1   **Evidence of climate change impacts on the iconic *Welwitschia mirabilis* in the Namib Desert**

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Abstract

16 Climate change represents an important threat to global biodiversity and African ecosystems are particularly

17 vulnerable. Recent studies predicted substantial variations of climatic suitability for *Welwitschia mirabilis*

18 under future conditions. Latitudinal/altitudinal range shifts are well-known responses to climate change but

19 not coherent patterns were documented. This study aims to verify whether welwitschia populations are

20 responding to climate change and if the assumption of a latitudinal/altitudinal shift is applicable. We

21 collected field data on welwitschia distribution, health condition, reproductive status, and plant size in

22 northern Namibia. We used ecological niche models to predict the expected geographic shift of climatic

23 suitability under future scenarios. For each variable, we compared the observed pattern with the expected

24 responses. Finally, we tested the presence of simple geographical gradients in the observed patterns. The

25 realized thermal niche of welwitschia will be almost completely unavailable in the next 30 years in northern

26 Namibia. Expected reductions of climatic suitability in the stand sites are strongly associated with indicators

27 of negative population conditions. The same population conditions does not fit any simple latitudinal or

28 altitudinal gradient. The observed pattern of population conditions mirrors the expected pattern of climate

29 change effect but no simple geographical gradient was relieved. Overall, we observed negative population

30 conditions in areas with stronger reductions of suitability. This makes welwitschia a suitable sentinel for

31 climate change effect in the Namib Desert ecosystems. Our approach to detect population responses to

32 climate change could be extensively adopted for selecting sentinel species in other regions and ecosystems.

Keywords

35 Global warming, climatic suitability, range shift, niche modeling, southern Africa

1. Introduction

Climate change is one of the strongest threats for ecosystems worldwide. Variations in the density of species, range shifts, and extinction events have been documented at local and global level (Cristofari et al., 2018; Parmesan and Yohe, 2003; Walther et al., 2002). Furthermore, changes in species diversity, ecosystem functioning, and service provision are expected for the future as a consequence of additional pressures on natural populations (Ge et al., 2015; e.g. Hole et al., 2009; Moritz and Agudo, 2013). In Africa, deep impacts by climate change were forecasted for animals (e.g. Garcia et al., 2012; Huntley and Barnard, 2012; Kirchhof et al., 2017), plants (Blach-Overgaard et al., 2015; e.g. Midgley et al., 2003; Midgley and Bond, 2015), and biodiversity conservation in general (Hole et al., 2009; Revermann et al., 2018). Arid regions of southern Africa seem to be particularly exposed to the effects of climate change (Midgley and Thuiller, 2011). For the quiver tree (*Aloidendron dichotomum* Klopper & Gideon 2013), climate-linked increases of mortality were observed, although this evidence is still controversial (Foden, 2002; Foden et al., 2007; Guo et al., 2011; Jack et al., 2016).

Recently, Bombi (2018) highlighted potential effects of climate change on welwitschia trees (*Welwitschia mirabilis* Hooker 1863; welwitschia) were highlighted. *Welwitschia mirabilis* is regarded as a living fossil, representing an ancient lineage of gymnosperm plants and it is recognized as a symbol of the Namib Desert biodiversity. This species has a peculiar morphology, being a long-living dwarf tree with only two leaves growing throughout the entire plant life (Roskov et al., 2019). This is also a key species in the Namib ecosystems, where it provides food, water, and refuge for many animal species (Henschel and Seely, 2000). The distribution of *W. mirabilis* is restricted to the central and northern Namib Desert, extending from the Kuiseb River in Namibia to the Nicolau River, north of Namibe, in Angola (Giess, 1969; Kers, 1967). In this area, welwitschia trees occur in four separated sub-ranges, three in western Namibia (Fig. 1A) (Bubenzer et al., 2004) and one in south-western Angola . Bombi (2018) showed that populations living in three Namibian subranges have experienced and will face rather different climatic conditions, and a significant reduction of climatic suitability is expected in the northernmost Namibian subrange under current climate change. In particular, the ongoing rise of temperature can drive the local climate out of the realized niche for the northern populations, thus increasing their extinction risk (Bombi, 2018). Although these findings were

63   potentially important for conservation planning, the study was based on low spatial resolution data available

64   at the national scale, thus limiting its utility at a finer scale for such purposes.

65   Distribution ranges shifts are well-known responses of species to climate change (Araújo and Rahbek, 2006;

66   Garcia et al., 2014; Parmesan, 2006). These shifts have been generally described as poleward and upward

67   movements of species to track suitable temperature conditions along latitudinal and altitudinal gradients

68   (Hickling et al., 2006; Parmesan et al., 1999; Thomas, 2010). However, in many cases documented

69   geographic patterns of response are complex and do not align with simple latitudinal and altitudinal shifts

70   (Fei et al., 2017). Indeed, the assumption of simple, uni-directional distribution shifts does not account for

71   intricate interactions among temperature, precipitation, and species-specific tolerances and can drive to

72   substantially underestimate the effect of climate change on species distributions (VanDerWal et al., 2012).

73   To overcome these drawbacks, one promising approach is based on the comparison of the species-specific

74   spatial pattern of expected responses, generated by predictive models, with the observed pattern of species

75   response measured in the field with appropriate metrics of population trends (Bombi et al., 2017). This

76   approach can increase our capacity of identifying the footprint of climate change on species dynamics.

77   The main aim of this study is to verify whether the observed geographic pattern of population conditions of

78   welwitschia trees in northwestern Namibia can be associated to the ongoing climate change. Secondarily, we

79   tested if the same pattern follows a latitudinal or altitudinal gradient in agreement with the assumption of a

80   poleward or upward range shift. More specifically, we want first to validate with field-based data the

81   predictions of potential impacts of climate change on *W. mirabilis*. Second, we want to assess whether the

82   simple assumption of a poleward/upward range shift is suitable for detecting climate change footprints in this

83   case. To do this, we compared the geographic pattern of population conditions, measured in the field, with

84   the expected pattern of response, predicted by ecological niche models. If climate change affects welwitschia

85   populations, we expect worst population conditions in sites where climatic suitability will decrease than in

86   sites where climatic suitability will increase. Moreover, if a poleward/upward range shift is the major

87   response to climate change we can expect a latitudinal or altitudinal trend in the observed patterns of

88   response. Since potential divergent responses to climate change by intraspecific lineages were evidenced

89   (Pearman et al., 2010) and different realized niche were described for each distinct Namibian subranges

90   (Bombi et al., 2017), we focused on populations in the northern subrange and considered them as an

91   independent ecological unit, with its own climatic niche and with its (sub)specific expected response. By

92   verifying our main and secondary hypotheses, we provide documented information to the long-term

93   conservation of *W. mirabilis* and further contribute to the scientific debate on the climate change impacts on

94   biodiversity.

95

2.   Materials and methods

96

2.1. Field data collection

97

98   During May 2019, we carried out a field expedition in the northernmost Namibian subrange of *W. mirabilis*,

99   as defined by the 'Digital Atlas of Namibia' (Bubenzer et al., 2004), in order to obtain information relevant

100   for the species conservation. During the expedition, we spent 10 full days searching for welwitschia trees

101   across the subrange by (1) driving at low speed along the available tracks (more than 330 km) while

102   recording the presence of plants in a ~30 m wide transect on each side of the vehicle, and (2) walking across

103   potentially suitable habitats (more than 65 km). The starting points and spatial extent of our walking transect-

104   based searches were informed by the knowledge of our local team members, who have an intimate

105   knowledge of the area. We are confident that the combination of local knowledge-informed searches and

106   systematic transects extending beyond the known range have allowed us to establish the extent and

107   characteristics of the majority of this sub-range.

108   During our transects, we collected detailed data on plant location, health condition, reproductive status, and

109   body size. Specifically, we recorded the precise coordinates (using a handheld GPS), the gender, and the

110   presence/absence of cones for almost all the individual plants we observed (just few, unreachable plants were

111   excluded). In sites with a sufficient number of plants, we also measured the stem diameters (minimum and

112   maximum along the two main axes of the stem) and the leaf length, and we recorded the health condition

113   (ranked as dead, poor, average, or good) for a random subset of ~60 plants. We ranked health condition on a

114   four-point scale (dead, poor, average, good) based on leaf color and the general aspect of the plant. Although

115   this is a relatively coarse scale, the brightness of the green color and the ratio of red/brown to green together

116   are a remarkably consistent and accurate indicator of good health condition as measured by photosynthesis

117   efficiency (Shuuya, 2016). The green color of the leaf is associated to the chlorophyll content and the

118   photosynthesis efficiency of the tissues (Menzies et al., 2016; Terashima et al., 2009), which is influenced by

119   environmental stress (Chaves, 1991; Munns et al., 2006). An estimate of health condition such as the above

120   is both a direct reflection of the environmental (including climatic) stress that the plant experiences and an

121   index of the likelihood that its resistance to parasites might be compromised (Mattson and Haack, 1987;

122   Schoeneweiss, 1978). We expected that changes in local climate will be visible in its leaf colour as a quick

123   proxy of plant health.

124

125   *2.2. Observed pattern of response*

126   For each welwitschia stand (defined *a posteriori*, through a GIS-based analysis, as a group of plants

127   separated from the other groups by a distance larger than the intra-group mean distance), we calculated three

128   categories of indicators of population response (derived from plant health, reproductive status, and size) from

129   the field-measured data. For each stand, we calculated the proportion of plants that were dead or in poor,

130   average and good condition. We also calculated the reproductive status (the proportion of plants in the stand

131   that had cones) and the plant size (average stem length, stem width, and leaf length).

132

133   *2.3. Expected pattern of response*

134   We used a spatially explicit approach based on ecological niche modeling to predict the geographic pattern

135   of plant response expected as a consequence of climate change. To do this, we defined our study area as a

136   bounding box three times larger than the latitudinal and longitudinal extent of the previously known

137   subrange of welwitschia in northern Namibia (Bubenzer et al., 2004). Inside this study area, we fitted models

138   on 1000 pseudo-presence/absence points by using climate data from the WorldClim databank (Hijmans et

139   al., 2005) at the spatial resolution of 30 arcsec (about 1 km). In order to control the model-associated

140   uncertainty, we adopted an ensemble forecasting approach (Araújo and New, 2007) in the *R*-based (R Core

141   Team, 2018) *biomod2* Package (Thuiller et al., 2016). In particular, we used Generalized Linear Models

142   (Mccullagh and Nelder, 1989), Generalized Additive Models (Hastie and Tibshirani, 1986), Generalized

143   Boosting Models (Ridgeway, 1999), Classification Tree Analyses (Breiman et al., 1984), Artificial Neural

144   Network (Ripley, 1996), and Random Forest (Breiman, 2001) methods.

145   Pseudo-presence/absence points were randomly generated across the study area and classified as presence or

146   absence points based on their position inside or outside the species extent of occurrence, generated as a

147   minimum convex polygon from our detailed distribution data. Multicollinearity among predictors was

148   reduced by discarding those with variance inflation factor higher than five (Belsley, 1991). Each independent

149   model was projected into the study area under current climatic conditions and three-fold cross-validated by

150   calculating the true skill statistic (TSS) (Allouche et al., 2006). Finally, we generated a single consensus

151   model of current suitability by calculating the TSS-weighted sum of the independent models. Future climate

152   suitability was predicted by projecting the models into future climatic conditions across the study area. All

153   the available scenarios of future (2050) climate from CMIP5 were utilized for projecting the models.

154   Suitability variation over time was calculated as the difference between future and current suitability and

155   assigned to the observed plant stands on the basis of their location.

156

157   *2.4. Association between observed and expected patterns*

158   For each variable, we tested the linkage between the observed and the expected patterns of responses by

159   adopting a null-model approach (Gotelli and Graves, 1996; Gotelli and Ulrich, 2012; Harvey et al., 1983).

160   First, we quantified the observed correlation between measured values and expected suitability variation in

161   the same sites (r_{obs}) by calculating the Pearson r. Second, we generated in *R* (R Core Team, 2018) (as all the

162   other analyses) 30,000 random permutations of the measured values and calculated the simulated correlation

163   with the expected suitability variation for each permutation (r_{sim}). Third, we calculated the probability of the

164   null hypothesis that the observed correlation was drawn at random from the distribution of the simulated

165   correlations (Gotelli, 2000). Finally, in order to control the familywise error rate due to multiple

166   comparisons, we corrected our *p* values adopting the approach proposed by Benjamini & Hochberg (1995).

167   These corrected *p* values (p_{corr}) measure the level to which the suitability variation (corresponding to the

168   expected response) due to climate change explains the actual responses observed in the different stands.

169   In addition, we tested whether the observed responses follows a general and simple geographic pattern. In

170   particular, we tested the hypothesis of a latitudinal (equator-to-pole) or altitudinal (low-to-high elevation)

171   range shift. To do this, we adopted the same approach used for testing the linkage between the observed and

172   the model-based expected patterns of responses. In particular, we contrasted each measured variable with the

173   stand latitudes and altitudes. We quantified the correlation between the measured variable and the

174   latitude/altitude, calculated the probability that the observed correlation comes randomly from the simulated

175   correlations after 30,000 random permutations, and corrected our p values with the Benjamini & Hochberg

176   (1995) approach. As a result, we obtained an estimation of the extent to which climate change effects can be

177   explained as a simple geographic gradient.

178

179   **3.   Results**

180   Overall, we recorded 1330 plants within the known distribution of *W. mirabilis* in northern Namibia. These

181   plants are clustered in 12 distinct stands, which are scattered across the central part of the known range at

182   elevations between 806 and 991 m above sea level (Fig. 1B). Our local team members, who know the area

183   and the species intimately from years of herding goats and cattle, could not point out any more locations than

184   the ones we recorded during the current study. We are thus confident that the plants that we recorded or

185   observed, and the resulting extent of occurrence, represent the majority of plants in this northern-Namibian

186   sub-range. The surface area of each recorded stand varied from 2000 – 825,000 m^2 and the number of plants

187   per stand varied between four and ~400. The extent of occurrence of welwitschia in the area covers about

188   215 km^2 and the inter-stand distance varied from 1.8 to 30 km (Fig. 1B). This is a markedly smaller area than

189   the distribution map previously published for the species in northern Namibia (Bubenzer et al., 2004) but a

190   significant improvement of the existing, but unpublished knowledge of plant location in the area.

191   The available climatic models revealed that the realized thermal niche of *W. mirabilis* in northern Namibia is

192   expected to become completely unavailable within its current extent of occurrence (Fig. 2A). In particular,

193   annual mean temperature within the stands will rise about 1.5 – 2.5 °C, with strong variations among the

194   different scenarios. In contrast, the total annual precipitation will likely remain relatively stable (Fig. 2B),

195   with small reductions or increments forecasted by different scenarios.

196

3.1. *Observed variation of plant parameters*

198 The most common class of health condition was 'average', with 50% of all the plants and a range between

199 32% and 74% across individual stands being found in this status. Plants in 'poor' condition were 32%

200 (range: 11-50%), but only 10% of all plants were in a 'good' condition (range: 0-30%). Seven percent of all

201 plants were dead (range: 0-30%) and 56% (range: 10-90%) had cones. Not all individuals could be sexed, but

202 among those that were, 56% were males, with a sex ratio (males/females) ranging between 0.6 – 1.7 across

203 stands. Stem length and stem width were highly variable, ranging from 2 to 100 cm (18.8 ± 14.1 cm; range:

204 10-33 cm) and from 0.3 and 55 cm (10.3 ± 9.8 cm; range 4.6-22 cm), respectively. Leaf length varied from

205 almost 0 cm (completely browsed plants) up to 93 cm (18.7 ± 13.4; range 11-40 cm).

206

3.2. *Expected pattern of species response*

208 The current climatic suitability for *W. mirabilis* is especially high in the eastern half of its extent of

209 occurrence (Fig. 3A). Some areas to the population's south, as well as a northwest-trending band to the north

210 are also predicted to be highly suitable (Fig. 3A), although plants have never been recorded from these areas

211 before, nor did we find any. Our models further predict that, in the future, the most suitable areas will occur

212 to the northwest of the current extent of occurrence (Fig. 3B). As a result, the plants within in the current

213 extent of occurrence would all experience a reduction of climatic suitability (Fig. 3C) and may thus respond

214 negatively. All the recorded stands are expected to face suitability reductions in the years to come, with

215 variable intensities between almost no reduction and complete reduction. Even those areas that are currently

216 suitable but where the species has not been recorded (Fig. 3A) will similarly experience reductions in

217 suitability (Fig. 3C). In contrast, positive responses may occur in the future suitable area to the northwest of

218 the current extent of occurrence (Fig. 3C).

219

3.3. *Observed* vs *expected patterns*

221 Stronger predicted reductions of climatic suitability in the stand sites are associated with lower plant health

222 condition, fewer plants with cones, and an increased number of dead plants. More specifically, the proportion

223 of plants in poor condition in each stand increases with the reduction of suitability (Fig. 4A). In contrast, the

224 proportion of plants in average and, marginally, of plants in good condition decreases as suitability variation

225 decreases (Fig. 4B and 4C). The proportion of plants with cones (i.e. a proxy of the potential population

226 recruitment) is lower in stands where stronger reductions of climatic suitability are expected (Fig. 4D). At

227 the same time, the proportion of dead plants (i.e. population mortality) is negatively correlated with the

228 expected variation of climatic suitability (Fig. 4E). However, neither the number of plants per stand (i.e.

229 population size) (Fig. 4F) nor plant body size (Fig. 4G, 4H, and 4I) is correlated with the suitability variation.

230 The observed geographic pattern of species response does not follow any simple geographic gradient.

231 Indeed, the latitude of welwitschia stands is not correlated with any measured variable (Table 1). Similarly,

232 altitude and the measured variables are not correlated (Table 1). Overall, no latitudinal or altitudinal variation

233 is occurring as a response to climate change.

234 **4. Discussion**

235 The results we obtained are coherent with our main hypothesis that the observed pattern of population

236 conditions of welwitschia trees in northern Namibia can be explained as consequences of climate change.

237 Differently, the secondary hypothesis that the geographic pattern of this response to climate change follows a

238 latitudinal or altitudinal gradient is not verified. These outcomes strongly suggest that the ongoing climate

239 change can cause significant alterations to welwitschia populations in the area, can produce important

240 changes (i.e. shifts, contraction) in the local species distribution, and can represent a not negligible threat for

241 the long term conservation of the species. On the other hand, these outcomes also evidence that the

242 potentially serious impact of climate change on this species would be undetected if searched with an

243 approach base on the simple assumption of poleward/upwards range shift.

244 Inter-stand variations of different population parameters are correlated to change in climatic suitability and

245 can be interpreted as effects of climate change. In this light, the high correlation between the variation of

246 climatic suitability and plant conditions can support a link among climate change, the distribution of plants

247 and the variation of plant health with observed increment of individuals in poor conditions and the reduction

248   of plants in average or good conditions. The loss of climatic suitability can be also put in relationship to the

249   population trends, by affecting recruitment (as suggested by the observed reduction of plants with cones) and

250   mortality (as suggested by the observed increase of dead plants). Even if we measured static parameters of

251   population condition, the pattern of these static measures is coherent with the dynamism of an ongoing range

252   shift from areas currently suitable to areas that will be suitable in the future. Indeed, negative population

253   dynamics, which can be detected as bad population conditions (i.e. scarce plant health, low reproduction

254   potential, high mortality), are typically associated with the trailing edge of a shifting species distribution. The

255   surprisingly clear relationships between observed and expected patterns could indicate one of the very first

256   cases of documented effects of climate change on austral species (Jack et al., 2016).

257   The higher proportion of dead plants, which suggests an increased mortality, coupled with the lower

258   proportion of plants with cones, which suggests a reduced population recruitment, in areas that suffer

259   stronger effects of climate change, is particularly worrisome because can imply a global negative trend in

260   population size, potentially driving to the local extinction of entire welwitschia stands. In addition, it is worth

261   noting that the linkage between mortality and suitability reduction could be even underestimated by our

262   approach because there are no ways to discriminate plants dead long time ago (i.e. not related to climate

263   change), from recently dead plants. Indeed, the inclusion of old deaths in our dataset could attenuate the

264   climate-related signal. The lack of linkage between suitability variation and plant number could mean that

265   the combination of increased mortality and reduced recruitment has not caused a reduction of population size

266   until now. Similarly, the absence of association between the plant body size and climate change suggests that

267   the altered rates of recruitment and mortality did not modified the age class structure of the stands.

268   Nevertheless, population dynamics of long living organisms can be slow and become evident only in the

269   long term.

270   As mentioned above, the visual estimation of the plant condition can be considered a rough estimation of

271   chlorophyll content of the leaves and thus of the plant photosynthetic efficiency. Alterations of

272   photosynthesis is a well-known effect of environmental stress (Chaves, 1991; Munns et al., 2006). Heat

273   stress in particular inhibits photosynthesis in tropical and subtropical plants (Larcher, 1995; Salvucci and

274   Crafts-Brandner, 2004). This effect can be stronger in arid environments, where the water shortage can

275   hamper the leaf temperature mitigation (Idso et al., 1982). On the other hand, other studies (Shuuya, 2016)

276 evidenced that, in other populations of *W. mirabilis*, rainfall is followed by an increase in condition. As a

277 result, we can hypothesize that the observed worsening of plant condition is associated to the complex

278 interaction between the significant increment of temperature, which is the main climate alteration expected in

279 the area (Fig. 2), and the constant but limited water availability in the desert environment. Anyway,

280 specifically designed experiments would be needed to tease apart the different possible forces that could

281 cause the observed responses.

282 Our results confirm the expectation of previous works on the potential impacts of climate change on

283 welwitschia populations in northern Namibia. The study of Bombi (2018), carried out at the national level

284 and at a much coarser spatial resolution, predicted a general reduction of climatic suitability for *W. mirabilis*

285 and suggested potential effects on population recruitment with consequent influences on population

286 structure. At the same time, the author evidenced that living welwitschia trees would have been probably

287 able to cope with the expected climate suitability reduction. On this point, the correlation we observed

288 between increased mortality and predicted influence of climate change would indicate a more worrisome

289 scenario, with a progressive degradation of the plant health and the potential long-term reduction of the

290 population size. This evidence should encourage specific management plans for northern Namibian

291 populations and take into consideration climate change among the conservation issues.

292 Quantitative data on the plant physiological performances (e.g. leaf growth rate, photosynthesis level, water

293 use efficiency) are required to obtain a more detailed picture of the occurring alterations and to clarify the

294 possible mechanistic linkage with climatic stress. Repeated measures of physiological parameters in different

295 sites would make possible following plant responses over time. The activation of programs for the long-term

296 monitoring of the species in the region would be particularly helpful, allowing critical situations to be

297 detected at early stages and planning effective recovery measures. Obviously, activities of long-term

298 monitoring in this remote area would be difficult and would require the involvement of local communities as

299 well as the provision of significant resources by local and international agencies aimed at the conservation of

300 desert ecosystems in Namibia.

301 Despite the great interest on *W. mirabilis*, which is considered a living fossil, for its morphological and

302 evolutionary uniqueness (Khoshoo and Ahuja, 1963), and an iconic species of the Namib desert, for its key-

303   role in this ecosystem, several aspects of the species distribution and biology are still to be clarified for a

304   science-based conservation strategy. First, the real level of geographic and genetic isolation of the different

305   subranges should be verified in order to identify intra-specific evolutionary and conservation units. Second,

306   an effort to census and make available the current knowledge on species distribution, demography, and

307   conservation should be undertaken. Indeed, a significant amount of this information is probably pulverized

308   into a plethora of unpublished datasets and field observations. Third, an analysis of the climate change

309   impacts should be extended to the other subranges and a science-based assessment of the conservation status

310   should be made at local and global level. This set of measures could significantly contribute at planning

311   conservation measures for the species that are effective on the long term.

312   The geographic pattern of response we observed in welwitschia is more complex than the simple

313   poleward/upward shift that was often observed for other species (Parmesan et al., 1999; Root et al., 2003;

314   Thomas, 2010). In the case of *W. mirabilis* populations of northern Namibia, the observed pattern of

315   population conditions, which can represent a response to climate change, follows local contingencies rather

316   than a simple latitudinal or altitudinal trend (Table 1). This could be associated with the small scale of the

317   study but is also in agreement with previous large-scale studies. These studies pointed out that specific

318   responses to climate change can be divergent (Fei et al., 2017) and that assuming a simplified

319   poleward/upward species movement can bring to underestimate climate change impacts (VanDerWal et al.,

320   2012). In our specific case, the linkage between climate change and population conditions, which is

321   suggested by our results, would have been completely undetected with a simplified, but frequently used

322   approach based on the assumption of poleward/upward shifts.

323   The comparison of the expected pattern of response to climate change, as predicted by suitability modeling,

324   with the observed patterns of population conditions, as measured in the field, appeared as a powerful approach

325   for detecting impacts on wild species. This approach, proposed by Bombi et al. (2017), allowed to indicate

326   climate change as one of the most probable drivers of the geographical variation of population features we

327   observed in the field. This study underlines the importance of considering species responses to climate change

328   as the emergent property of the different effects on individual populations. At a higher biodiversity level,

329   ecosystem responses to climate change can be considered as the emergent property of the effects on individual

330   species. Such a hierarchical relationship provides direction for the application of spatial explicit approaches

331 such as the one used in this study, to multiple species and across diverse ecosystems. In this light, it can be

332 advocated the setting of a large scale program for the identification of sentinel species of climate change

333 effects, which allows to detect, estimate, and follow the climate change impacts on biodiversity and to improve

334 the long-term conservation of species at the ecosystem level.

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491   Table 1. Correlation between the measured variables and the stand latitude and altitude.

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|	Latitude		Altitude	
	r_{obs}	p_{corr}	r_{obs}	p_{corr}
Proportion of plants in poor conditions	-0.342	0.496	0.293	0.332
Proportion of plants in average conditions	-0.083	0.375	0.039	0.33
Proportion of plants in good conditions	0.258	0.425	-0.418	0.463
Proportion of plants with cones	0.425	0.151	-0.492	0.201
Proportion of dead plants	0.275	0.356	-0.048	0.066
Number of plants	-0.669	0.06	0.096	0.461
Stem length	0.521	0.26	-0.131	0.461
Stem width	0.542	0.177	-0.279	0.225
Leaf length	-0.243	0.102	0.573	0.3765

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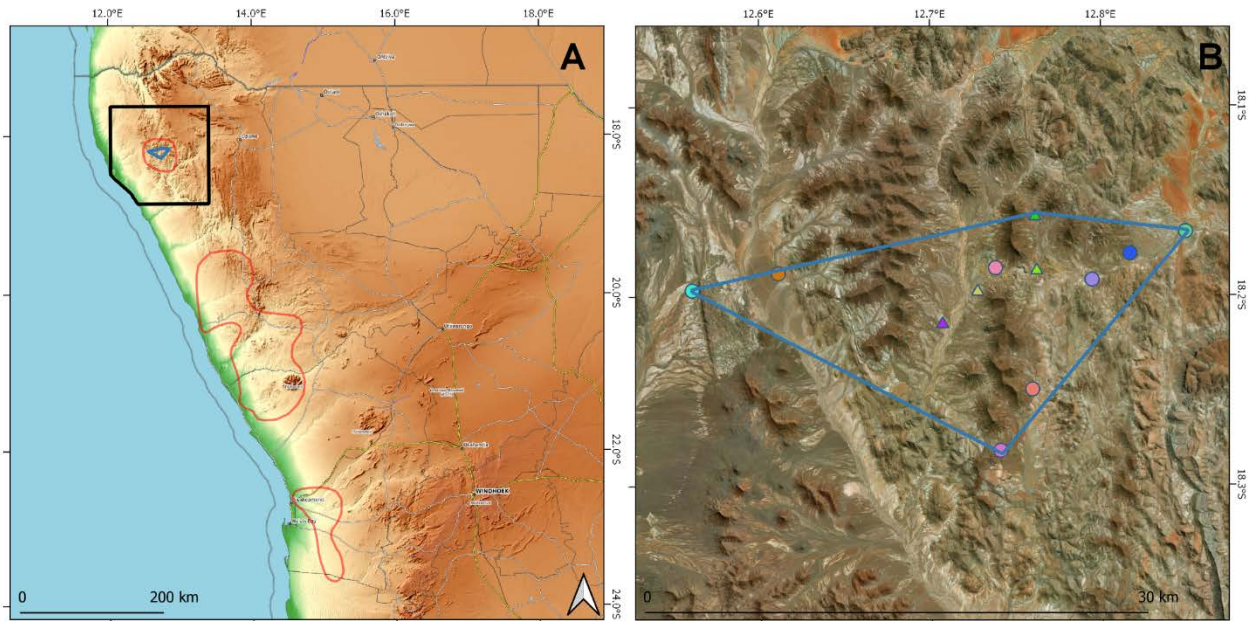
Figure 1. Distribution of *Welwitschia mirabilis* in Namibia and location of the study area (A) and position of detected plant stands inside the observed extent of occurrence (B). In A, the black polygon indicates the study area and the red polygons show the known species distribution. In B, the colored triangles are the plant locations that were known before our study and the colored circles are the new occurrences. In both the maps, the blue polygons represent the boundaries of the observed extent of occurrence in Northern Namibia.
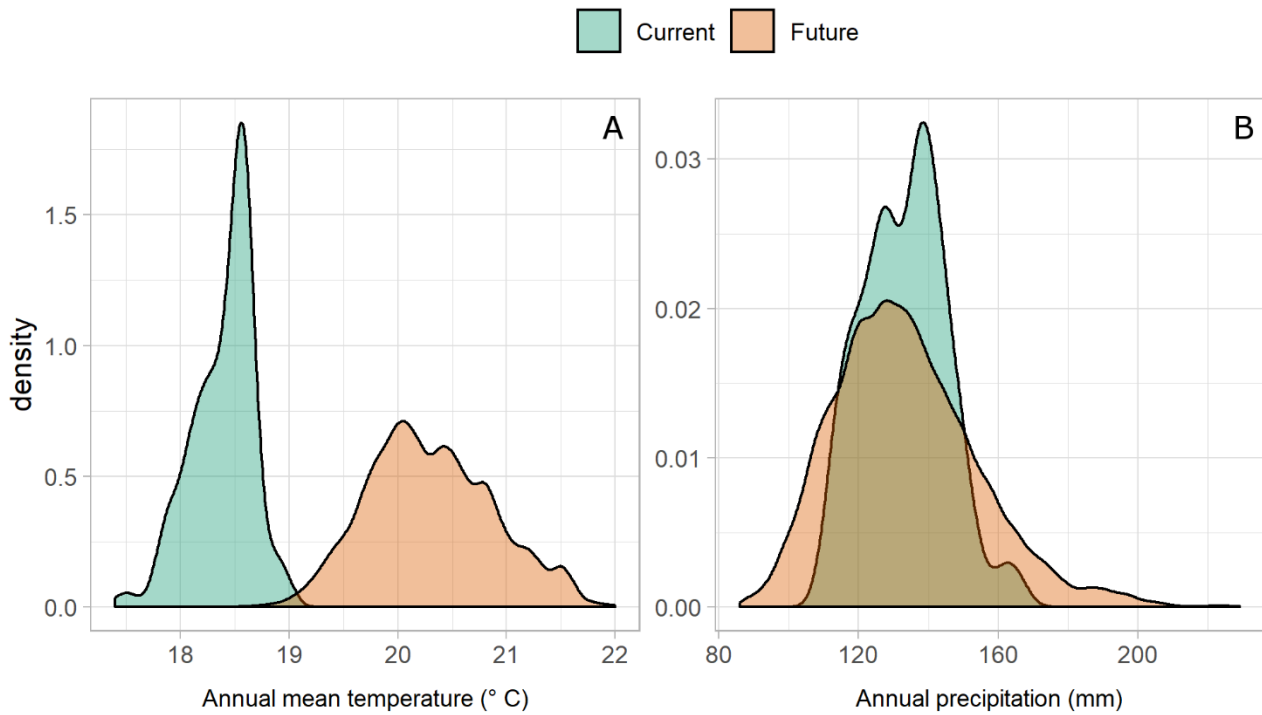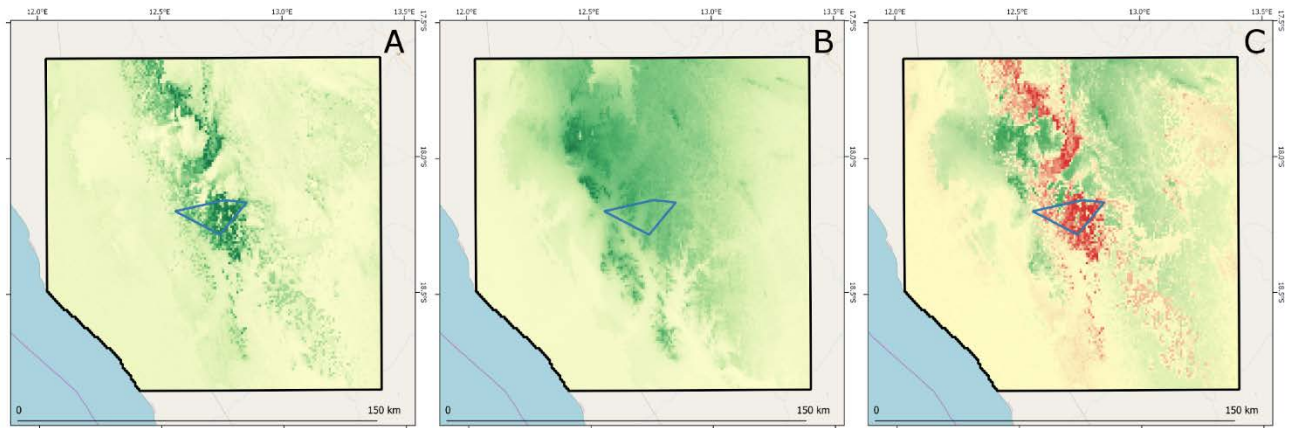
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508   Figure 2. Distribution of current climatic data (i.e. realized climatic niche of *Welwitschia mirabilis*) in the

509   extent of occurrence (in green) and expected future values (in orange) for annual mean temperature (A) and

510   annual precipitation (B).

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Figure 3. Climatic suitability for *W. mirabilis* in the study area under current (A) and future (B) climatic conditions (green shades indicate growing suitability). Expected suitability variation from climate change (C) (red and green shades indicate negative and positi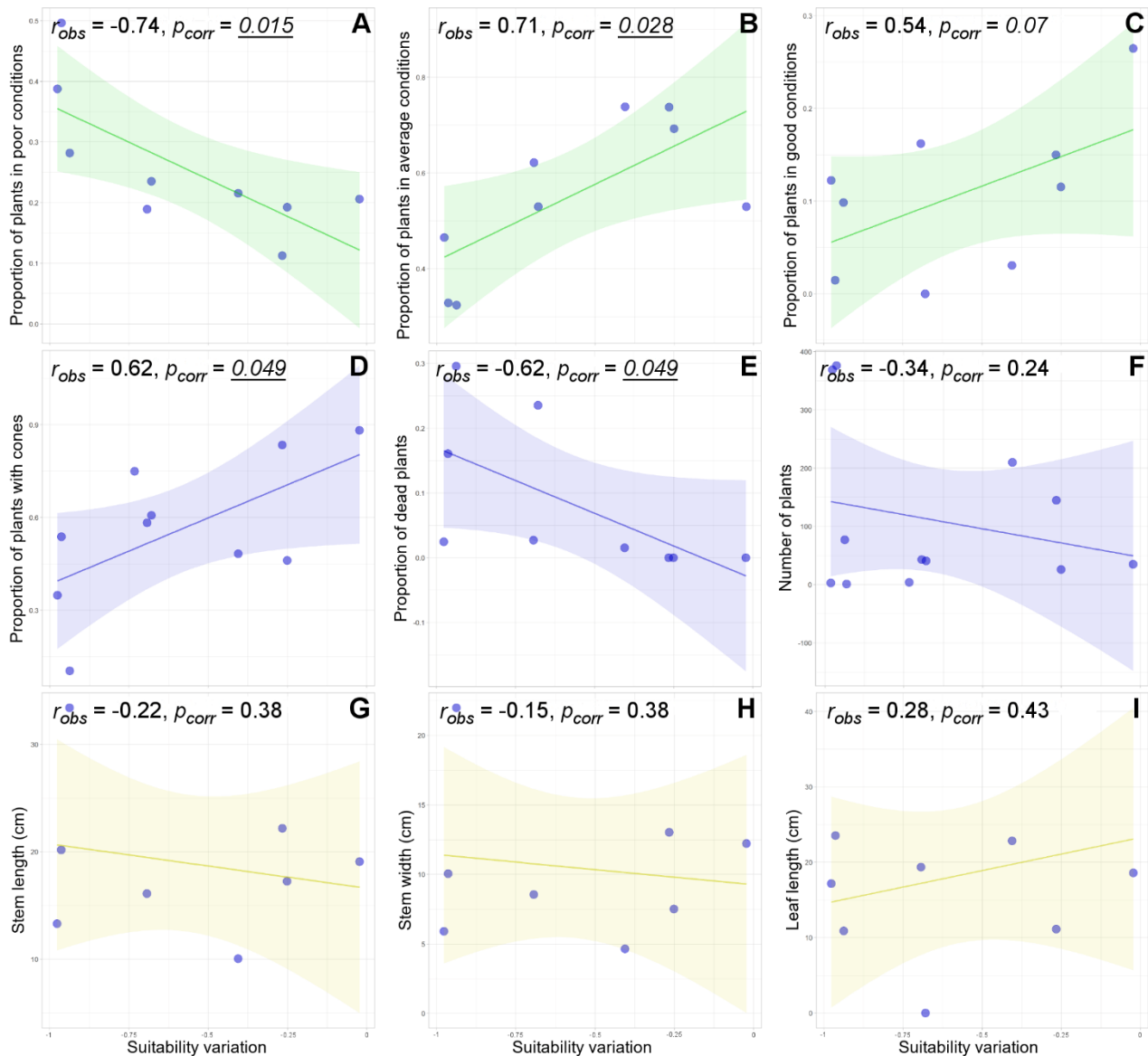ve variations respectively). In all the maps, black polygons indicate the study area and the blue polygons represent the boundaries of the observed extent of occurrence in Northern Namibia.

Figure 4. Population features as functions of the expected suitability variation in the stands. In green (first row), features related to plant health condition: proportion of plants in poor (A), average (B), and good (C) conditions. In blue (second row), features related to potential population trends: proportion of plants with cones (D) and of dead plants (E), and number of plants per stand (F). In yellow (third row), features related to plant body size: stem length (G) and width (H), and leaf length (I). In all the plots, blue dots are values for plant stands. Note that suitability variation values (X-axis) are all negative; thus, the reduction of suitability increases from right to left.