plants, herbaceous plants, rock, block, stone, bare soil and litter,
441 respectively.
- 442 • **Fig. S2:** Environmental and response variables prediction by GJAM model.
- 443 • **Fig. S3:** GJAM analysis of sensitivity of *Astragalus tragacantha* total density ("all stages") and
444 size stages to ecological gradients obtained by OMI. Plant size increased from D10 to Dsup200
- 445 • **Fig. S4:** Cluster of species and *Astragalus tragacantha* size stages based on response to
446 ecological gradients (β coefficients of GJAM model). This figure helps to find species having the
447 same model response than *A. tragacantha*.

448

449 **Bibliography**

450 Abdel Samad, F., Medail, F., Baumel, A., Yakovlev, S.S., Roukoz, A., Tohme, G., Tohme, H., Bou Dagher
451 Kharrat, M., 2020. New insights on the conservation status of the endangered coastal endemic plant
452 *Astragalus berytheus* (Fabaceae) in Lebanon. Oryx 1–3. <https://doi:10.1017/S0030605320000149>.

453 Affre, L., Dumas, P.J., Dumas, E., Laffont-Schwob, I., Tatoni, T., 2015. Regard écologique sur le recul
454 stratégique : atouts et risques pour la diversité végétale péri-urbaine marseillaise. VertigO Hors-Série
455 21, 13p. <https://doi.org/10.4000/vertigo.15748>.

456 Allen, J.R., Forrest, M., Hickler, T., Singarayer, J.S., Valdes, P.J., Huntley, B., 2020. Global vegetation
457 patterns of the past 140,000 years. *J. Biogeogr.* 47, 2073–2090. <https://doi.org/10.1111/jbi.13930>.

458 Baer, K.C., Maron, J.L., 2019. Declining demographic performance and dispersal limitation influence
459 the geographic distribution of the perennial forb *Astragalus utahensis* (Fabaceae). *J. Ecol.* 107, 1250–
460 1262. <https://doi.org/10.1111/1365-2745.13086>.

461 Baer, K. C., Maron, J. L., 2020. Ecological niche models display nonlinear relationships with
462 abundance and demographic performance across the latitudinal distribution of *Astragalus utahensis*
463 (Fabaceae). *Ecol. and Evol.* 10, 8251–8264. <https://doi.org/10.1002/ece3.6532>.

464 Barbour, M.G., 1978. Salt spray as a microenvironmental factor in the distribution of beach plants at
465 point Reyes, California. *Oecologia* 32, 213–224.

466 Becker, T., 2010. Explaining rarity of the dry grassland perennial *Astragalus exscapus*. *Folia Geobot.*
467 45, 303–321.

468 Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L., Thuiller, W., 2012. Niche breadth, rarity and
469 ecological characteristics within a regional flora spanning large environmental gradients. *J. Biogeogr.*,
470 39, 204–214. <https://doi.org/10.1111/j.1365-2699.2011.02581.x>

471 Brown, J. H., 1984. On the relationship between abundance and distribution of species. *Am. Nat.*,
472 124, 255–279.

473 Bullied, J.W., van Acker, R.C., Bullock, P.R., 2012. Review: Microsite characteristics influencing weed
474 seedling recruitment and implications for recruitment modeling. *Can. J. Plant Sci.* 92, 627–650.
475 <https://doi.org/10.4141/cjps2011-281>.

476 Clark, J.S., Nemergut, D., Seyednasrollah, B., Turner, P.J., Zhang, S., 2017. Generalized joint attribute
477 modeling for biodiversity analysis: Median-zero, multivariate, multifarious data. *Ecol. Monogr.* 87,
478 34–56. <https://doi.org/10.1002/ecm.1241>

479 Cogoni, D., Fenu, G., Porceddu, M., Bacchetta, G., 2014. *Astragalus gennarii* Bacch. Et Brullo. in:
480 Rossi, G., Bacchetta, G., Fenu, G., Foggi, B., Gennai, M., Gargano, D., Montagnani, C., Orsenigo, S.,
481 Peruzzi, L. (Eds.), Schede per una Lista Rossa della Flora vascolare e crittogamica Italiana. *Inf. Bot. Ital.*
482 46, 103–105.

483 De Caceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and
484 statistical inference. *Ecology* 90, 3566–3574.

485 Davies, C.E., Moss, D., Hill, M.O., 2004. EUNIS Habitat Classification Revised 2004. Report to
486 European Environment Agency, European Topic Centre on Nature Protection and Biodiversity. pp 1–
487 307.

488 Delauge, J., Meyer, D., Noble, V., Chondroyannis, P., 2013. Le portail des données naturalistes
489 SILENE1 en région Provence-Alpes-Côte d’Azur. Les données environnementales en libre accès,
490 Netcom. 27, 245-253. <https://doi.org/10.4000/netcom.1362>.

491 Dolédec, S., Chessel, D., Gimaret-Carpentier, C., 2000. Niche separation in community analysis: A new
492 method. *Ecology* 81, 2914–2927. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2)
493 [9658\(2000\)081\[2914:NSICAA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2914:NSICAA]2.0.CO;2).

494 Doxa, A., Albert, C.H., Leriche, A., Saatkamp, A., 2017. Prioritizing conservation areas for coastal plant
495 diversity under increasing urbanization. *J. Environ. Manage.* 201, 425–434.
496 <https://doi.org/10.1016/j.jenvman.2017.06.021>.

497 Dray, S., Dufour, A.B., 2007. The ade4 package: Implementing the duality diagram for ecologists. *J.*
498 *Stat. Softw.* 22, 1–20. <http://www.jstatsoft.org>.

499 European Commission, 2013. Interpretation Manual of European Union Habitats-EUR 28. Version
500 April 2013. DG Environment –Nature and biodiversity,144 p.

501 Fenu, G., Cogoni, D., Ulian, T., Bacchetta, G., 2013. The impact of human trampling on a threatened
502 coastal Mediterranean plant: the case of *Anchusa littorea* Moris (Boraginaceae). *Flora* 208, 104–110.
503 <https://doi.org/10.1016/j.flora.2013.02.003>.

504 Fenu, G., Bacchetta, G., Charalambos, S. C., Fournaraki, C., del Galdo, G. P. G., Gotsiou, P., Kyratzis, A.,
505 Piazza, C., Vicens, M., Pinna, M. S., de Montmollin, B., 2019. An early evaluation of translocation
506 actions for endangered plant species on Mediterranean islands. *Plant Divers.* 41, 94–104.
507 <https://doi.org/10.1016/j.pld.2019.03.001>.

508 Frankham, R., Bradshaw, C.J.A., Brook, B.W., 2014. Genetics in conservation management: revised
509 recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biol.*
510 *Conserv.* 170, 56–63. <https://doi.org/10.1016/j.biocon.2013.12.036>.

511 Gaston, K.J., 1994. *Rarity*. Chapman & Hall, London.

512 Gauthier, P., Bernard, C., Thompson, J.D., 2019. Exploring vulnerability of listed Mediterranean plants
513 in relation to risks of population loss. *J. Nat. Conserv.* 51, 125736.
514 <https://doi.org/10.1016/j.jnc.2019.125736>.

515 Hanski, I., Kouki, J., Halkka, A., 1993. Three explanations of the positive relationship between
516 distribution and abundance of species. In Ricklefs, R.E., Schluter, D., (eds) *Species diversity in*
517 *ecological communities: historical and geographical perspectives*. University of Chicago Press,
518 Chicago, pp 108–116.

519 Hanski, I., Ovaskainen, O., 2002. Extinction debt at extinction threshold. *Conserv. Biol.* 16, 666–673.
520 <https://doi.org/10.1046/j.1523-1739.2002.00342.x>.

521 Hardion, L., Baumel, A., Dumas, P.J., Duong, N., Affre, L., Taton, T., 2010. Phylogenetic relationships
522 and infrageneric classification of *Astragalus tragacantha* L. (Fabaceae), inferred from nuclear
523 ribosomal DNA Internal transcribed spacers data (nrDNA ITS). *Ecol. Mediterr.* 36, 99–106.

524 Hardion, L., Dumas, P.J., Abdel Samad, F., Bou Dagher Kharrat, M., Surina, B., Affre, L., Médail, F.,
525 Bacchetta, G., Baumel, A., 2016. Geographical isolation caused the diversification of the
526 Mediterranean thorny cushion-like *Astragalus* L. sect. *Tragacantha* DC. (Fabaceae). *Mol. Phylogenet.*
527 *Evol.* 97, 187–195. <https://doi.org/10.1016/j.ympev.2016.01.006>.

528 Heywood, V.H., 2014. An overview of in situ conservation of plant species in the Mediterranean. *Fl.*
529 *Medit.* 24, 5–24. doi: 10.7320/FIMedit24.005.

530 Jombart, T., 2008. Adegenet: A R package for the multivariate analysis of genetic markers.
531 Bioinformatics 24, 1403–1405. <https://doi.org/10.1093/bioinformatics/btn129>.

532 Kassambara, A., 2016. ggcorrplot: Visualization of a Correlation Matrix using 'ggplot2'. R Package. URL
533 [http://www.sthda.com/english/wiki/ggcorrplotversion 0.1, 1](http://www.sthda.com/english/wiki/ggcorrplotversion%200.1).

534 Kienberg, O., Becker, T., 2017. Differences in population structure require habitat-specific
535 conservation strategies in the threatened steppe grassland plant *Astragalus exscapus*. Biol. Conserv.
536 211, 56–66. <https://doi.org/10.1016/j.biocon.2017.05.002>.

537 Laffont-Schwob, I., Dumas, P.J., Pricop, A., Rabier, J., Miché, L., Affre, L., Masotti, V., Prudent, P.,
538 Tatoni, T., 2011. Insights on metal-tolerance and symbionts of the rare species *Astragalus*
539 *tragacantha* aiming at phytostabilization of polluted soils and plant conservation. Ecol. Mediterr.
540 Rev. Int. Ecol. Med. 37, 57–62.

541 Le Berre, M., Diadema, K., Pires, M., Noble, V., Debarros, G., Gavotto, O., 2017. Hiérarchisation des
542 enjeux de conservation de la flore en région Provence-Alpes-Côte-d'Azur. Rapport inédit,
543 CBNMed,CBNA, Région Provence-Alpes-Côte d'Azur, 30 pages.

544 Le Berre, M., Noble, V., Pires, M., Médail, F., Diadema, K., 2019. How to hierarchise species to
545 determine priorities for conservation action? A critical analysis. Biodivers. Conserv. 28, 3051–3071.

546 Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby,
547 M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion degradation, and recovery potential of estuaries
548 and coastal seas. Science 312, 1806–1809. <https://doi.org/10.1126/science.1128035>.

549 Martín-Queller, E., Albert, C.H., Dumas, P.J., Saatkamp, A., 2017. Islands, mainland, and terrestrial
550 fragments: How isolation shapes plant diversity. Ecol. Evol. 7, 6904–6917.
551 <https://doi.org/10.1002/ece3.3150>.

552 Mendoza-Fernández, A.J., Pérez-García, F.J., Martínez-Hernández, F., Medina-Cazorla, J.M., Garrido-
553 Becerra, J.A., Calvente, M. E. M., Romero, J.S., Mota, J.F., 2014. Threatened plants of arid ecosystems
554 in the Mediterranean Basin: A case study of the south-eastern Iberian Peninsula. Oryx, 48, 548-554.
555 <https://doi.org/10.1017/S0030605313000495>.

556 Mendoza-Fernández, A. J., Martínez-Hernández, F., Salmerón-Sánchez, E., Pérez-García, F. J., Teruel,
557 B., Merlo, M. E., Mota, J. F., 2021. The Relict Ecosystem of *Maytenus senegalensis* subsp. *europaea* in
558 an Agricultural Landscape: Past, Present and Future Scenarios. Land, 10, 1.
559 <https://doi.org/10.3390/land10010001>.

560 Ovaskainen, O., Meerson, B., 2010. Stochastic models of population extinction. TREE 11, 643–652.
561 <https://doi.org/10.1016/j.tree.2010.07.009>.

562 Orsenigo, S., Montagnani, C., Fenu, G., Gargano, D., Peruzzi, L., Abeli, T., Alessandrini, A., Bacchetta,
563 G., Bartolucci, F., Bovio, M., Brullo, C., Brullo, S., Carta, A., Castello, M., Cogoni, D., Conti, F., Domina,
564 G., Foggi, B., Gennai, M., Gigante, D., Iberite, M., Lasen, C., Magrini, S., Perrino, E.V., Prosser, F.,
565 Santangelo, A., Selvaggi, A., Stinca, A., Vagge, I., Villani, M., Wagensommer, R.P., Wilhelm, T.,
566 Tartaglioni, N., Duprè, E., Blasi, C., Rossi, G., 2018. Red Listing plants under full national responsibility:
567 Extinction risk and threats in the vascular flora endemic to Italy. Biol. Conserv. 224, 213–222.
568 <https://doi.org/10.1016/j.biocon.2018.05.030>.

569 Ouborg, N.J., Vergeer, P., Mix, C., 2006. The rough edges of the conservation genetics paradigm for
570 Plants. J. Ecol. 94, 1233–1248. <https://doi.org/10.1111/j.1365-2745.2006.01167.x>.

571 Padilla, F.M., Pugnaire, F.I., 2007. Rooting depth and soil moisture control Mediterranean woody
572 seedling survival during drought. *Funct. Ecol.* 21, 489–495. <https://doi.org/10.1111/j.1365->
573 2435.2007.01267.x.

574 Pogorzelec, M., Bronowicka-Mielniczuk, U., Serafin, A., Parzymies, M., 2020. The importance of
575 habitat selection for the reintroduction of the endangered *Salix lapponum* L. in eastern Poland. *J.*
576 *Nature Conserv.* 54, 125785. <https://doi.org/10.1016/j.jnc.2020.125785>

577 Pouget, M., Youssef, S., Dumas, P.J., Baumberger, T., San Roman, A., Torre, F., Affre L., Médail F.,
578 Baumel, A., 2016. Spatial mismatches between plant biodiversity facets and evolutionary legacy in
579 the vicinity of a major Mediterranean city. *Ecol. Indicators* 60, 736–745.
580 <https://doi.org/10.1016/j.ecolind.2015.07.017>.

581 QGIS Development Team, 2020. QGIS Geographic Information System. Open Source Geospatial
582 Foundation Project. Available at: <http://qgis.osgeo.org>.

583 Robert-Peillard F., Syakti, A.D., Coulomb, B., Doumenq, P., Malleret, L., Asia, L., Boudenne, J.-L., 2015.
584 Occurrence and fate of selected surfactants in seawater at the outfall of the Marseille urban sewage
585 system. *Int. J. Env. Science Tech.* 12, 1527–1538.

586 Roberts, D.W., 2013. Package ‘labdsv’: Ordination and Multivariate Analysis for Ecology. R Package.
587 URL: <http://ecology.msu.montana.edu/labdsv/R/>

588 Romey, C., Vella, C., Rochette, P., Andrieu-Ponel, V., Magnin, F., Veron, A., Talon, B., Landuré, C.,
589 D’Ovidio, A-M., Delanghe, D., Ghilardi, M., Angeletti, B., 2015. Environmental imprints of landscape
590 evolution and human activities during the Holocene in a small catchment of the Calanques Massif
591 (Cassis, southern France). *Holocene* 25, 1454–1469. <https://doi.org/10.1177/0959683615585838>.

592 Salducci, M.D., Folzer, H., Issartel, J., Rabier, J., Masotti, V., Prudent, P., Affre, L., Hardion, L., Tatoni,
593 T., Laffont-Schwob, I., 2019. How can a rare protected plant cope with the metal and metalloid soil
594 pollution resulting from past industrial activities? Phytometabolites, antioxidant activities and root
595 symbiosis involved in the metal tolerance of *Astragalus tragacantha*. *Chemosphere* 217, 887–896.
596 <https://doi.org/10.1016/j.chemosphere.2018.11.078>.

597 Sau, S., Fois, M., Fenu, G., Cogoni, D., Bacchetta, G., 2014. *Astragalus genargenteus* Moris. *Inf. Bot.*
598 *Ital.* 46, 285–321.

599 Sau S., Fenu, G., Cogoni, D., Bacchetta, G., 2015. *Astragalus thermensis* Vals. *Inf. Bot. Ital.* 47, 99–140.

600 Scheele, B.C., Foster, C.N., Banks, S.C., Lindenmayer, D.B., 2017. Niche contractions in declining
601 species: mechanisms and consequences. *TREE* 32, 346–35.
602 <https://doi.org/10.1016/j.tree.2017.02.013>

603 Schoeman, D., Dugan, J., Jones, A., Scapini, F., Schlacher, T., Lastra, M., Jones, A., Scapini, F.,
604 McLachlan, A., 2008. Sandy beach ecosystems: key features, sampling issues, management
605 challenges and climate change impacts. *Mar. Ecol.* 29, 70–90. <https://doi.org/10.1111/j.1439->
606 0485.2007.00204.x

607 Schurr, L., Affre, L., Flacher, F., Tatoni, T., Le Mire Pecheux, L., Geslin, B., 2019. Insights on pollen flow
608 and pollination activity for the conservation of a fragmented plant species (*Astragalus tragacantha*,
609 Fabaceae). *Biod. Conserv.* 28, 1389–1409.

610 Small, C., Nicholls, R.J., 2003. A global analysis of human settlement in coastal zones. *J. Coast. Res.*
611 19, 584–599. <https://www.jstor.org/stable/4299200>.

612 Suc, J.-P., Popescu, S.-M., Fauquette, S., Bessedik, M., Jiménez-Moreno, G., Bachiri Taoufiq, N.,
613 Zheng, Z., Médail, F., Klotz, S., 2018. Reconstruction of Mediterranean flora, vegetation and climate
614 for the last 23 million years based on an extensive pollen dataset. *Ecol. Mediterr.* 44, 53–85.

615 Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt.
616 *Nature* 371, 65–66.

617 Valsecchi, F., 1994. Sul complesso *Astragalus tragacantha* L. (Leguminosae) nel Mediterraneo.
618 *Webbia* 49, 31–41. <https://doi.org/10.1080/00837792.1994.10670568>.

619 Youssef, S., Baumel, A., Médail, F., 2009. The demographic structure of *Armeria arenaria* (Pers.)
620 Schult. (Plumbaginaceae), a biological indicator of conservation state of the littoral flora of the
621 Maures (Var, France). *Candollea* 64, 245–256.

622 Youssef, S., Baumel, A., Véla, E., Juin, M., Dumas, E., Affre, L., Tatoni, T., 2011. Factors underlying the
623 narrow distribution of the Mediterranean annual plant *Arenaria provincialis* (Caryophyllaceae). *Folia*
624 *Geobot.* 46, 327–350.

625

626

627 **Figures**

628 **Fig. 2:** Study area in Provence that encompass all French populations of *Astragalus tragacantha* L.,
629 1753. The black dots on the map are indicating all *A. tragacantha* occurrences detected by our survey
630 in 2019. Pictures: Calanques habitats and *A. tragacantha* cushions, Marseille, France.

631

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

634

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

640

641 **Tables**

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

644

645 **Table 2:** Proportion of crossed classes of the mean individual diameter and mean individual foliar
646 necrosis rate calculated for the 4,919 individuals of *Astragalus tragacantha* counted in Provence.

647

648 **Table 3:** Significant positive or negative responses of *Astragalus tragacantha* population
649 parameters to ecological gradients estimated by GJAM. "All stages" indicates that all individuals were
650 considered whereas "D0-10" to "Dsup200" indicate that individuals were organized as size stages
651 according to the mean individual diameter (cm) from the smallest to the biggest individuals. Dead
652 individuals were removed.

653

654

655

656

657 Table 1

658

Sector	Sub-sector	Total number of individuals	Percentage of total number of individuals	Minimum density (individual/100 m ²)	Maximum density (individual/100 m ²)	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 Queyrans	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
	Escalette	186	3.78%	1	14	0.5	3.88	48	0.48 ha
	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
	La Cayolle	2	0.04%	1	1	0	1.00	2	0.02 ha
	Sablères Anjarre	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
	Total	8	0.16%	1	3	0	1.50	6	0.06 ha
	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
	Fort Pomègues	133	2.7%	1	8	0	1.82	73	0.73 ha
	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
	Calanque de Morgiret	662	13.46%	1	22	4.7	3.39	195	1.95 ha
	Calanque du Berger	35	0.71%	1	9	0	3.50	10	0.1 ha
	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	0	1.85	20	0.2 ha
	Total	570	11.59%	1	17	0	1.78	170	1.7 ha
	Six-Fours-les-plages								
	Cap Nègre	1	0.02%	1	1	0	1.00	1	0.01 ha
	Total	569	11.57%	1	17	0.9	2.56	169	1.69 ha
	Amphitria	431	8.76%	1	17	0.7	2.91	101	1.01 ha
	Bau Rouge	13	0.26%	1	5	7.7	2.60	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
	Total in France	4,919	100%	1	34	4.5	2.5	1,571	15.71 ha

659

660 Table 2

661

	Mean diameter				
Foliar necrosis rate	Inferior to 10cm	Between 10 and 50 cm	Between 51 and 100 cm	Between 101 and 200 cm	Superior to 200 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%

662

663 Table 3

Ecological gradient	from negative pole	to positive pole	All stages	D10	D50	D100	D200	Dsup200
OMI_1	high elevation, wood	lowland, 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

664 **ns= non significant value*

665