European plants lagging behind climate change pay a climatic debt in the North, but are favoured in the South

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1 **European plants lagging behind climate change pay a climatic debt in the**

2 **North, but are favored in the South**

3

4 **Short title:** Climatic debts and bonuses in European plants

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22   **Abstract:**

23   **For many species, climate change leads to range shifts that are detectable, but often**

24   **insufficient to track historical climatic conditions. These lags of species range shifts behind**

25   **climatic conditions are often coined "climatic debts", but the demographic costs entailed**

26   **by the word "debt" have not been demonstrated. Here we used opportunistic distribution**

27   **data for ~4,000 European plant species to estimate the temporal shifts in climatic**

28   **conditions experienced by these species and their occupancy trends, over the last 65 years.**

29   **The resulting negative relationship observed between these two variables provides the**

30   **first piece of evidence that European plants are already paying a climatic debt in Alpine,**

31   **Atlantic and Boreal regions. In contrast, plants appear to benefit from a surprising**

32   **"climatic bonus" in the Mediterranean. We also find that among multiple pressures faced**

33   **by plants, climate change is now on par with other known drivers of occupancy trends,**

34   **including eutrophication and urbanization.**

Introduction

Climate change is recognized as a major threat for biodiversity (Sala *et al.* 2000). Species have two main ways to persist under such change: they can track their climatic optimum in space (geographic range shift) or they can respond adaptively to survive and reproduce in a altered environment (Chevin *et al.* 2010), i.e. modify their climatic optimum. Concerns about the capacity of species to achieve one or the other quickly enough have increased (Parmesan 2006; Chevin *et al.* 2010; Hoffmann & Sgrò 2011), with many studies showing that living organisms are currently moving poleward and upward in response to climate warming (Parmesan 2006; Kelly & Goulden 2008; Devictor *et al.* 2012; Lenoir *et al.* 2020). Yet, most studies so far have shown that range shifts are rarely as fast as climate change (Menéndez *et al.* 2006; Devictor *et al.* 2012; VanDerWal *et al.* 2013; Lenoir *et al.* 2020), i.e. climate variables move faster through space than most species do. This lag of species movements behind climate change is often coined a "climatic debt" (Devictor *et al.* 2012; Monsinjon *et al.* 2019; Lenoir *et al.* 2020). It can be evidenced by a temporal change in the so-called "climatic niche" of a species, as measured by the average of one or several climatic variables throughout its range (VanDerWal *et al.* 2013), hereafter "species climatic indices" (SCIs).

The consequences of species shifting their ranges slower than the movement of suitable climate conditions, however, remain to be quantified. First, the resulting temporal change in the climatic conditions experienced by a species need not necessarily translate into a "debt": most species can and do also respond to climate change via adaptive plastic or evolutionary trait changes, which could be sufficient to sustain populations despite changing climatic conditions (Hoffmann & Sgrò 2011), albeit the most recent meta-analysis to date suggests otherwise (Radchuk *et al.* 2019). Thus, to verify the existence of a true climatic debt, one needs to demonstrate that the spatial lag of species behind changing climate conditions results in decreased individual fitness or population growth; this has not yet been done. Second, most

60   species face additional threats beyond climate change, e.g. habitat loss or pollution, which may

61   be the dominant drivers of current species loss (Maxwell *et al.* 2016). Thus, a climatic debt,

62   should it exist, might be of little consequence for population trends compared to other drivers.

63   However, few studies so far have compared quantitatively the impact of different drivers across

64   a large number of species, and none has included the climatic debt.

65   Costs associated with the putative climatic debt remain poorly investigated likely because

66   the climatic debt concept has been developed at the community level mostly (Bertrand *et al.*

67   2011; Devictor *et al.* 2012), while cost estimation is easier at species level, e.g. via an

68   assessment of species persistence. By shifting the concept of climatic debt from community to

69   species level, one can correlate delayed spatial responses (i.e. temporal trends in SCIs) with

70   species persistence. Under climate warming, if both species movements and adaptive responses

71   are insufficient, we expect (1) an increase in the temperature SCI of a given species over time

72   (limited spatial response) and (2) a negative relationship between the temporal trend in SCI for

73   temperature and the species persistence (limited adaptive response, Radchuk *et al.* 2019). The

74   latter observation only is suggestive of costs at individual and population levels, i.e. a climatic

75   debt. Alternatively, uncorrelated SCI trends and species persistence would indicate an absence

76   of climatic debt, which could be explained by adaptive responses buffering limited spatial

77   responses or by species insensitivity to temperature (Rodríguez-Sánchez *et al.* 2012). This logic

78   applies similarly to other climatic variables beyond temperature, such as precipitation.

79   Here we examine the temporal shifts in the climatic conditions experienced by a species

80   throughout its range, as measured by SCI trends, and occupancy trends, for more than 4,000

81   European plant species over the last 65 years, using a large dataset of opportunistic distribution

82   records. These two elements allowed us to verify the existence of a climatic debt, which we

83   estimate via the relationship between occupancy and SCI trends, and to compare its strength to

84   other potential drivers of occupancy trends besides climate change via a trait-based approach.

Methods

Data collection; trends in SCIs and species occupancy

Plant database

We focused on the most common vascular plant species in geographical Europe, i.e. with at least 500 records in the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org) between 1950 and 2014 within a rectangle bounded by longitudes [-13°, 34°] and latitudes [34°,75°]. We downloaded all species sightings during the time period from 1951 through 2014, excluding 1950 as this year contains data not precisely dated, but corresponding to the mid-twentieth century. The DOIs associated with the extraction are presented in the Supplementary methods. We considered only records from the European mainland, stopping at 34° of longitude because there were too few data to the East of this meridian (Fig. S1). Note that the area also includes the western part of Turkey. This yielded a dataset containing 111,549,494 occurrence records, characterized by a species name, a location and a date. Of these, we analyzed temporal trends in species climatic indices (SCIs) and occupancy only for the species observed in at least 20 years between 1951 and 2014 and with at least one record between 1951 and 1980. We removed crop species and considered invasive species separately (see Supplementary methods), because the drivers of their occupancy trends are likely different from those for non-invasive species. This selection resulted in 4,120 native and naturalized plant species (listed in Table S1), plus 58 invasive species.

Bioclimatic variables

Climate change is not limited to increases in annual mean temperature; hence we characterized the climatic conditions with three bioclimatic variables related to temperature and three bioclimatic variables related to precipitation, because temperature and precipitation are strong predictors of plant distribution (Franklin *et al.* 2013). We used previously published European time series (Fréjaville & Benito Garzón 2018) to extract annual mean temperature,

110   maximum temperature of the warmest month, minimum temperature of the coldest month,

111   annual precipitation, precipitation of the wettest month, and precipitation of the driest month.

112   These bioclimatic variables are the same as in Worldclim (bio1, 5, 6, 12, 13, 14) but with annual

113   data. For computational reasons we aggregated 1kmx1km raster cells, which decreased spatial

114   resolution from 1 to about 100km² (~10km×10km).

115   *Calculation of annual species climatic indices and their temporal trends*

116   Species climatic indices (SCIs) are often calculated as the average of a climatic variable,

117   e.g. temperature, across a species range (Devictor *et al.* 2012). However, the heterogeneity of

118   opportunistic datasets can bias this index (Loiselle *et al.* 2008; Beck *et al.* 2014). Because we

119   are interested in inter-annual comparisons, we corrected a temporal bias in the spatial

120   distribution of sampling pressure: the average latitude and longitude of the GBIF records both

121   decrease significantly with time. To reduce such bias we defined annual SCI as the mean

122   climatic variable of all 100km² cells occupied by a given species, while weighting the

123   contribution of each cell by the ratio of the number of records of this species on the number of

124   records of all plant species for the given year and grid cell. Such method enables estimations of

125   the SCIs that are more independent from the sampling pressure than a weighting by the number

126   of records of the given species only (Fig. S2).

127   Following the method above, we calculated one SCI for each bioclimatic variable, species

128   and year. We then assessed the temporal trend in each SCI and species separately, using the

129   following linear model:

130   $$SCI_k = \mu + \beta \times year_k + \varepsilon_k \qquad (1)$$

131   where SCI_k is the species climatic index of year k, μ is the grand mean (intercept), β is the year

132   effect and ε_k is an error term (independent and identically distributed, following $N(0,\sigma^2)$).

133   Observations (SCI_k) are weighted by the square root of the number of grid cells included in

134   their calculation for each year, which gives greater weight to years with more data. We finally

135   estimated the phylogenetic signal in SCI trends (Supplementary Methods).

136   *Occupancy trends*

137   To model the temporal occupancy trends, we first discretized the dataset spatially and

138   temporally, to define areas occupied or not by a species for a given time period. Such

139   discretization then allowed us to estimate variation in occupancy probability among time

140   periods by taking the sampling pressure into account. As for SCI calculation, we used a grid

141   cell of about 10km×10km to discretize the dataset spatially, and we aggregated records

142   temporally by years. For each year, a grid cell is considered as visited by at least an observer if

143   it contains at least one plant species record. Non-visited cells are discarded. A visited cell is

144   considered as occupied by a species if it contains at least one record of the given species in the

145   given year, and unoccupied otherwise. We obtained a dataset composed of annual presences

146   and pseudo-absences in each 10km×10km grid cell.

147   Before analyzing the data, we discarded all grid cells visited only one year, to improve

148   occupancy estimations by decreasing the confusion between grid cell and year effects (Isaac *et*

149   *al.* 2014). To save computing time, for each species we removed non-informative grid cells, i.e.

150   cells with no record of the species over the whole study period. Finally, to estimate a yearly

151   occupancy probability (*p*), we explained remaining presences and pseudo-absences for each

152   species separately using the following binomial generalized linear model with a logit link:

153
$$\log\left(\frac{p_{ik}}{1-p_{ik}}\right) = \mu + \beta_1 \times year_k + \beta_2 \times \log(SL_{ik}) + \varphi_i \qquad (2)$$

154   Where p_{ik} is the occupancy probability of grid cell i for year k, μ is the intercept of the model,

155   β_1 is the year effect (i.e. the occupancy trend), and φ_i a random grid cell effect. Finally, β_2 is

156   the effect of the logarithm of the species list length (SL_{ik}, i.e. the number of species observed

157   in a given grid cell and year), used as a proxy for the sampling pressure (Isaac *et al.* 2014).

158   Those models were implemented using the R package *glmmTMB* (Brooks *et al.* 2017). We

159   estimated occupancy trends for all 4,120 native and naturalized species, as well as for the 58

160   invasive species. This latter step allowed us to verify that occupancy trend estimates were large

161   and positive for invasive species (Fig. S3), confirming that the data and statistical methods to

162   estimate occupancy trends yield results consistent with known species trends. As for SCI trends,

163   we estimated the phylogenetic signal in occupancy trends (Supplementary Methods).

164   *Additional potential drivers of occupancy trends*

165   To compare the strength of the climatic debt with that of other potential drivers of occupancy

166   trends, we tried to include all additional drivers in the analysis of the relationship between

167   occupancy trends and SCI trends (see below). We used the plant and global change literature to

168   identify potential drivers of plant trends, which we took into account via species traits: historical

169   climatic niche (Martin *et al.* 2019), lifespan (Martin *et al.* 2019), habitat affinity (Aronson *et*

170   *al.* 2014; Buse *et al.* 2015), nitrophily (Sala *et al.* 2000; Bobbink *et al.* 2016), moisture

171   preferences (Moeslund *et al.* 2013) and pollinator dependency (Biesmeijer *et al.* 2006). We

172   detail all calculations for these traits in Supplementary Methods.

173   Species traits, SCI and occupancy trends are available in Table S1.

174   ***Evidencing the climatic debt: relationship between SCI trends and occupancy trends***

175   *Analysis at continental scale*

176   As explained above, a climatic debt can be revealed by a negative relationship between

177   species occupancy trends and SCI trends. To assess this relationship between SCI trends and

178   occupancy trends, while controlling for the species traits cited above, we used linear models.

179   We first checked the correlations among the six SCI trends and six historical climatic niche

180   indices. We noticed high correlations ($r > 0.7$) among historical temperature indices, among

181   historical precipitation indices, among SCI trends related to temperature and among SCI trends

182   related to precipitation (Fig. S4). In order to avoid multicollinearity issues, we retained only the

183   two most used and integrative bioclimatic variables, both for the historical climatic niche and

184   for SCI trends: annual mean temperature and annual precipitation.

185   In summary, we considered the following correlates of occupancy trends: SCI trends related

186   to annual mean temperature and annual precipitation, historical climatic index related to annual

187   mean temperature and annual precipitation, nitrophily and moisture Ellenberg indicator values,

188   pollinator dependency, habitat affinity and lifespan. To be able to compare the strength of

189   relations across explanatory variables, we scaled them before using the Phylogenetic

190   Generalized Least Squares regression, except for habitat affinity and lifespan, as we wanted to

191   extract the effect on the intercept for the first and as the second is a qualitative variable. We

192   used the *caper* R package (Orme *et al.* 2013) to implement models controlling for phylogenetic

193   signal in the residuals:

194     $\Delta O_{sj} = \mu + \beta_1 \times \Delta SCI_{bio1_s} + \beta_2 \times \Delta SCI_{bio12_s} + \beta_3 \times BCI_{bio1_s} + \beta_4 \times BCI_{bio12_s} + \beta_5 \times$

195     $ME_s + \beta_6 \times NE_s + \beta_7 \times Poll_s + \theta_j + \sum_{i=1}^{h} \beta_{habitat_i} \times Habitat_i + \varepsilon_{sj}$ (3)

196   Where ΔO_{sj} is the occupancy trend of species *s* with lifespan class *j*, μ is the grand mean

197   (intercept), β_1 and β_2 are the slopes of SCI trends, β_3 and β_4 are the effects of historical climatic

198   niche indices, BCI_{bio1} and BCI_{bio12}, related to annual mean temperature and annual

199   precipitation respectively. β_5 and β_6 are the effects of Ellenberg indicator values for moisture

200   and nitrogen respectively. β_7 is the effect of pollinator dependency, θ_j is the qualitative lifespan

201   effect and $\beta_{habitat_i}$ is the effect of affinity to habitat *i*, with six habitat classes ($h = 6$, Table S2),

202   woodland being the reference habitat. Finally, ε_{sj} is an error term, after correction by Pagel's λ

203   value at the likelihood maximum.

204   This model included all species matching the phylogeny and with full trait data ($n = 2,013$).

205   To add the 67 species that were not in the phylogeny but for which all traits were available, we

206   also performed a linear mixed-effect model similar to the phylogenetic regression but including

207   random taxonomic effects of class (φ_c) and of family nested in class (φ_f) instead of a

208   phylogeny:

209      $\Delta O_{sjcf} = \mu + \beta_1 \times \Delta SCI_{bio1_s} + \beta_2 \times \Delta SCI_{bio12_s} + \beta_3 \times BCI_{bio1_s} + \beta_4 \times BCI_{bio12_s} + \beta_5 \times$

210      $ME_s + \beta_6 \times NE_s + \beta_7 \times Poll_s + \theta_j + \sum_{i=1}^{h} \beta_{habitat_i} \times Habitat_i + \varphi_c + \varphi_f + \varepsilon_{sjcf}$ (4)

211   This linear mixed-effect model was weighted by the inverse of the standard errors associated

212   with the occupancy trends.

213   *Analysis by biogeographic region and time period*

214   To examine the spatial variation in climatic debt, we also conducted the same analysis

215   within biogeographic regions. We focused on the five biogeographic regions with at least 1,000

216   species: Alpine, Atlantic, Boreal, Continental and Mediterranean regions. For each region, as

217   for the main analysis, we retained only species with at least 20 years of data.

218   We re-calculated SCI and occupancy trends within each region independently, using the

219   same method as above, but including only plant records from the focal biogeographic region.

220   With these new estimates, we assessed regional climatic debts as the relationship between SCI

221   and occupancy trends, using the same models as in the European analysis (equations (3) and

222   (4)) but removing the random effect of taxonomic class φ_c, to avoid singularities. While SCI

223   and occupancy trends were calculated within biogeographic regions, we considered other

224   species traits as constant throughout Europe.

225   Finally, to confirm that the costs of the shifts in experienced climatic conditions occur only

226   after the acceleration of climate change (1980-2000, Fig. S5) we performed the same set of

227   analyses on the earliest data, as detailed in Supplementary Methods. Results are shown in Fig.

228   S6.

229   *Combining the effects of precipitation and temperature SCI trends to estimate an overall*
230   *climatic debt*

231   To combine the effects of annual precipitation and temperature SCI trends on occupancy

232   trends for each biogeographic region, we multiplied each unscaled effect of SCI trends by the

233   observed change in the corresponding climatic indices. This yielded a measure of the effective

234   cost/bonus due to a given SCI trend, i.e. to the lag of species behind climate change. For each

235   region, we then summed the values of effective cost/bonus for temperature and precipitation to

236   measure the overall climatic debt/bonus over the study period. We also calculated the relative

237   contribution of precipitation and temperature SCI trends to the overall debt/bonus by dividing

238   each by the sum of the absolute values of both.

239   **Results**

240   ***Temporal trends in Species Climatic Indices***

241   During the study period (1951-2014), all SCIs change significantly, in direct relation with

242   climate change. All bioclimatic variables related to temperature and precipitation increase on

243   average over the study area, but with substantial spatial heterogeneity for precipitation (Fig.

244   S5). Consistently with the trends in bioclimatic variables related to temperature, we show that

245   the temperature SCIs increase over time for a large majority of species (Fig. 1). Precipitation

246   SCIs also increase over time on average (Fig. 1, Table S3), but the distribution of precipitation

247   SCI trends is closer to zero, with more numerous negative trends than for temperature SCIs.

248   Temperature and precipitation SCI trends are not significantly correlated (Fig. S4), probably

249   due to the fact that annual precipitation and temperature trends exhibit contrasting spatial

250   distributions (Fig. S5c-d). We also find a significant phylogenetic signal in all SCI trends (Fig.

251   S7).

252
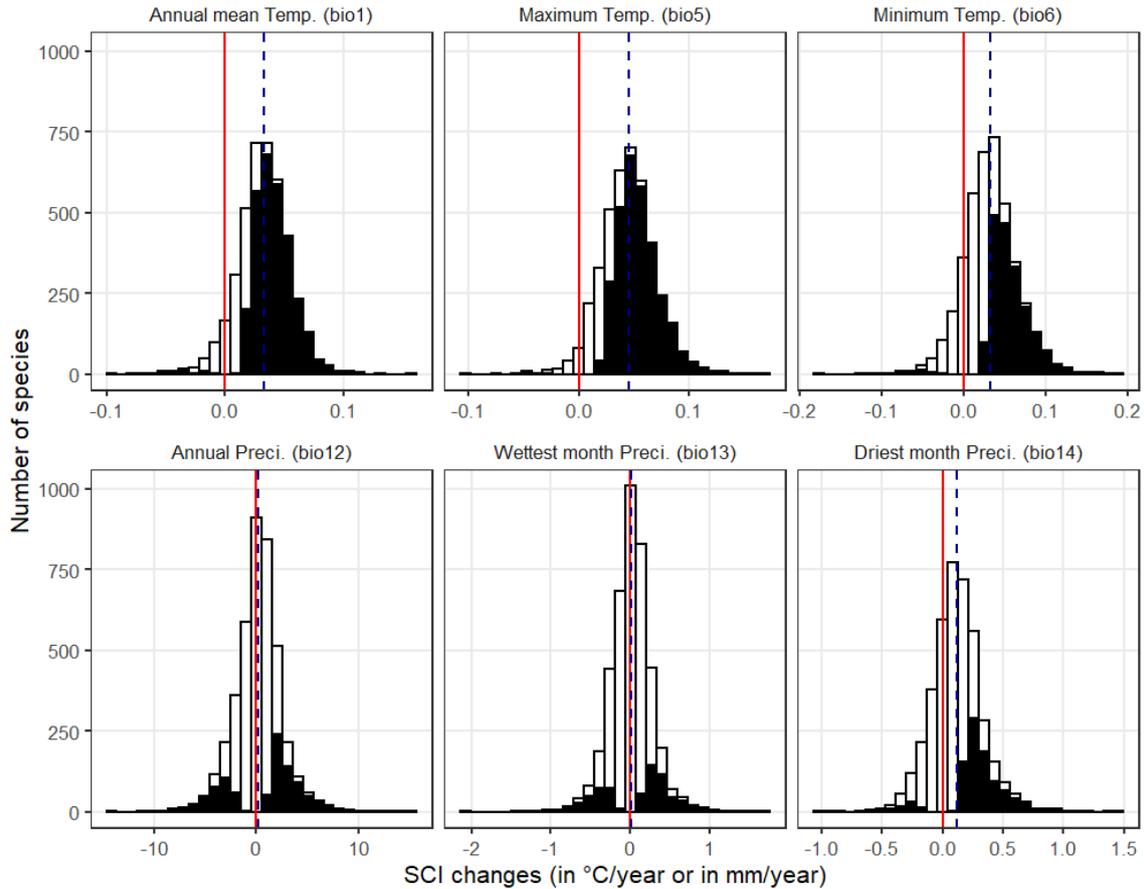
Figure 1: Linear trends in species climatic indices (SCIs) for all species (n=4,120). *The first row shows the trends in temperature SCIs and the second row the trends in precipitation SCIs over time. The WorldClim abbreviation for bioclimatic variables is indicated in parentheses atop each panel. The vertical red line indicates zero (no change across years) while the vertical dashed blue lines show the average values across the 4,120 species. Filled bars represent the count of species with significant trends (p-value<0.05) whereas open bars represent the count of species with non-significant trend (p-value>0.05).*

Occupancy trends and their drivers

The average trend in occupancy over all native and naturalized species is slightly positive: $0.0048 \pm 3.29 \ 10^{-4}$ year^{-1} (mean $\pm$ SE), but the number of species with significant increase in the occupancy estimates (1,721 species, 42%) is comparable to the number of species with significant decline in occupancy (1,519 species, 37%). The average positive trend over all species (Fig. 2a) is mainly explained by the skewed distribution of trends towards positive values, with a couple of species exhibiting strong increases even after exclusion of invasive species (Fig. S3). Furthermore, we find that plant occupancy trends exhibit a strong

phylogenetic signal both before (Pagel's λ = 0.62, p-value<0.01; *n*=2,785) and after (Pagel's λ = 0.45, $CI_{95\%}$ = [0.32,0.57]; *n*=2,013) considering species traits.
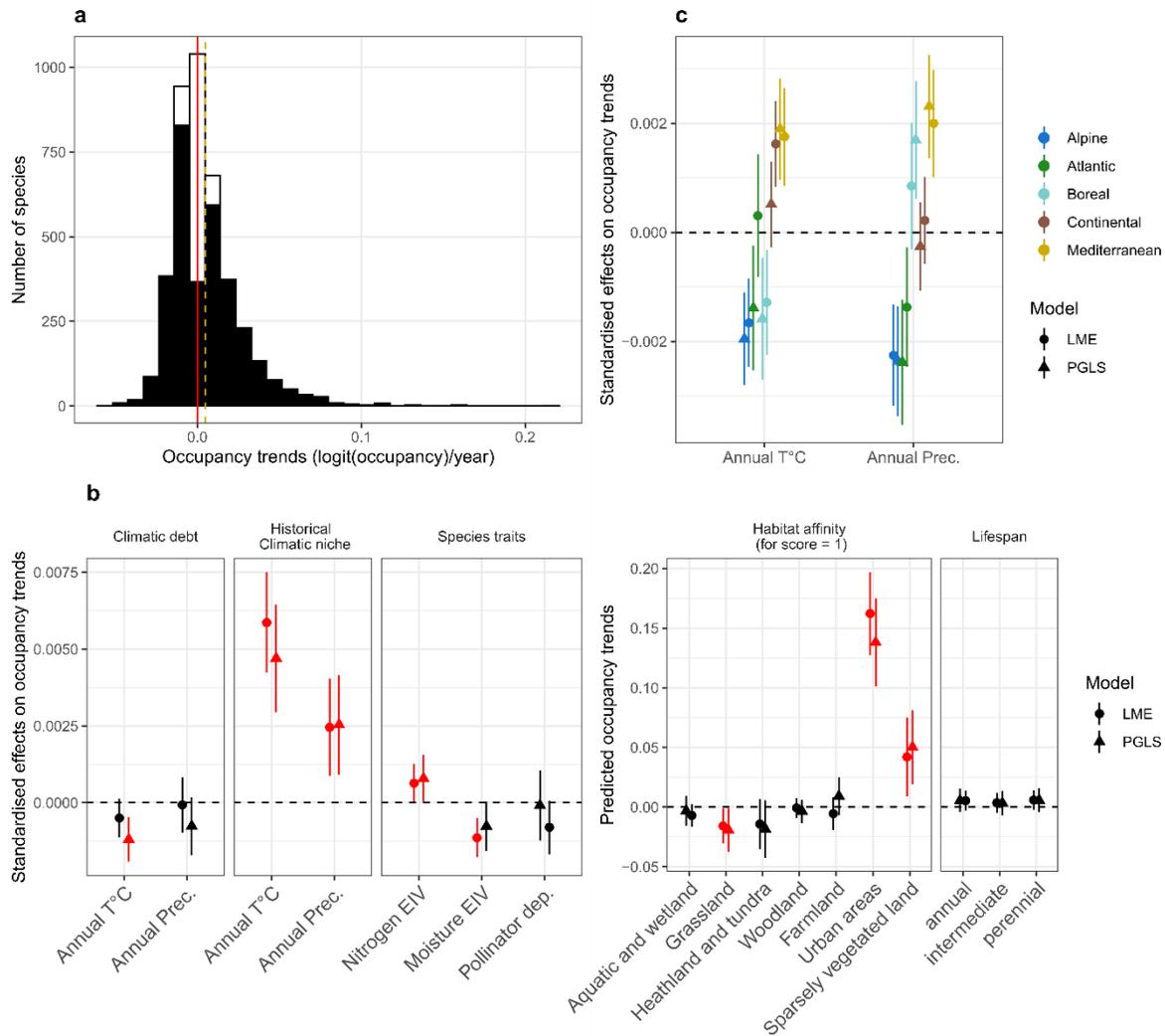
Figure 2: ***Occupancy trends of native and naturalized European plant species and their correlates.*** *(a) Histogram of occupancy trends, on a logit scale y^{-1}. The red vertical line indicates zero while the vertical dashed yellow line shows the average value (n=4,120). Filled bars represent the count of species with significant trends (p-value<0.05) whereas open bars represent the count of species with non-significant trends (p-value>0.05). (b) The three left panels represent the estimates (±$CI_{95\%}$) from phylogenetic regressions (PGLS, n=2,013) and linear mixed-effect model (LME, n= 2,080, see Methods) explaining occupancy trends with temporal trends in species climatic indices (SCIs) and other species traits. The two right panels show predicted averaged occupancy trends (±$CI_{95\%}$) for annual species with complete affinity for each habitat (habitat affinity score = 1 and lifespan = annual), and for lifespan categories, predicted at the average of all other variables. Red symbols represent significant effects while black symbols represent non-significant correlations. (c) Estimates (±$CI_{95\%}$) from PGLS and LME of the effect of standardized temperature and precipitation SCI trends on occupancy trends, for each biogeographic region.*

The analysis of the correlates of species occupancy trends reveals that plant species pay a

climatic debt, but only in some parts of Europe. While at the continental scale, the negative

288   relationship between SCI trends and occupancy trends is not significant (Fig. 2b), analysis by

289   biogeographic regions reveals significant correlations, with a strong heterogeneity among

290   regions and across bioclimatic variables. Regarding temperature, in the two coldest

291   biogeographic regions (i.e. Boreal and Alpine regions), a temporal increase in temperature

292   throughout a species range, a consequence of an insufficient range shift to keep pace with

293   historical climatic conditions, is associated with more negative occupancy trends over time (Fig.

294   2c). Surprisingly, in the warmest Mediterranean region, the opposite pattern is observed:

295   species that have experienced a temperature increase throughout their range tend to increase

296   (Fig. 2c), suggesting that climate change elicits a bonus instead of a debt in this area. Regarding

297   precipitation, plant species occupancy trends are negatively related with precipitation SCI

298   trends in the Alpine and Atlantic regions with the highest rainfall, while this relationship tends

299   to be positive in the drier Boreal, Mediterranean and Continental regions (Fig. 2c).

300   These contrasting consequences of lagging behind climate change come in addition to

301   expected effects of the historical climatic niche (Fig. 2b), that however vary in space. At the

302   continental scale, species from rainy and warm historical niches exhibit higher occupancy

303   trends. However, within biogeographic regions, the advantage of warm historical niches was

304   observed only in cooler parts of Europe (Boreal, Atlantic and Alpine regions, Fig. S8).

305   Similarly, the benefit of rainy niches is seen in Boreal and Continental regions only (Fig. S8),

306   where rainfall has increased the most (Fig. S5), while species with dry niches seem to be favored

307   in the Alpine region with decreasing precipitation (Fig. S8).

308   The overall consequences of climate change, combining both temperature and precipitation

309   variables, are a climatic debt in Alpine, Atlantic and Boreal regions (Fig. 3a), but a climatic

310   bonus in the Mediterranean (Fig. 3a), driven mostly by temperature changes but with a

311   significant contribution of precipitation locally (Fig. 3b,c). In the Continental region the

312   observed lags in range shifts did not have any overall significant effect on plant persistence

313 (Fig. 3a), although when combining all the non-significant effects, lags in range shifts tended

314 to benefit plants there, similarly to the Mediterranean region (Fig. S9). The examination of the

315 relative contributions of temperature and precipitation SCI trends to the climatic debt/bonus

316 shows that temperature is generally the major driver (Fig 3c), except in the Atlantic region,

317 where precipitation shifts are the only significant driver of estimated climatic costs.

318 Importantly, SCI and occupancy trends are not significantly related during 1951-1990 (Fig. S6),

319 when climate was relatively stable.

320   Finally, plant occupancy trends are also expectedly related to other drivers beyond climate

321 change. At a continental scale, nitrophily and urban affinity are significant correlates of plant

322 occupancy trends (Fig. 2b). We also find a negative but non-significant effect of pollinator

323 dependency on occupancy trends (Fig. 2b). A majority of the remaining variables, such as most

324 habitat affinities except urban affinity and moisture preferences, have contrasting effects on

325 occupancy trends across biogeographic regions (Fig. S8).
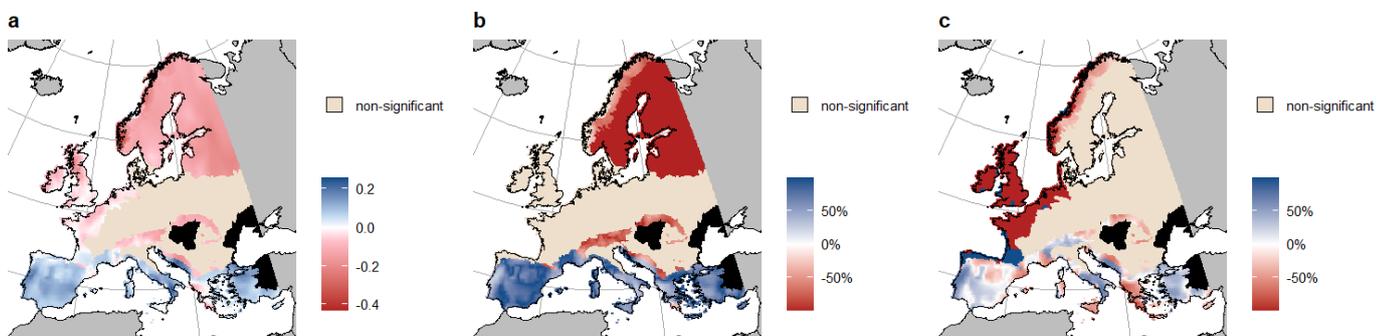
326 ***Figure 3: Climatic debt/bonus in Europe and its climatic drivers.*** *(a) Climatic debt/bonus*
327 *averaged over all species over the last 65 years. The gradient from white to red indicates a*
328 *climatic debt (cost of climate change in terms of species occupancy), while the gradient from*
329 *white to blue indicates a climatic bonus (benefits of climate change in terms of species*
330 *occupancy); white represents no cost of range shift lags on average for plants. Relative*
331 *contribution of trends in species climatic indices (SCIs) related to (b) temperature and (c)*
332 *precipitation to the climatic debt/bonus, in percentage. Black regions are biogeographic*
333 *regions with too few data. The maps were generated using only predictions for effects of SCI*
334 *trends that are significant in both the phylogenetic regression and the linear mixed-effect model*
335 *averaged over these two models.*

Discussion

Our study of the consequences of climate change for plant species first confirms a spatial lag in species responses to climate change, evidenced by an increase in both temperature and precipitation SCIs (Fig.1) suggesting that species are not moving fast enough to track their historical climatic conditions (i.e. to keep constant SCIs). Those SCI trends are phylogenetically structured, which could be explained by the already known climatic niche conservatism in plants (Prinzing Andreas *et al.* 2001; Preston & Sandve 2013; Hawkins *et al.* 2014; Liu *et al.* 2015) but also by the phylogenetic structure in the ability of plant species to track their optimum spatially via colonization (Baeten *et al.* 2015). Furthermore, we also find that temperature and precipitation exhibit contrasting temporal trends in Europe, inducing uncorrelated SCI changes and possibly leading to a spatial trade-off for European plants between tracking precipitation and temperature historical conditions, as has been shown along the elevation gradient (Crimmins *et al.* 2011).

Analyses within biogeographic regions reveal that the lag in species response to temperature change translated into a climatic debt in the North but a surprising climatic "bonus" in the South, resulting in no overall significant signal for a climatic debt at the European scale. However, differences between northern and southern Europe are consistent with a climatic debt at a continental scale: species that track climate change spatially, i.e. with SCI trends close to zero, have positive occupancy trends on their leading edge (northern margins) but negative trends on their trailing edge (southern margins). In addition, among-region differences also match regional patterns of correlations between occupancy trends and historical climatic niche, suggesting that climate could have distinctive effects among regions.

In Boreal and Alpine regions, the effect of temperature SCI trends comes in addition to an effect of the historical climatic niche, with larger occupancy trends for species from historically warmer area. This pattern is consistent with previous results on French plants (Martin *et al.*

361 2019), and its significance only in the cooler parts of Europe (Fig. S8) confirms the well-known

362 stronger effect of climate warming at higher latitudes (Parmesan 2007). Occupancy trends

363 correlate significantly both with temperature SCI trends and temperature of the historical niche

364 in cooler parts of Europe, suggesting that climate is an important driver of species persistence

365 in these areas. In contrast, the surprising climatic bonus in the Mediterranean region is

366 consistent with the absence of correlation between the historical climatic niche and occupancy

367 trends there, suggesting that climate is currently not a strong driver of plant occupancy trends

368 in this area, as previously shown for colonization patterns (Normand *et al.* 2011). This

369 unexpected climatic bonus, which is generally overlooked, could be caused by changes in

370 competitive interactions, an important driver of species responses to climate change (Alexander

371 *et al.* 2015), although we cannot exclude a role of other types of interspecific interactions, such

372 as facilitation or herbivory (Descombes *et al.* 2020). Plants with limited or no northward shift

373 (i.e. plants with an increasing temperature SCI) may benefit from competitive release associated

374 with the range shift of more mobile species, without being in competition with novel

375 competitors from southern regions, because of the numerous geographic barriers limiting plant

376 colonization in the Mediterranean region (Normand *et al.* 2011). These apparent benefits may

377 however disappear when focusing on the whole Mediterranean region: here we ignored the

378 southern margin of many Mediterranean plants, located in Northern Africa, a region with few

379 plant records. Moreover, this climatic bonus is likely to be reversed by sustained climate

380 change on the longer term, when climatic conditions exceed the climatic tolerance of species.

381 In addition to these effects of temperature, the climatic debt can also be driven by changes

382 in precipitation, albeit to a lesser extent. When we combine the effects of temperature and

383 precipitation SCI trends, we show that the inability of plant species to track their historical

384 climatic conditions has been costly in the Alpine, Atlantic and Boreal regions, but beneficial in

385 the Mediterranean region. These patterns substantiate further the notion of climatic debt in the

386   former areas, and confirm the climatic bonus in the Mediterranean, although lags behind climate

387   are most often interpreted as a climatic debt there (Bertrand *et al.* 2016). The effects of lagging

388   behind changing precipitation are variable however. In relatively dry biogeographic regions, a

389   decrease in the annual precipitation SCI of plant species over the past decades is associated

390   with negative, or less positive, occupancy trends, which suggests that climate change causes

391   water-deficit stress with detrimental consequences for plant population dynamics, a well-known

392   phenomenon (Breshears *et al.* 2005; Allen *et al.* 2010; Zhao & Running 2010). This applies to

393   the Mediterranean region, in which precipitation shifts can be as important a driver as

394   temperature changes, although it is widely overlooked in climatic debt assessments.

395   In contrast, in relatively wet areas, plant occupancy trends seem to be hindered by an

396   increase in annual precipitation SCI, which suggests water-excess stress, via e.g. waterlogging.

397   Such consequence of climate change, via an increase in precipitation, is less documented but

398   has been shown to drive downhill shifts in plant species elevation against temperature changes

399   in mountain areas (Crimmins *et al.* 2011). Their general contribution to the climatic debt

400   relative to temperature is however moderate, except in the Atlantic region.

401   Beyond the effects of climate change, our results also strongly suggest that nitrogen

402   deposition and urbanization are important disturbances for plants (Aronson *et al.* 2014; Bobbink

403   *et al.* 2016). However, while nitrogen deposition is sometimes cited as the first driver of changes

404   in plant species composition (Bobbink *et al.* 2016), our results challenge this statement: by

405   assessing response traits simultaneously, we find stronger links of occupancy trends with

406   historical climatic niche or urban affinity than with nitrophily. Hence, our results are consistent

407   with the recent acceleration of climate change in Europe and suggest that climate warming has

408   caught up with urbanization and nitrogen deposition to become an important driver of plant

409   persistence. We thus provide further evidence that biodiversity is often affected by multiple

410   global change drivers rather than by single threats (Brooks *et al.* 2017). Consistent with

411 previous results and with the pollinator decline (Biesmeijer *et al.* 2006), we find a negative

412 effect of pollinator dependency on occupancy trends, but the latter is non-significant. This lack

413 of signal for an effect of pollinator loss on plant occupancy trends may be attributable to

414 contrasting plant trends depending on the group of pollinators (Biesmeijer *et al.* 2006).

415 Here we show that plants are under multiple pressures from global change, and that plant

416 occupancy trends exhibit a strong phylogenetic signal, which entails a risk of important

417 evolutionary history losses associated with the forecasted extinctions. In particular, in some

418 regions plant persistence is already affected by climate change and the resulting climatic

419 debt/bonus, while these climate-related costs/benefits are often considered long-term. The

420 climatic debt/bonus evident here is an integrative measure of all ecological and evolutionary

421 costs/benefits associated with climate change, which we are not able to partition. For example,

422 the costs we observe in Northern Europe could be due to insufficient adaptive response to buffer

423 a spatial lag, to the arrival of novel competitors (Alexander *et al.* 2015), and/or to the

424 demographic cost of an ongoing adaptive response (Lynch & Lande 1993) buffering the spatial

425 lag. As plant adaptation to climate change opens the door to a possible evolutionary rescue for

426 species that track their climatic optimum poorly in space (Gonzalez *et al.* 2013), assessing the

427 contribution of ecological and evolutionary mechanisms of the climatic debt or bonus is a

428 remaining key challenge to predict future effects of climate change on plants.

429 Although this study tackled two dimensions of the species climatic niches simultaneously,

430 our estimation of the climatic debt faces some limitations. First, we examined average climatic

431 conditions only, thereby probably underestimating the cost of climate change, which also

432 includes changes in variability, such as in the frequency of extreme events. Moreover, other

433 environmental conditions beyond climate have changed during the last decades, such that their

434 effects are difficult to unravel. Our climatic debt/bonus measure is thus integrative, likely

435 including costs related to interactions between climate change and other drivers. For example

436   landscape alteration can hinder species tracking of their historical climatic conditions (Bertrand

437   *et al.* 2016; Gaüzère *et al.* 2017). We used a correlative approach on the basis of species traits,

438   while taking phylogeny into account: the remaining phylogenetic signal in plant occupancy

439   trends points to a likely omission either of some drivers or of synergistic effects among drivers.

440   These could be investigated through local studies.

441   Finally, we present the first overview of plant occupancy trends at continental scale. This

442   was made possible by the use of opportunistic data, which are often the only data source to

443   obtain long time-series at large spatial extent (Biesmeijer *et al.* 2006; Bartomeus *et al.* 2019),

444   together with statistical methods aiming to correct the potential biases associated with those

445   data (Isaac *et al.* 2014). The fact that we find strong positive trends for invasive species suggests

446   that trends estimated from GBIF data provide an accurate picture of actual changes in species

447   occupancy. However, finding independent datasets and methods that allow turning the clock

448   back and studying past effects of global change on biodiversity is a major challenge to confirm

449   our results and anticipate future threats for biodiversity.

Author Contributions

458

459 FD designed the study, extracted the data and performed all the statistical analyses. GM and

460 FD extracted and compiled species traits. FD and EP wrote the paper with contributions from

461 GM.

Competing interests

462

463 The authors declare no competing interests.

Data availability statement

464

465 R scrips used to perform the analysis are available here: https://github.com/f-

466 duchenne/European-plants-lagging-behind-climate-change-. All data supporting the analysis,

467 excepting row data from the GBIF, can be downloaded here:

468 http://doi.org/10.5281/zenodo.4550500.

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