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

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5

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

7

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9 **survey of *Astragalus tragacantha* L. (Fabaceae)**

10

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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

41 Rare plant specialists are often weak competitors that found refuge in harsh environments
42 where they can be locally abundant (Youssef et al., 2011; Boulangeat et al., 2012). However,
43 compared to widespread species, they are expected to be more vulnerable to environmental
44 changes due to a restricted niche and/or less ability to disperse (Brown, 1984; Hanski et al., 1993;
45 Gaston, 1994). Knowing the drivers of vulnerability of rare plant species remain a challenging issue
46 for conservationists who aim to preserve and strengthen their natural populations (Heywood, 2014;
47 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
66 origin from the Near East probably during the Pliocene (5.3 to 2.6 million years before present) and
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-Plantaginietum 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
83 Park, has recently launched a LIFE Habitats Calanques project (LIFE16 NAT / FR / 000593, 2017-2022)
84 for the large-scale restoration of degraded coastal habitats. This project included *A. tragacantha* of
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 Calanques 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

110 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

131 10%; between 10 and 50%; more than 50%; and dead individual (i.e., 100%). A grid of 100 m² squares
132 (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
136 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**

141 Ecological data are composed of the floristic and environmental relevés obtained from a
142 recent study (Pouget et al., 2016) and those acquired for this study during spring 2019. The 499
143 relevés, situated within 2 km from seashore, encompass the ecological gradient from rocky shoreline
144 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. $\varnothing > 20$
150 cm, stone i.e. $\varnothing < 20$ 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% ≤ cover < 50%, 4: 50% ≤ cover < 75%, 5: cover ≥ 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
160 absence of *A. tragacantha* and used the “multipatt” function of the indicpecies packages in R
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.

165

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*
182 total density (number of individuals counted in each 100 m² plots) we used the coordinates of each
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
206 were summarized in a table to show the response of *A. tragacantha* to ecological gradients.
207 Scripts and data of our analyses are deposited in DRYAD database (doi:10.5061/dryad.bzkh1898p). We
208 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).
210

211 **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
	Total	1,054	21.43%	1	18	1	2.85	370	3.7 ha
Pomègues (Frioul archipelago)	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
Ratonneau (Frioul archipelago)	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
	Total	569	11.57%	1	17	0.9	2.56	169	1.69 ha
Cap Sicié	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

212

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 “Calanques littoral” sector and 25.1% on
 218 Frioul archipelago (“Pomègues” and “Ratonneau”) indicating that the areas in the vicinity of
 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 Calanques 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
 225 the lower populations isolation, whereas sectors “Six-fours-les-plages” and “Cap Sicié”, holding a
 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 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%

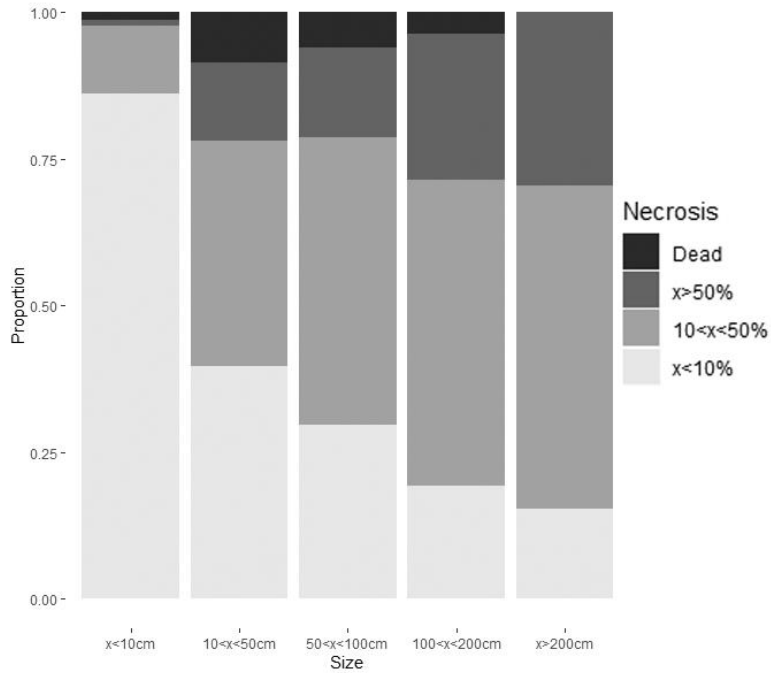
232

233 Among the 4,919 individuals, 4,614 are alive (e.g. with necrosis ratio inferior to 100%) and
 234 37.7% present a mean diameter between 50 and 100 cm which is the most abundant size stage
 235 (**Erreur ! Source du renvoi introuvable.**). Overall, the mean proportion of individuals inferior to 10
 236 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%.

239 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).

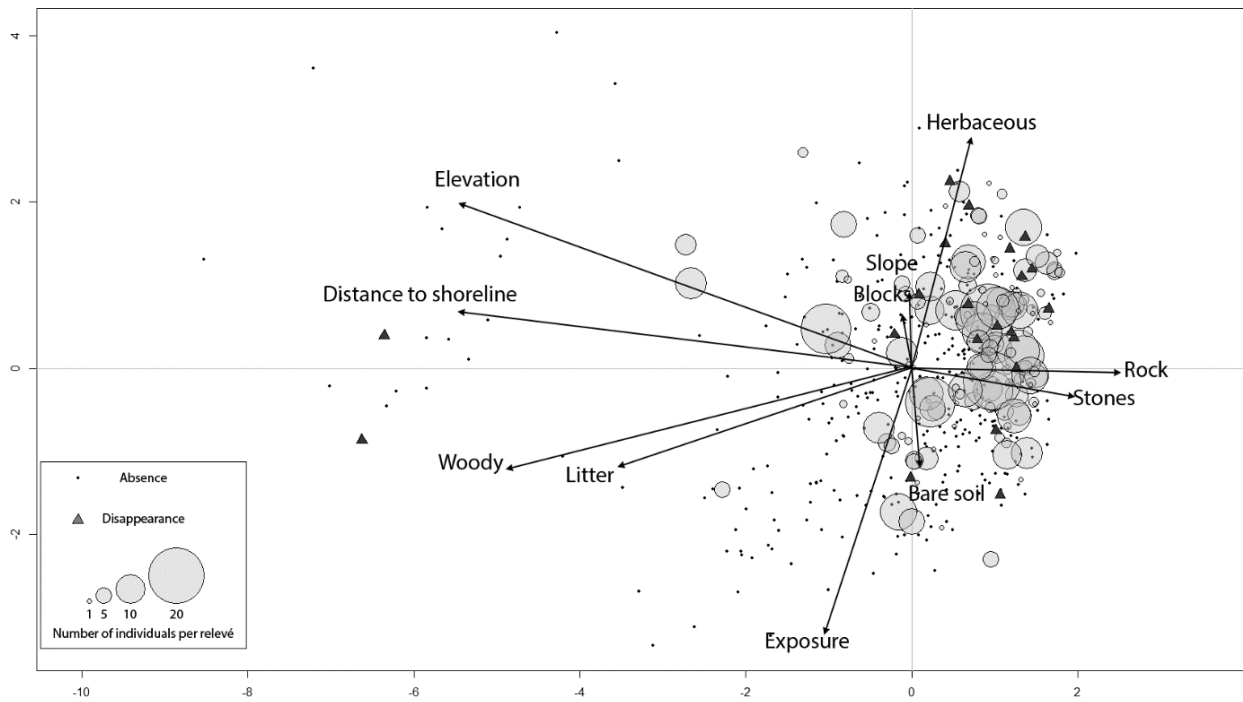
245

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
252 value, these companion plant species of *A. tragacantha* are *Catapodium marimum* (L.) C.E. Hubbard,
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.*
267 *tragacantha* is higher on the right part (Fig. 3). These sites are situated in opened littoral biotopes.
268



269

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

275

276 Analyses of niche parameters show that over all plant species, the mean standardized
 277 marginality is 31 with a 95% confidence interval between 28 and 38. The mean residual tolerance is
 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*
 283 *halepensis* Miller (marginality = 9, residual tolerance = 75), or *Pistacia lentiscus* L. (marginality =5.8,
 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

290 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,

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
 310 **Table 3:** Significant positive or negative responses of *Astragalus tragacantha* population
 311 parameters to ecological gradients estimated by GJAM. “All stages” indicates that all individuals were
 312 considered whereas “D0-10” to “Dsup200” indicate that individuals were organized as size stages
 313 according to the mean individual diameter (cm) from the smallest to the biggest individuals. Dead
 314 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

315 *ns= non significative value

316
 317 The differences among size stages appeared also clearly when they are clustered with the
 318 other species based on their responses to ecological gradients (Fig. S4 in sup. mat.). The first three
 319 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 maritimum*, *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 populations (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.

351 At first glance, the low frequency of smallest and biggest individuals (4.3% and 3.3%), with
352 most intermediate sizes individuals (Table 2), suggests a stable population type by comparison to the
353 demography of *Astragalus exscapus* L., an endangered steppe grassland species (Kienberg and
354 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.

369 A final point of concern is that only the small individuals have low ratio of necrosis. Above 10
370 cm of diameter, all size stages show a necrosis rate superior to 10% of their cushion. We counted
371 also 305 individuals having a 100% foliar necrosis ratio and which are probably dead. Representing
372 6.2% of the total number of individuals they suggest that mortality rate is strong. Such important
373 foliar necrosis rate was not observed in closely related species of *A. tragacantha* living on deeper
374 soils (A. Baumel com. pers.). Deciphering between polluted sea sprays and water stress deficit as
375 causes for foliar necrosis is an important issue that deserves an *ad hoc* study.

376

377 **4.2. Is population vulnerability caused by a restricted niche breadth?**

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

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

390 plant community indicating that the regeneration niche is more restricted than the current realized
391 niche. Soil depth is important for germination (Bullied et al., 2012) and studies on *Astragalus* species
392 underline the importance of seed dispersal toward bare soil areas for recruitment (Becker, 2010;
393 Baer and Maron, 2019, 2020). Indeed, sufficiently deep soil allowing water retention is required for
394 the seed emergence whereas once taller adult individuals develop their root system, soil depth
395 become less crucial for their survival, especially under Mediterranean climate (Padilla and Pugnaire,
396 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*
424 populations and (re)introduction in favorable habitats are therefore needed.

425

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432

433 **Supplementary materials**

434 Data sets and R scripts were deposited 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 (β coefficients of GJAM model). This figure helps to find species having the
452 same model response than *A. tragacantha*.

453

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631

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: Calanques 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,
642 black dots are relevés without *A. tragacantha*, grey circles are relevés with *A. tragacantha*, the
643 diameter being proportional to the number of individuals within the relevé. Triangles indicate plots
644 where *A. tragacantha* disappeared between 2007 and 2019.

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:** Significant 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

661

662 Table 1

663

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
	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
	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

664

665 Table 2

666

	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%

667

668 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

669 **ns= non significant value*

670