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1 Alejandro G. Fernández de Castro*¹, Vicente Rozas², Javier Fuertes Aguilar¹ & Juan
2 Carlos Moreno Saiz^{3,4}

3 Demographic and dendrochronological evidence reveals highly endangered status of a
4 paleoendemic woody mallow from the Canary Islands

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6 ¹Departamento de Biodiversidad y Conservación, Real Jardín Botánico-CSIC, Calle
7 Claudio Moyano 1, 28013 Madrid, Spain.

8 *Corresponding author, jano@rjb.csic.es, telephone number: 635434879

9 ²Departamento de Ciencias Agroforestales, E. U. de Ingenierías Agrarias, Universidad
10 de Valladolid, Campus Duques de Soria, 42004 Soria, Spain.

11 ³Departamento de Biología (Botánica), Universidad Autónoma de Madrid, Calle
12 Darwin 2, 28049 Madrid, Spain.

13 ⁴Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM) Universidad
14 Autónoma de Madrid, 28049 Madrid, Spain.

15

16 **ABSTRACT**

17 *Navaea phoenicea* (Malvaceae) is a flagship shrub species endemic to Tenerife Island in
18 the Canary archipelago and is included as Endangered on the Spanish Red List. We
19 conducted a comprehensive census and monitored the structure of 8 accessible
20 populations over ten years to develop a stage-based demographic matrix model and
21 performed deterministic and stochastic projections. To determine the longevity of
22 individuals, we conducted a dendrochronological study on 10 collected dry samples.
23 The censuses showed a clear, gradual decline, and the total population was around half
24 that in previous studies. The yearly finite growth rate was strongly correlated with
25 annual rainfall. Survival rates of seedlings were low, and high elasticity values were
26 allocated to the larger, reproductive individuals, which showed the highest survival
27 rates. The age of the oldest individual was 32 years, while the average age inferred from
28 dendrochronology was 18 years. These results point to a lower longevity of individuals
29 with respect to the values calculated by demographic models. The findings of this study
30 suggest the importance of the preservation of reproductive individuals and their habitat,
31 as well as the need to re-adopt legal measures of greater protection for the species.

32 **Keywords:** Canary Islands, Macaronesian bird-flower element, matrix modelling,
33 *Lavatera*, *Navaea phoenicea*, Malvaceae, stochastic models.

34 **1. Introduction**

35 The characteristics of volcanic archipelagos make insular biota more vulnerable to
36 extinction due to isolation and limited potential habitat, resulting in a large number of
37 endangered species (Courchamp et al. 2014; Harter et al. 2015). Conservation biology
38 has thus focused on oceanic islands, given the higher species diversity in these small
39 territories (Kier et al. 2009). One paradigmatic case is the Canary archipelago, whose

40 early colonization by African and later European settlers led to a dramatic disturbance
41 of natural habitats (De Nascimento et al. 2009; Fernández-Palacios et al. 2011). The
42 Canary Islands, as part of the Mediterranean-Macaronesian hotspot (Médail and Quézel,
43 1999), hosts a large plant diversity with approximately 50% of endemic taxa (Reyes-
44 Betancort et al. 2008). The main threats to biodiversity identified in the archipelago
45 include severe habitat reduction combined with strong fragmentation, grazing by
46 introduced herbivores and competition with invasive plant species (Bañares-Baudet et
47 al. 2004; Caujapé-Castells et al. 2010; Gangoso et al. 2006). Thus, 25% of the Canarian
48 flora fall within an IUCN category of risk (Bañares-Baudet et al. 2004; Moreno-Saiz
49 2008; Moreno-Saiz et al. 2015; Muñoz-Rodríguez et al. 2016). Whereas population
50 genetics (Caujapé-Castells 2010) along with reproductive biology and autecology
51 approaches (Anderson et al. 2015) have accounted for most of the efforts, studies
52 focusing on demographic parameters account to date for little more than a dozen species
53 (Iriondo et al. 2009; Marrero-Gómez et al. 2005; 2007; 20015).

54 Within the endangered flora of the Canary Islands, we focus on a relic,
55 paleoendemic species. *Navaea phoenicea* (Vent.) Webb & Berthel. (Malvaceae) is a
56 rare shrubby mallow restricted to reduced areas in Tenerife Island. The species shows a
57 rare bird-pollination system, making it part of the Macaronesian bird flower element
58 (Fernández de Castro et al. 2017). The natural history of the species and its role in the
59 ecosystems makes it a flagship species for conservation measures. *Navaea phoenicea*
60 has been recognized either as a vulnerable (Rodríguez-Núñez et al. 2004) or endangered
61 taxon (Gómez-Campo, 1996; Moreno-Saiz 2008) based on IUCN criteria. However, its
62 populations have been downgraded to the legal status of 'Species of special interest for
63 the Canarian ecosystems', a category for unthreatened species managed 'by virtue of

64 their relationship to the ecosystems of the protected areas in which they are located'
65 (Gobierno de Canarias 2010).

66 Prior evaluations conducted for this plant identified as the main endangerment
67 factors the inability to disperse seeds, grazing, competition with exotic species and
68 habitat loss (Rodríguez-Núñez et al. 2004). These risk assessments, however, were
69 based only on visual evidence, which caused them to reach conclusions not supported
70 by long-term studies. Demographic parameters, such as the structure and viability of the
71 populations, are thus far unknown. The aim of this paper is to shed light on these
72 questions to assess the conservation status of the species. For this purpose, a detailed
73 population survey over 10 years was conducted along with a dendrochronological study
74 to perform a population viability analysis (PVA) to determine long-term trends. The
75 objectives were: 1) to model population dynamics and examine which life stages
76 contribute to their growth rates; 2) to assess the relationship between climate and
77 demography; and 3) to model extinction probability to guide conservation strategies.

78 **2. Materials and methods**

79 *2.1. Study site and species*

80 *Navaea phoenicea* represents an independent lineage within the tribe Malveae
81 (Escobar García et al. 2009). It is a large-sized shrub, exemplifying a case of insular
82 woodiness within its lineage (Carlquist 1974; Lens et al. 2013). Flowers are pollinated
83 by non-specialist passerine birds (Fernández de Castro et al. 2017). The seeds are dry
84 schizocarps that disperse mostly by barochory, with germination rates remaining very
85 low without manual scarification.

86 The habitat of *N. phoenicea* are the steep slopes of the transition between the
87 sclerophyllous forests of the Thermomediterranean dry belt, characterized by the

88 occurrence of *Maytenus canariensis*, *Pistacia atlantica*, and *Juniperus phoenicea*, and
89 the Mesomediterranean subhumid laurel forests, where is frequent the presence of
90 *Apollonias barbujana* and *Visnea mocanera* (del Arco Aguilar & Rodríguez Delgado,
91 2018), which has been severely reduced by human activities (del Arco Aguilar et al.
92 2010). Within these habitats, populations are restricted to northern cliffs of the two old
93 volcanic paleoislands of Tenerife, the Anaga (East) and Teno (West) mountain massifs,
94 resulting in two fragmented population groups composed of 8 and 7 subpopulations,
95 respectively (figure 1). A census carried out for the Red Book counted as many as 1,410
96 mature individuals (Rodríguez Núñez et al. 2004).

97 2.2. Demographic survey

98 All known subpopulations and nearby areas (figure 1) were intensively prospected
99 in January 2006 and all individuals recorded. The inaccessibility and instability of the
100 ravines necessitated the use of binoculars on several occasions. The 8 most accessible
101 subpopulations were delimited as survey plots for annual demographic monitoring. All
102 individuals within the plots were tagged, georeferenced, and measured for the following
103 biometric parameters: basal diameter of the stem, total height and crown surface. The
104 cylindrical biovolume was calculated as the product of total height by crown surface.
105 Flower production and number of branches were also quantified. Futher, we calculated
106 the correlations between all biometric parameters to determine if the stem diameter
107 could be considered as a reliable size estimator.

108 In every annual sampling, from 2006 to 2015, plots were visited in search of new
109 seedlings, and biometric parameters were measured yearly for every recorded
110 individual. Surveys were performed at the end of the flowering season in late February.
111 Reproductive data coupled with biometry were used to establish the threshold between

112 life stages (see results): 1) seedlings (S), considered as first year individuals; 2) juvenile
113 (V); 3) young reproductive (RI) as flowering individuals of stem diameter <5.8 cm; and
114 4) mature reproductive (RII), flowering individuals with stem diameter ≥ 5.8 cm. The
115 5.8 cm diameter threshold dividing RI and RII classes was selected as the increment in
116 flower production was maximal at this point under a GAM model (see results). These
117 classes were used to estimate the transition matrices for demographic modeling over the
118 period of the study. To account for significant differences in seedling survival between
119 localities and years, generalized linear models (GLM) were employed. For recruitment,
120 we assumed that reproductive capacity was directly proportional to tree size. We
121 therefore used the sum of stem diameters as a covariate in the model following Pierson
122 & Turner (1998). With respect to seedling survival, we fitted a GLM with localities and
123 years as predictors. The fate of seedlings (death or survival the next year) was used as a
124 dependent variable following a binomial distribution.

125 2.2. *Deterministic matrix modeling*

126 Projection matrices to calculate transition probabilities between life stages were
127 built using the *popbio* package (Milligan and Stubben 2007), implemented in R
128 software (R Core Team 2013). To account for fecundity estimates we took the approach
129 of Caswell (2001). First, the seed production of each individual was calculated based on
130 the number of flowers, which was counted weekly in the sampling periods from 2007-
131 2009. The total number of flowers was modeled as a response variable in a linear
132 regression against the basal diameter of the stem. The model was used to estimate the
133 total number of flowers of each individual for subsequent sampling years, where
134 population censuses occurred only at the end of the flowering period. The total number
135 of flowers of each individual was multiplied by the mean number of ovules per flower
136 and the average fructification rate (21 and 0.18, respectively; Fernández de Castro,

137 unpublished results). Second, the average number of seedlings that emerged the next
138 year was divided by the average total number of seeds produced every year, as an
139 estimate of the rate of seedlings established per seed. Finally, the number of seeds
140 produced annually by each individual was multiplied by the mean rate of seedling
141 production, as the individual estimate of fecundity. Lefkovitch transition probability
142 matrices were calculated, followed by yearly lambda (λ) values of finite growth and
143 bootstrap λ values along with elasticity matrices. Analyses were conducted for the
144 ensemble of individuals and separately for the two populations, Teno and Anaga.

145 2.3. *Average generation time*

146 A demographic parameter relevant for population genetic models based on the
147 coalescent and population dynamics is the average generation time. The calculation of
148 this parameter is based on the ages at first and last reproduction (α and ω) The average
149 time between generations of repeated reproducers is roughly estimated as $T = (\alpha + \omega)/2$
150 (Pianka 2011).

151 2.4. *Stochastic simulation of population dynamics*

152 Stochastic simulations were conducted again with the *popbio* package, which
153 implements equations for stochastic models from Morris and Doak (2002). To account
154 for potential environmental variability affecting growth rates, three scenarios were
155 developed to assign probabilities to each year. One stable scenario where all yearly
156 matrices were weighted equally; a negative scenario where matrices of years with $\lambda < 0$
157 were given twice the weight of those of years with $\lambda > 0$; and a third, positive scenario
158 where conversely, years with positive growth were given double weight in the
159 stochastic simulations. Models were run with 50.000 iterations. Quasi-extinction

160 probabilities were calculated assuming an extinction threshold of $N=100$ (a reduction of
161 90% the censused individuals) and a temporal horizon of 100 years.

162 2.5. *Climatic variables*

163 To calculate the correlation between population growth and climate parameters, datasets
164 of available weather stations from the Spanish Meteorological Agency (AEMET) were
165 collected and filtered by location and time span of climate records. Only stations within
166 the northern slopes of Teno and Anaga massifs within the altitude range of *Navaea*
167 *phoenicea* were considered (400-600 m a.s.l.), one in Teno massif and 5 in Anaga
168 (figure 1). Here, the following approach was taken to explore which kind of procedure
169 is more informative about the environmental influence on population growth. On the
170 one hand, only one station was kept as a proxy of the general climate variation for the
171 whole Anaga massif. On the other, data from the five stations were used to interpolate a
172 raster map for each monthly variable for every year at 500 m resolution. Calculations
173 were conducted using the geoR package in R (Ribeiro and Diggle 2015). The values
174 obtained for the centroid cell of all subpopulations in Anaga were then used as a climate
175 proxy. Monthly, quarterly, average and total annual precipitation values, and maximum,
176 minimum and average monthly temperature in Teno and Anaga separately, were used to
177 test the significance of the correlation between λ and climate values.

178 2.6. *Dendrochronological analyses*

179 Given the current conservation status of the species, only dead individuals were used in
180 the dendrochronological assessment. Samples were obtained from the beginning of the
181 survey to 2009. Stems from dead individuals were sliced at their base and manually
182 sanded and processed to clarify the tree rings in the stem. Then, individual growth rings
183 were counted and measured by means of a Velmex sliding-stage micrometer. For each

184 sample, we measured rings along three radii, and an the average ring width series from
185 every individual was calculated. Those individuals whose year of death was known
186 were used to establish a master chronology. Dead individuals found at the beginning of
187 the study for which death year was unknown, were matched to the highest correlation
188 coefficient with the master chronology. All calculations were performed with the dplR
189 package in R (Bunn 2008).

190 AEMET meteorological station data were used to explore the relationships between
191 climate time series and stem growth. The set of meteorological records was filtered to
192 select stations accounting for data for the life-time period of the sampled specimens.
193 Finally, two stations were chosen as climate proxies (figure 1) for Anaga and Teno
194 specimens. The correlation with annual precipitation was analyzed to explore the effects
195 of climatic variables on growth rate. These correlations were calculated for the annual
196 precipitation of the same year, and for the previous and the two previous years.

197 **3. Results**

198 *3.1. Demographic survey and population dynamics*

199 The initial survey detected 840 individuals, about half of the 1,410 counted in the
200 previous census (figure 1). However, the survey in inaccessible locations with
201 binoculars could only account for flowering individuals, but not seedlings or juveniles,
202 which could not be easily detected. The starting number of individuals within the
203 accessible studied plots was 347 in total, 163 from Anaga and 184 from Teno. Annual
204 growth inferred from the differences between diameters measured in consecutive years
205 was on average 1.92 mm ($SD=1.01$). The number of flowers and logarithm of the
206 biovolume were significantly correlated with basal stem diameter ($F=910.5$, $p<0.001$,
207 $R^2=0.857$; $F=558$, $p<0.001$, $R^2=0.780$, $n=349$, supplementary figure 1a and b,

208 respectively). Diameter was therefore considered a valid measure to establish size
209 classes and life stages. Proportion of seedling survival in the plots from one year to the
210 next ranged from 0 to 100% with a mean of 0.15. Survival rate significantly varied
211 between years ($F_{9,147}=5.477$, $P=0.0026$) and subpopulations ($F_{12,144}=3.337$,
212 $P=0.000046$). For recruitment, the minimum ratio of seedlings emerged/seeds produced
213 ranged from 0 to $0.587 \cdot 10^{-3}$. Linear models also detected significant differences for
214 both predictors (sub-population: $F_{9,147}=3.292 \cdot 10^{-8}$, $P=2.017 \cdot 10^{-7}$; M year: $F_{9,144}=5.097 \cdot 10^{-9}$,
215 $P=3.806 \cdot 10^{-16}$).

216

217 3.2. *Deterministic matrix modeling, fecundity and survival rates*

218 The average λ value for the total population was 0.994, ranging from 0.982 (2012)
219 to 1.022 (2010) (table 1, supplementary table 1). Bootstrapped values ranged overall
220 from 0.985 to 1. In Teno and Anaga, the average λ was 0.992 and 0.994, respectively,
221 and bootstrapped values ranged from 0.937 to 1 in Teno, and 0.962 to 1 in Anaga. Three
222 transitions showed $\lambda > 1$ in Anaga (2009-2010 2010-2011 and 2014-2015), two in Teno
223 (2009-2010 2013-2014), and one for the ensemble (2009-2010). Figure 2a represents
224 the values of fecundity, transition rate to the next stage and survival rates within a given
225 stage. No reversion to previous stages was observed over ten years. Survival rates were
226 higher in the reproductive stages. The transition from seedling to juvenile, i.e., seedling
227 survival, showed low values (0.153). Fecundity was higher in mature reproductive
228 individuals RII than in young reproductive individuals RI (table 1). As a result of an
229 average $\lambda < 1$, the deterministic matrix model projected a population decrease (figure 2b).
230 The current population structure differed from the stable structure defined by the
231 population matrix only between RI and RII individuals as the distributions of their

232 proportions became inverted. Distributions of seedlings and juvenile individuals
233 decreased slightly (figure 2b). The time spent in each stage by an individual, estimated
234 from the projection matrix, indicated that *Navaea phoenicea* is a long-lived species: by
235 definition 1 year in the seedling stage, and an average of 4 years in the juvenile stage,
236 24 as young reproductive and 25.5 as mature reproductive. This was in sum 55 years.
237 The times estimated for the mature reproductive stage were mostly less in Anaga (18 yr)
238 than in Teno (30 yr). Average generation time for *Navaea phoenicea* is $T = 16.8$ yr.

239 Elasticities were high for the survival of young reproductive and mature
240 reproductive individuals. More frequently, annual elasticity matrices assigned higher
241 values to the survival of young reproductive individuals than to mature ones. However,
242 these values varied widely, i.e. in several periods elasticity of survival of mature
243 individuals reached 1, while in others, conversely, young reproductive individuals also
244 achieved a value of elasticity of 1. The elasticity of transition between stages or
245 fecundity showed very low values.

246 No monthly variables of temperature or precipitation presented significant
247 correlations with yearly λ values. On the contrary, total annual precipitation showed a
248 strong relationship with λ (figure 4). In Teno, Pearson R^2 was 0.764 ($t=3.35$, $df=8$,
249 $p=0.0109$). In Anaga, where two distinct approaches were used, results differed. In
250 contrast with Teno, there was a weak correlation for a single station ($R^2=0.401$, $t=1.24$,
251 $df=8$, $p=0.249$). For the centroid of the interpolated values, however, correlation was
252 strong ($R^2=0.818$, $t=4.026$, $df=8$, $p=0.004$).

253 3.3. *Stochastic projections*

254 Table 2 summarizes stochastic projections under the defined negative, stable and
255 positive scenarios for a temporal horizon of 100 years. Growth rates calculated for

256 stochastic projections showed that at any of the three defined scenarios, both in total and
257 for each population, their values were always <1 , although in the positive scenario λ
258 was 0.999. Quasi-extinction probabilities varied between scenarios (supplementary
259 figure 2, table 2). Under the negative scenario, the probability was over 0.938 in all
260 cases. Under the stable scenario, probability in both Teno and Anaga was over 0.973
261 when considered separately, but not when considered together (0.154). Finally, the
262 positive scenario gave a null probability of quasi-extinction to the population ensemble,
263 low for Teno (0.184) and intermediate for Anaga (0.570). For shorter time horizons, the
264 probabilities for the two populations separately began to increase after 25 years, not
265 before.

266 Projected population numbers at the end of the simulations were highly variable
267 (supplementary figure 2). For both Anaga and Teno considered separately, in only the
268 positive scenario was the most probable number of effectives over 100. Accounting for
269 the total population, the most probable population numbers were 121 in the negative
270 scenario, 181 in the stable, and 315 in the positive scenario.

271 3.4. *Dendrochronological analyses*

272 Ten samples from dead individuals were obtained during the time period 2005-
273 2008, eight in Anaga and two in Teno. Two dry individuals were found at the beginning
274 of the fieldwork, while the other eight were collected during the annual population
275 sampling. Although the tree-ring chronological series were generally very short (figure
276 3a), growth rings are characterized by semi-ring porosity and the boundaries can be
277 unequivocally identified by a band of marginal parenchyma (figure 3b). The oldest
278 sample was REP01 at 32 years and the youngest was TAB04 at 11 years. The mean age
279 of sampled individuals inferred from rings was 18.09, below the times inferred from the

280 projection matrix. On average, annual growth rate was 2.011 mm ($SD=1.17$), slightly
281 higher than growth rate measured at the stem base. Pearson correlation among the
282 individual growth rates was 0.61.

283 Correlations between average ring growth per population and any of the time
284 series of annual precipitation were very weak (supplementary table 2). Figure 3c shows
285 the relationship between ring growth and total precipitation for the period 1978-2010. In
286 Anaga, the correlation between growth and precipitation only appeared to be significant
287 in the period 1999-2001, and in Teno between 2004 and 2006. However, in some parts
288 of the chronological series, a time lag in the covariation between rainfall and growth
289 could be observed, suggesting that a stronger relationship between climate and growth
290 may occur, but weakly coupled and with a certain preconditioning of climate on growth
291 rates variable across years.

292 **4. Discussion**

293 This study provides a census of *Navaea phoenicea* and a long-term population
294 survey predicting a slow decline of the species in the coming decades. These concerning
295 results offer insights both on the size structure of the population and the effect of
296 climate constraints on population trends. The study on this particular endemic species in
297 the thermophilous shrubland of Tenerife contributes to the understanding of its risk
298 factors and offers clues for the management of the habitat.

299 *4.1. Size and population structure*

300 There is a large discrepancy between the census in our study and a previous one
301 taken for the Spanish Red Book (Rodríguez Núñez et al. 2004). Our number is just over
302 half of the individuals previously estimated. Based on the number of mature individuals,
303 this new census would qualify the species as threatened in the IUCN category VU D1.

304 Such an effective decrease is not likely to have happened, given the slow decline trend
305 found here and the near absence of dead mature individuals at the beginning of our
306 study. Instead, discrepancies are more likely due to the use of different estimation
307 methods and the existence of look-alike species at the same locations.

308 The sample size that could be surveyed within plots represent a fraction of
309 approximately half of the total census. The population structure based on size in *Navaea*
310 *phoenicea* was dominated fundamentally by mature individuals. Because in most years
311 annual surveys were performed once, it is very likely that annual data only accounts for
312 a fraction of total seedlings in the population, although the sampling time was chosen to
313 maximize the number of seedlings emerged from the seed bank. Accounting for the total
314 number of seedlings emerged throughout the year may confer to the species population
315 the classical J-shaped distribution curve of frequency of each stage. Under this 4 stage-
316 based classification of individuals, collected data would classify the populations as
317 ‘senile’ (Oostermeijer et al., 1994). Juvenile individuals were present in very low
318 numbers and were scarcer than seedlings. One of the main threats to the Canarian flora
319 is grazing, which may more intensely affect seedlings, yet for *Navaea phoenicea* the
320 elasticity values for seedling survival does not ensure the persistence of the species.

321 4.2. *Projected population trends and drivers. Reasons for concern?*

322 The variability of finite growth rate across years and locations was below one,
323 indicating a declining tendency. This trend is partly due to the longevity and relatively
324 slow growth of individuals, which drives small variations in population numbers and
325 transitions between years. The deterministic modeling predicted less than 100
326 individuals within the next century meaning a reduction of 30% of the population in 50
327 years, insufficient to be considered threatened under IUCN criteria.

328 The comprehensive COMPADRE database (Salguero-Gómez et al. 2015) shows
329 that other pertinent PVAs are scarce for the Malvaceae. Similarly, there have only been
330 14 PVAs carried out in Canarian plants (Iriondo et al. 2009; Kyncl et al. 2006; Marrero-
331 Gómez et al. 2007 2005), across all environments. Demographic monitoring on
332 Canarian species has shown great variations in their population trends, ranging from
333 $\lambda=0.603$ for *Laphangium teydeum* (Asteraceae, Marrero Gómez et al. 2015) to $\lambda=1.247$
334 for *Helianthemum juliae* Wildpret (Cistaceae, Marrero Gómez et al. 2007), both
335 endemic to the Cañadas del Teide National Park in Tenerife. *Navaea phoenicea* showed
336 an intermediate $\lambda=0.994$ and by far the lowest fluctuation in annual population growth
337 trends among the studied Canarian taxa. For these three species, as for some others, the
338 highest elasticities were associated with survival rates of mature individuals. Likewise,
339 survival of juvenile individuals was associated with rainfall amounts.

340 Accounting for stochasticity under different scenarios of population growth, only
341 the positive scenario did not predict an early quasi-extinction event. The probabilities
342 are dependent on two arbitrary inputs, namely the time period for the calculation and the
343 initial number of individuals. The models were run accounting only for individuals
344 within survey plots, which represent approximately 50% of the total estimated
345 population, thus the actual quasi-extinction probability should be lower. In the three
346 scenarios, however, the average stochastic λ was always below 1, indicating a likely
347 decrease in the number of effectives regardless of the environmental variability.
348 Stochastic models allow for the assessment of IUCN criterion E for probability of
349 extinction within a time period. Given the long lifespan of cohorts estimated by the
350 matrix models, extinction probability would only increase significantly after 25 years,
351 but in the time period within 5 generations. Therefore, *Navaea phoenicea* should be

352 included in EN category under this criterion, i.e. >20% of extinction probability in less
353 than 20 years or 5 generations.

354 The causes of the decline may be two-fold. First, demographic analysis showed a
355 strong relationship between precipitation and λ , where years with precipitation >550
356 mm drove a positive population growth. Overall, the elasticity analysis showed that
357 individual reproductive stages are crucial for the survival of populations as they had
358 significantly higher values than any transition or fecundity values in the average
359 matrices. On the other hand, the congruence between recruitment and rainfall has been
360 found for other species in different climate regimes and habitats in Tenerife (Fernández-
361 Lugo et al. 2015; Marrero-Gómez et al. 2007). This evidence is consistent with the fact
362 that juveniles show a high survival rate; once the critical seedling stage is passed. A
363 second possible factor is seedling predation as a direct driver against recruitment.

364 Although grazing is considered a recurrent risk factor for the Canarian flora
365 (Gangoso et al. 2006; Moreno-Saiz et al. 2015), our evidence for this is uncertain,
366 especially confronted with findings for the noticeable effect of rainfall. In a preliminary
367 experiment performed between exclusion and non-exclusion plots, we found significant
368 differences in recruitment, but the small sample size and short-term nature of the assay
369 prevents sound conclusions. Because recruitment and seed survival vary significantly
370 between populations and years, there may be several local factors affecting recruitment.

371 The high elasticity attributed to reproductive individuals indicates a requirement
372 for the conservation of the species, which can be translated into recommendations for
373 habitat conservation. This presents challenges for decision-makers, as land management
374 on islands can be particularly difficult (Fernandes et al. 2015). However, under the
375 current trend of populations and probabilities this may not be enough in the long term.

376 Since recruitment appears to rely largely on climate, it is necessary to assess current and
377 future trends of precipitation. Trends from preindustrial times until the present show a
378 significant decrease in the precipitation for the Canary Islands when measuring
379 tendencies at the regional scale (Niang et al. 2014) but not significant at the
380 Macaronesian scale (Cropper and Hanna 2014). Projections of IPCC5 scenarios (IPCC
381 2013) predict a significant decrease in the rainfall of 20% by 2100 under the worst
382 emissions scenario. IPCC 5 scenarios have not been downscaled for the Canary Islands,
383 which is needed given the complexity of climate in oceanic islands when representing
384 microclimate variables that operate at finer scales (Harter et al. 2015). For instance, the
385 effect of trade winds, which are crucial for rainfall regime and water balance, may be
386 very difficult to model for the present climate and to downscale future scenarios.
387 Specifically, a downward shift of the cloud forest has been predicted resulting from the
388 incidence of trade winds (Sperling et al. 2004), which would in turn favor populations
389 of *Navaea phoenicea* if rainfall is increased in the lower limit of its altitudinal range. On
390 the other hand, the species distribution shows a certain altitudinal variation, with
391 subpopulations located at the lower edge of the thermophilous shrubland limited by the
392 coastal desert, and others near or within the laurel forest, although a sufficient sampling
393 size could not be retrieved to test the effect of elevation on the growth rate apportioned
394 by subpopulations. Therefore, the fate of populations may be asymmetric depending on
395 the distribution under scenarios of intense climate change, but can present an
396 opportunity to carry out assisted migration.

397 4.3. *Coupling dendrochronology and population viability analysis*

398 Although evolutionary implications of insular woodiness in *Navaea phoenicea*
399 are beyond the scope of this paper, accounting for tree rings and stem growth allowed
400 us to confirm the existence of true woodiness in a species disregarded in previous

401 studies (Lens et al. 2013). Rings can be easily visualized and measured. Because of the
402 conservative approach to an endangered species, sample size achieved throughout the
403 period was very low, and therefore these results should be considered with caution.

404 The correlation between chronological series was satisfactory, but there was weak
405 evidence of the effect of climatic variables on tree growth. Microclimatic variations
406 linked to complex topography are a generalized factor in oceanic islands (Harter et al.
407 2015; Irl et al. 2015). Therefore, the climate proxies may misrepresent the local climatic
408 conditions that affect tree growth. Similar results are found for tree species (Rozas et al.
409 2013). Measures of annual growth taken in the sampling plots were inconsistent with
410 width increments measured from tree rings. There was no correlation between age and
411 basal diameter. Age therefore, as often occurs in the vast majority of species studied,
412 can be considered a poor predictor of the reproductive ability of individuals, which is in
413 turn rather correlated with size. A second incongruence found between matrix modeling
414 and this dendrochronological study is their difference in the survival rates. Even with
415 the limited sample size, the mean age of dead individuals was 18 years and the oldest
416 individual, which also had the second largest trunk, was 32. On the contrary, the matrix
417 modeling gave much higher estimates of survival in each stage. One possible
418 explanation is that individuals in the dendrochronological study were sampled in more
419 optimal years. Since conservation strategies rely partially on the assurance of
420 survivorship of the largest individuals, this incongruence must be taken into account as
421 a caution measure, if living times extracted by matrix modeling are overestimated.

422 4.4. *Concluding remarks for conservation strategies*

423 This study identifies a population decline driven by a lack of recruitment in the
424 driest years, which were frequent in the survey period. The application of IUCN criteria

425 through this study provides evidence to maintain *Navaea phoenicea* in the EN category.
426 Our study calls into question the justification for the reduction in its protection and, on
427 the contrary, warns about the future of a plant whose habitats are fragmented and
428 unprotected or covered by 'low intensity' figures of land protection (Rural Park and
429 Protected Landscape). Projected governmental evaluation in 2018 (A. Bañares com.
430 pers.) should incorporate these new data and draw up a recovery plan in line with the
431 real risks faced by the species.

432 The rate of decline, although clear, is modulated by the long lifespan cycle of the
433 species. Even in the absence of this risk of rapid decay, which would better suggest a
434 long-term conservation strategy, it is necessary to address the remaining risk factors.
435 Population numbers are very low and subject to catastrophic events as the stochastic
436 models showed. These may be natural processes frequent in the oceanic archipelagos,
437 such as landslides or volcanic episodes, but can also be human-induced impacts. An ex-
438 situ reproduction program, as well as an adequately storage of genotyped germplasm,
439 could act as a supporting measure in the event of climate-change related hazards, such
440 as prolonged drought or a source of population reinforcement programs. This was
441 already suggested by Rodríguez-Núñez et al. (2004) for some localities. There are
442 currently three germoplasm banks hosting seeds (Jardín Botánico Viera y Clavijo in
443 Gran Canaria island, and Real Jardín Botánico, in Madrid). The first two preserve live
444 individuals. Besides, other individuals are maintained by private initiatives with no
445 information of their origin. Grazing, together with non-climatic factors affecting
446 seedling survival for instance, must be still investigated accurately. Habitat preservation
447 and competition with invasive species must be addressed as well, as part of the
448 conservation practices for reproductive individuals and to acknowledge natural and
449 anthropogenic mortality causes. Climate-induced changes in vital rates may be more

450 difficult to manage. Besides an assisted approach, habitat conservation should not only
451 contribute to the preservation of reproductive individuals, it should preserve bird
452 pollinators and ensure reproductive fitness, which may improve with higher visit rates
453 of efficient pollinators. Although time-consuming, PVAs prove to be useful for a better
454 understanding of the risk factors that threaten populations. Given the singularity of the
455 island biota and the conservation status, it is therefore necessary to improve the use of
456 these methods.

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464

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- 600
- 601

602

603 **Table 1.** Average projection and elasticity matrices, average and minimum-maximum
 604 bootstrapped λ values for the complete period for Teno, Anaga and the total population
 605 ensemble. S=seedling, J = juvenile, RI=young reproductive, RII=mature reproductive. N=mean
 606 time spent in each stage.

Projection					Elasticity				λ	BS. λ
Teno										
	S	J	RI	RII	S	J	RI	RII		
S	0.000	0.000	0.092	0.284	0.000	0.000	0.010	0.010	0.992	0.985 1.000
V	0.185	0.7599	0.000	0.000	0.020	0.065	0.000	0.000		
RI	0.000	0.192	0.963	0.000	0.000	0.020	0.653	0.000		
RII	0.000	0.000	0.016	0.946	0.000	0.000	0.012	0.210		
N	1	4.71	21	30						
Anaga										
	S	J	RI	RII	S	J	RI	RII		
S	0.000	0.000	0.083	0.297	0.000	0.000	0.002	0.013	0.994	0.937 1.000
V	0.110	0.787	0.000	0.000	0.016	0.062	0.000	0.000		
RI	0.000	0.158	0.951	0.001	0.000	0.016	0.386	0.000		
RII	0.000	0.000	0.0375	0.966	0.000	0.000	0.014	0.486		
N	1	4.18	27.30	18.63						
Total										
	S	J	RI	RII	S	J	RI	RII		
S	0.000	0.000	0.089	0.291	0.000	0.000	0.006	0.012	0.994	0.962 1
V	0.153	0.775	0.000	0.000	0.010	0.067	0.000	0.000		
RI	0.000	0.177	0.959	0.000	0.000	0.002	0.523	0.000		
RII	0.000	0.000	0.024	0.957	0.000	0.000	0.013	0.339		
N	1	4.44	24.65	23.54						

607

608 **Table 2.** Results of stochastic projections for a 150 year horizon. Approximate λ values and
 609 projected number of effectives are displayed in bold between the 95% confidence interval. For
 610 quasi-extinction probabilities, only the mean value is provided as variation was almost 0 in the
 611 three scenarios.

		Negative scenario	Stable scenario	Positive scenario
Teno	λ	0.989	0.993	0.999
	Projected population numbers	25±8	57±20	163±59
	quasi-extinction probability	0.99	0.973	0.184
Anaga	λ	0.990	0.993	0.994
	Projected population numbers in 150 years	45±8	63±11	101±18
	quasi-extinction probability	1.000	0.997	0.570
Total	λ	0.990	0.994	0.999
	Projected population numbers (mean ± SD)	121±22	181±37	315±67
	quasi-extinction probability	0.938	0.154	0.000

612

613

614

615 **FIGURE CAPTIONS**

616 **Figure 1.** Location of Tenerife Island, sampling plots (in red) and situation of
617 meteorological stations. Asterisks denote the stations used as individual climate proxies
618 to determine correlations between λ and tree ring growth with climatic parameters.

619 **Figure 2.** a) Life cycle of *Navaea phoenicea*. Dashed lines represent fecundity, dotted
620 lines represent survival, and solid lines represent transitions to the next stage; b)
621 Deterministic trajectory projection of *N. phoenicea* monitored populations from the
622 number of individuals in 2015 for a period of 150 years; c) Yearly λ growth rates for
623 Anaga and Teno populations (black line) and yearly total precipitation values for
624 meteorological stations (dashed lines).

625 **Figure 3.** a) Quasi-extinction probabilities for a 100 year period performed for Anaga
626 and Teno populations separately and the population ensemble. The probabilities
627 predicted by the stochastic model for the three scenarios (negative, stable and positive)
628 are plotted against time. b) Density of frequency of population numbers at year 100
629 predicted by the model for the three scenarios.

630 **Figure 4.** a) Complete transversal section of a stem with visible rings; b) Detail of three
631 rings with two tree-ring boundaries. Arrows indicate visible limits between rings; c)
632 Index of growth per individual through time. Dashed lines represent total precipitation.
633 Grey frames show years with high correlation between growth and precipitation.
634 Arrows indicate possible time offsets in the potential relationship between precipitation
635 and growth, if it actually happens. d) Growth rate index for all the individuals sampled.

636

637 **Supplementary figure 1:** Relationships between diameter at the stem height and a)
638 number of flowers and b) logarithm of biovolume.

639 **Supplementary figure 2:** Stochastic projections of *Navaea phoenicea* populations for a
640 100 years period. a) Quasi-extinction probabilities in 100 years; b) Relative frequency
641 of the total number of effectives after 100 years.

Lambda ANAGA					Elasticity					Lambda TEND					elasticity matrix					TOTAL projection					Elasticity matrix						
2006	2007	0.9878049	S	projection matrix	0	0	0.06696293	0.2372005	0	0	0	0	0.972973	0	0	0.06536824	0.2390435	0	0	0	0	totalambda	0.9880427	0	0	0.06593664	0.2380747	0	0	0.00053565	0.00694362
				Y	0	0.8461538	0	0	0	0	0	0	0.1621622	0.93548387	0	0	0	0	0	0	0.1016949	0.8947368	0	0	0.00747927	0.07	0	0			
				YR	0	0.1153846	0.88888889	0	0	0	0	0	0	0.06451613	0.90769231	0	0	0	0	0	0	0.0877193	0.9009901	0	0	0.007	0.07653098	0			
				MR	0	0	0.08333333	0.9878049	0	0	0	1	0	0	0	0.972973	0	0	0	1	0	0	0.02970297	0.9807692	0	0	0.00694362	0.82312718			

0.07870608
0.17874983
0.44972796
0.29281613
0.1426649
0.153843
0.1532608
0.5502313
0.15566178
0.08920541
0.31136515
0.44376766
0.08351326
0.01434954
0.9021372
0
0.1042481
0.14094
0.5984531
0.1563588
0.1288524
0.0135274
0.6616234
0.1959968
0.14407587
0.02844333
0.56924772
0.25823308
0.18177048
0.04223654
0.30075157
0.47524141
0.1346749
0.0535893
0.5673297
0.2444061
0.1388909
0.08768799
0.5067126
0.26670852

Temporal series	ANAGA	TENO	TOTAL
Same year	-0.202	-0.228	-0.213
1 previous year	-0.017	-0.205	0.137
2 previous years	0.103	-0.116	0.141

0.07870608
0.17874983
0.44972796
0.29281613
0.1426649
0.153843
0.1532608
0.5502313
0.15566178
0.08920541
0.31136515
0.44376766
0.08351326
0.01434954
0.9021372
0
0.1042481
0.14094
0.5984531
0.1563588
0.1288524
0.0135274
0.6616234
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0.02844333
0.56924772
0.25823308
0.18177048
0.04223654
0.30075157
0.47524141
0.1346749
0.0535893
0.5673297
0.2444061
0.1388909
0.08768799
0.5067126
0.26670852

Figure 1

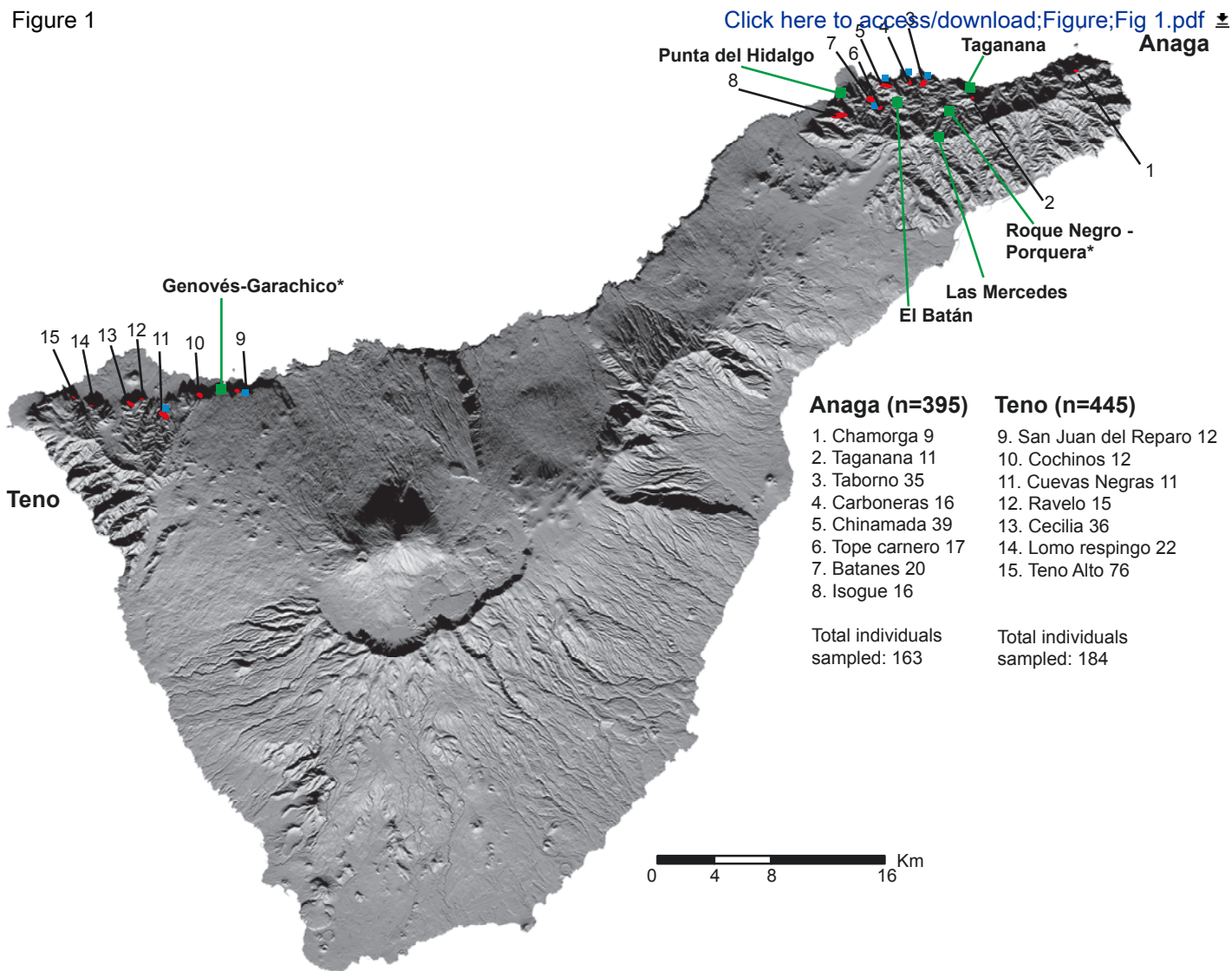
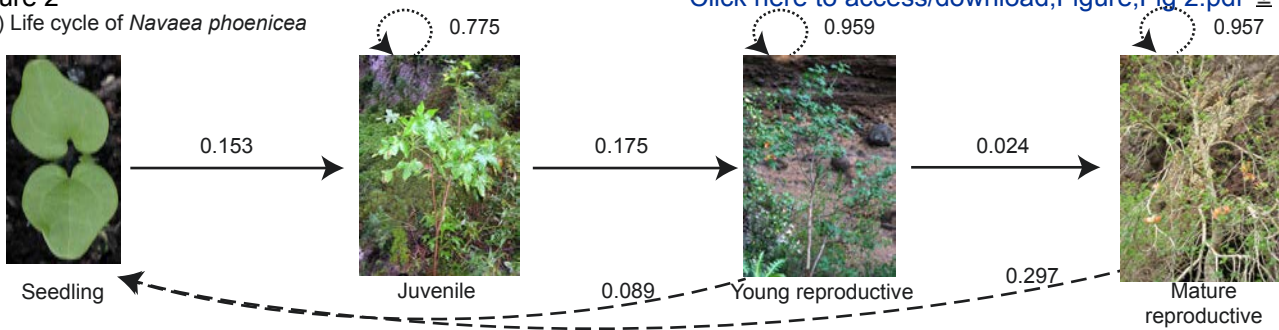
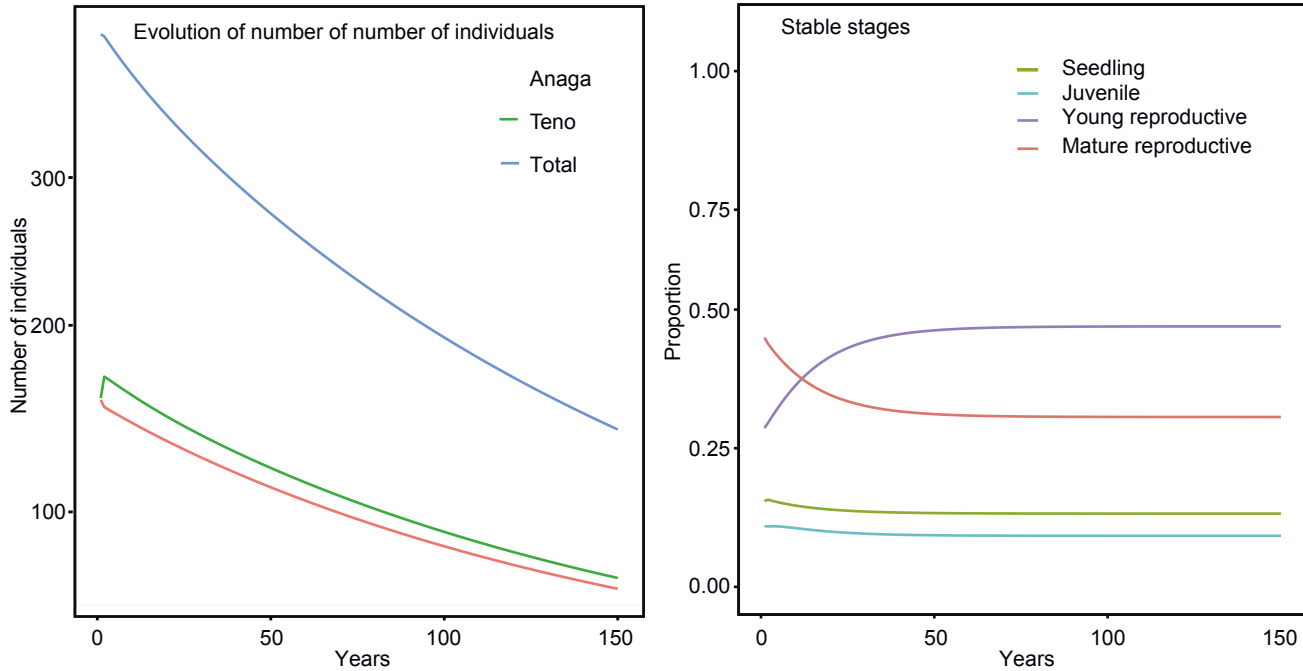


Figure 2

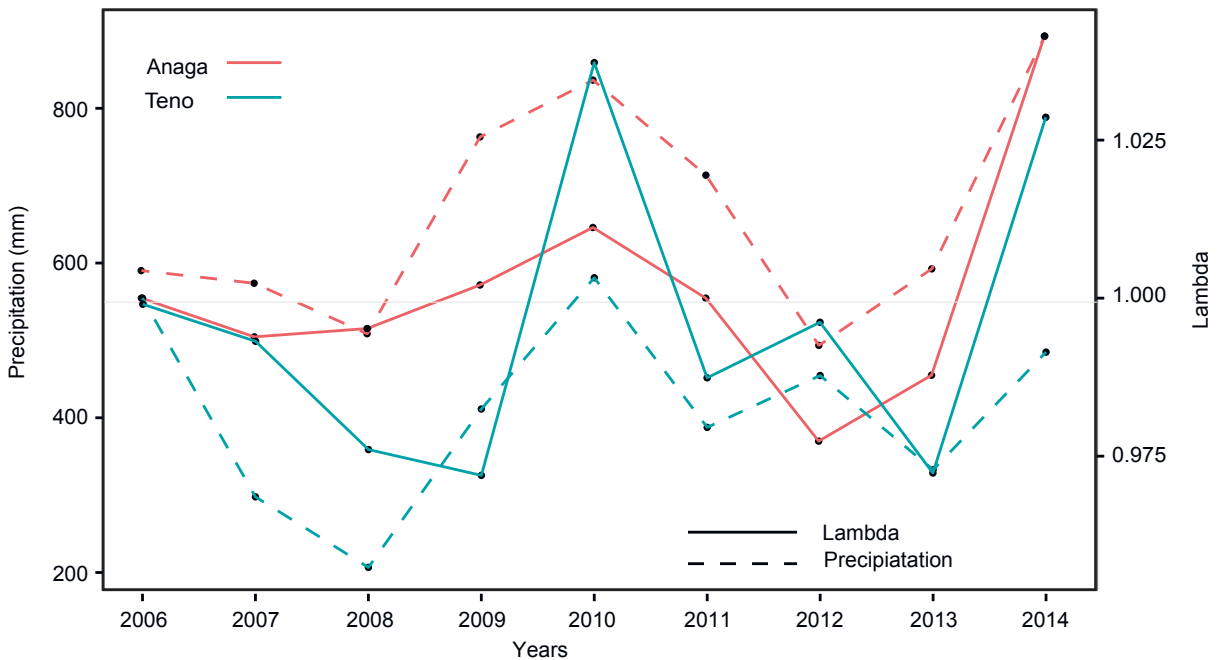
a) Life cycle of *Navaea phoenicea*



b) Deterministic trajectories

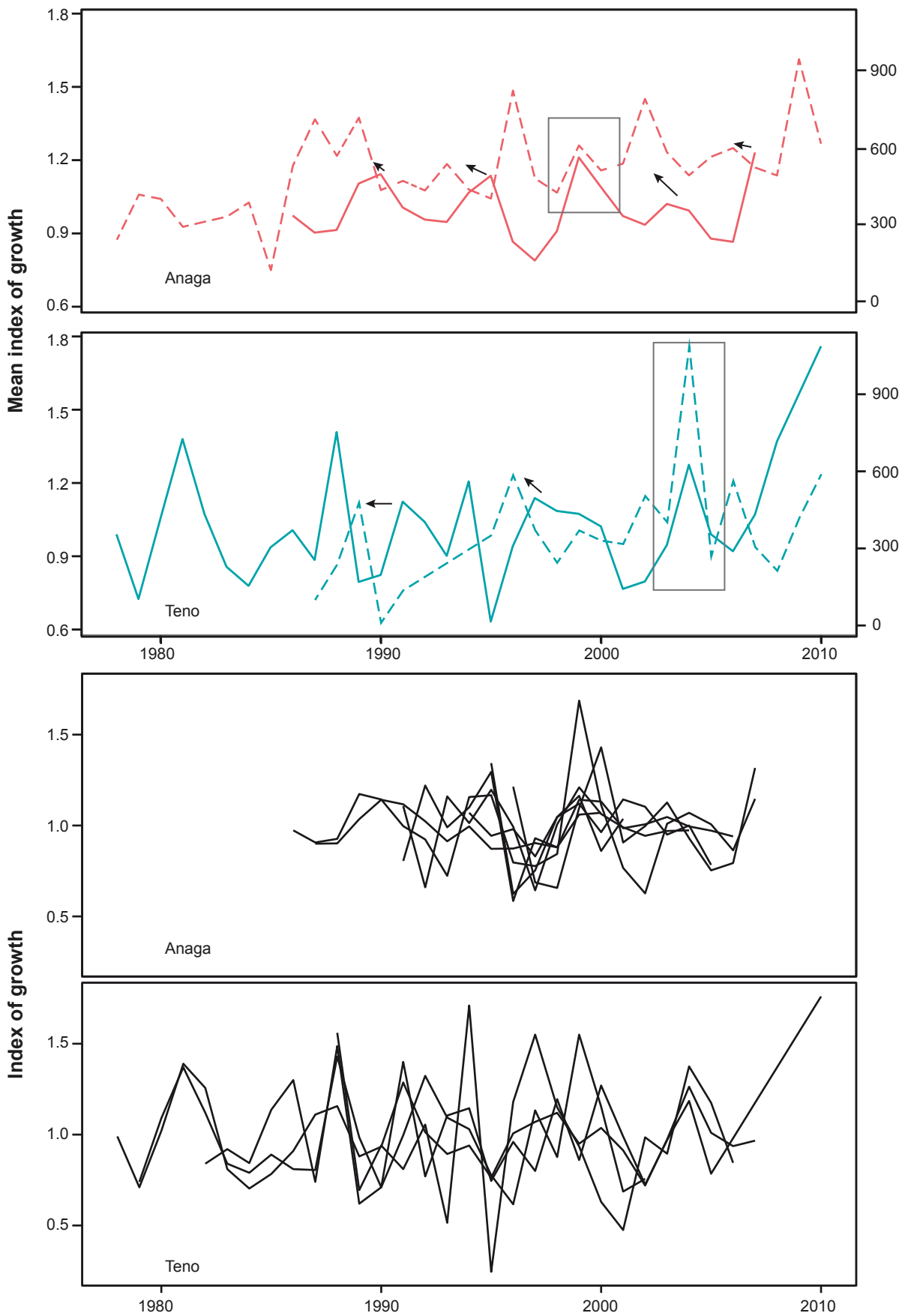


c) Variation of lambda values and precipitation across years

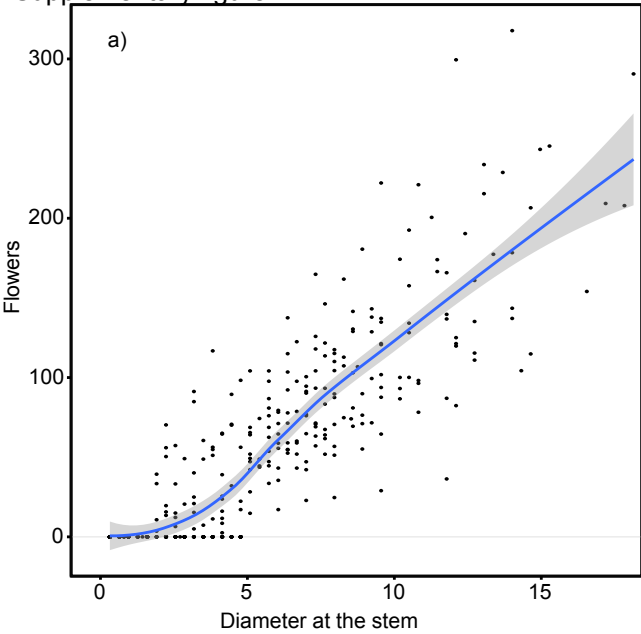




c) Index of growth



Supplementary figure 1



[Click here to access/download;Figure;Sup.fig1.pdf](#)

