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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

5

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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.**

35 **Introduction**

36 Climate change is recognized as a major threat for biodiversity (Sala *et al.* 2000). Species
37 have two main ways to persist under such change: they can track their climatic optimum in
38 space (geographic range shift) or they can respond adaptively to survive and reproduce in a
39 altered environment (Chevin *et al.* 2010), i.e. modify their climatic optimum. Concerns about
40 the capacity of species to achieve one or the other quickly enough have increased (Parmesan
41 2006; Chevin *et al.* 2010; Hoffmann & Sgrò 2011), with many studies showing that living
42 organisms are currently moving poleward and upward in response to climate warming
43 (Parmesan 2006; Kelly & Goulden 2008; Devictor *et al.* 2012; Lenoir *et al.* 2020). Yet, most
44 studies so far have shown that range shifts are rarely as fast as climate change (Menéndez *et al.*
45 2006; Devictor *et al.* 2012; VanDerWal *et al.* 2013; Lenoir *et al.* 2020), i.e. climate variables
46 move faster through space than most species do. This lag of species movements behind climate
47 change is often coined a “climatic debt” (Devictor *et al.* 2012; Monsinjon *et al.* 2019; Lenoir *et*
48 *al.* 2020). It can be evidenced by a temporal change in the so-called “climatic niche” of a
49 species, as measured by the average of one or several climatic variables throughout its range
50 (VanDerWal *et al.* 2013), hereafter “species climatic indices” (SCIs).

51 The consequences of species shifting their ranges slower than the movement of suitable
52 climate conditions, however, remain to be quantified. First, the resulting temporal change in the
53 climatic conditions experienced by a species need not necessarily translate into a “debt”: most
54 species can and do also respond to climate change via adaptive plastic or evolutionary trait
55 changes, which could be sufficient to sustain populations despite changing climatic conditions
56 (Hoffmann & Sgrò 2011), albeit the most recent meta-analysis to date suggests otherwise
57 (Radchuk *et al.* 2019). Thus, to verify the existence of a true climatic debt, one needs to
58 demonstrate that the spatial lag of species behind changing climate conditions results in
59 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.

85 **Methods**

86 *Data collection; trends in SCIs and species occupancy*

87 *Plant database*

88 We focused on the most common vascular plant species in geographical Europe, i.e. with at
89 least 500 records in the Global Biodiversity Information Facility (GBIF) database
90 (<https://www.gbif.org>) between 1950 and 2014 within a rectangle bounded by longitudes [-13°,
91 34°] and latitudes [34°,75°]. We downloaded all species sightings during the time period from
92 1951 through 2014, excluding 1950 as this year contains data not precisely dated, but
93 corresponding to the mid-twentieth century. The DOIs associated with the extraction are
94 presented in the Supplementary methods. We considered only records from the European
95 mainland, stopping at 34° of longitude because there were too few data to the East of this
96 meridian (Fig. S1). Note that the area also includes the western part of Turkey. This yielded a
97 dataset containing 111,549,494 occurrence records, characterized by a species name, a location
98 and a date. Of these, we analyzed temporal trends in species climatic indices (SCIs) and
99 occupancy only for the species observed in at least 20 years between 1951 and 2014 and with
100 at least one record between 1951 and 1980. We removed crop species and considered invasive
101 species separately (see Supplementary methods), because the drivers of their occupancy trends
102 are likely different from those for non-invasive species. This selection resulted in 4,120 native
103 and naturalized plant species (listed in Table S1), plus 58 invasive species.

104 *Bioclimatic variables*

105 Climate change is not limited to increases in annual mean temperature; hence we
106 characterized the climatic conditions with three bioclimatic variables related to temperature and
107 three bioclimatic variables related to precipitation, because temperature and precipitation are
108 strong predictors of plant distribution (Franklin *et al.* 2013). We used previously published
109 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
$$SCI_k = \mu + \beta \times year_k + \varepsilon_k \quad (1)$$

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:

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

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:

$$\begin{aligned} 194 \Delta O_{sj} = & \mu + \beta_1 \times \Delta SCI_{bio1s} + \beta_2 \times \Delta SCI_{bio12s} + \beta_3 \times BCI_{bio1s} + \beta_4 \times BCI_{bio12s} + \beta_5 \times \\ 195 ME_s + & \beta_6 \times NE_s + \beta_7 \times Poll_s + \theta_j + \sum_{i=1}^h \beta_{habitat_i} \times Habitat_i + \varepsilon_{sj} \quad (3) \end{aligned}$$

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:

$$209 \Delta O_{sjcf} = \mu + \beta_1 \times \Delta SCI_{bio1s} + \beta_2 \times \Delta SCI_{bio12s} + \beta_3 \times BCI_{bio1s} + \beta_4 \times BCI_{bio12s} + \beta_5 \times \\ 210 ME_s + \beta_6 \times NE_s + \beta_7 \times Poll_s + \theta_j + \sum_{i=1}^h \beta_{habitat_i} \times Habitat_i + \varphi_c + \varphi_f + \varepsilon_{sjcf} \quad (4)$$

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*

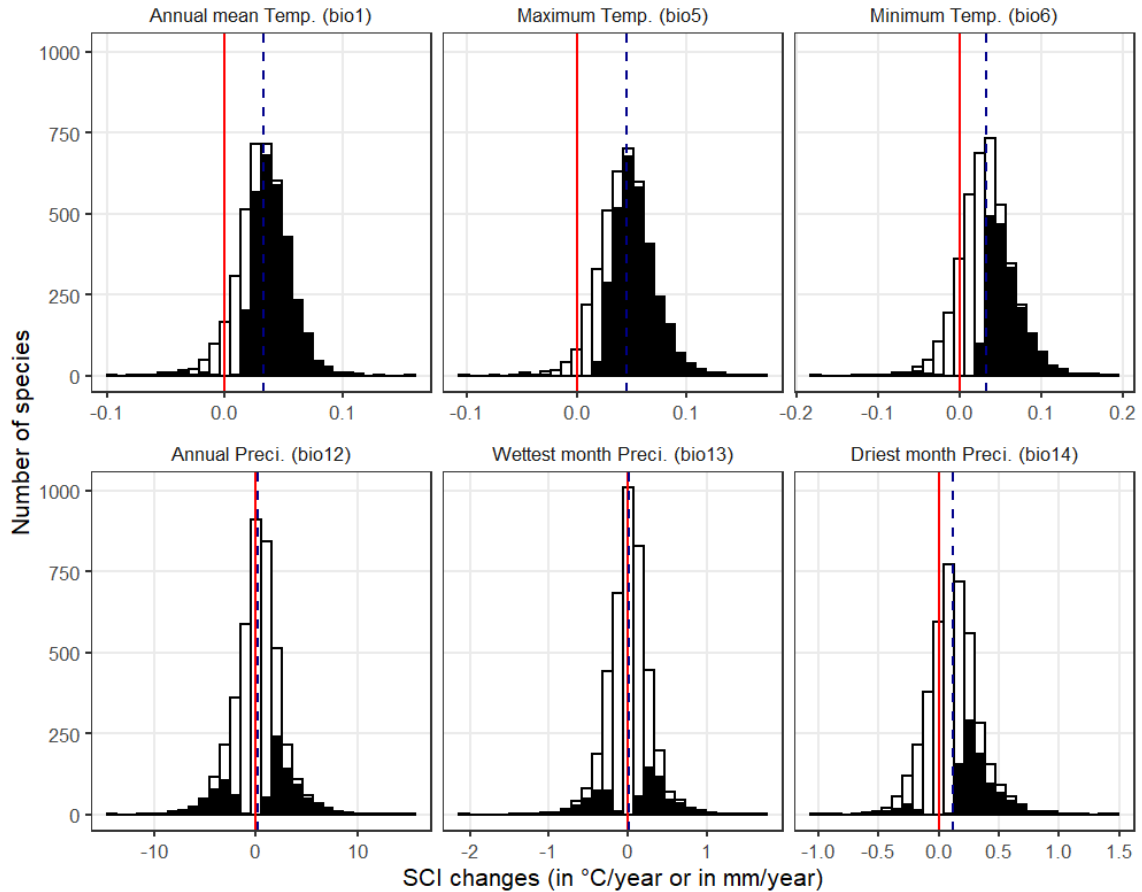
231 To combine the effects of annual precipitation and temperature SCI trends on occupancy
232 trends for each biogeographic region, we multiplied each unscaled effect of SCI trends by the
233 observed change in the corresponding climatic indices. This yielded a measure of the effective
234 cost/bonus 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



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

260

261

Occupancy trends and their drivers

262

The average trend in occupancy over all native and naturalized species is slightly positive:

263

$0.0048 \pm 3.29 \cdot 10^{-4} \text{ year}^{-1}$ (mean \pm SE), but the number of species with significant increase in

264

the occupancy estimates (1,721 species, 42%) is comparable to the number of species with

265

significant decline in occupancy (1,519 species, 37%). The average positive trend over all

266

species (Fig. 2a) is mainly explained by the skewed distribution of trends towards positive

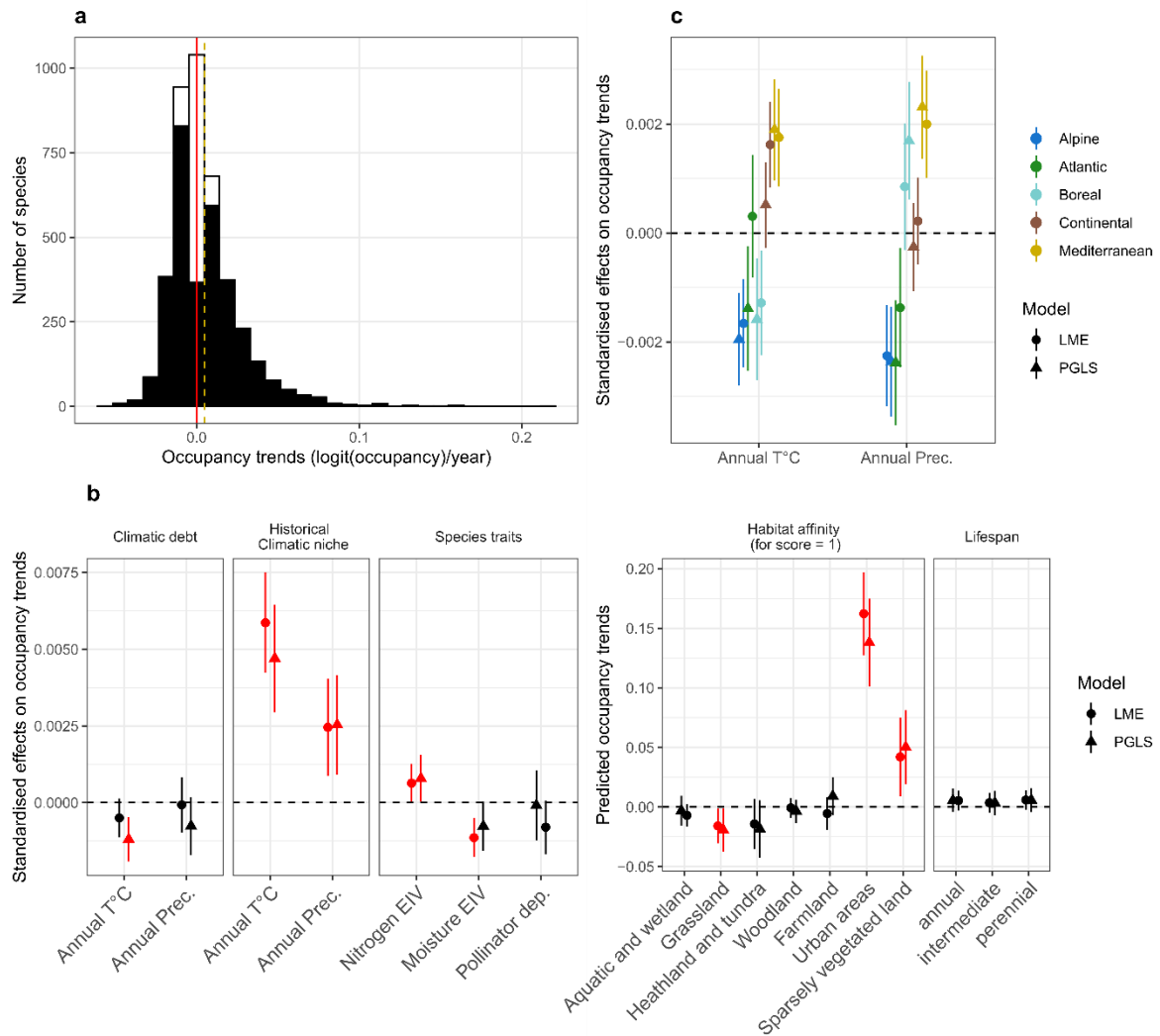
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values, with a couple of species exhibiting strong increases even after exclusion of invasive

268

species (Fig. S3). Furthermore, we find that plant occupancy trends exhibit a strong

269 phylogenetic signal both before (Pagel's $\lambda = 0.62$, p -value <0.01 ; $n=2,785$) and after (Pagel's λ
 270 $= 0.45$, $CI_{95\%} = [0.32,0.57]$; $n=2,013$) considering species traits.



271 **Figure 2: Occupancy trends of native and naturalized European plant species and their**
 272 **correlates.** (a) Histogram of occupancy trends, on a logit scale y^{-1} . The red vertical line
 273 indicates zero while the vertical dashed yellow line shows the average value ($n=4,120$). Filled
 274 bars represent the count of species with significant trends (p -value <0.05) whereas open bars
 275 represent the count of species with non-significant trends (p -value >0.05). (b) The three left
 276 panels represent the estimates ($\pm CI_{95\%}$) from phylogenetic regressions (PGLS, $n=2,013$) and
 277 linear mixed-effect model (LME, $n=2,080$, see Methods) explaining occupancy trends with
 278 temporal trends in species climatic indices (SCIs) and other species traits. The two right panels
 279 show predicted averaged occupancy trends ($\pm CI_{95\%}$) for annual species with complete affinity
 280 for each habitat (habitat affinity score = 1 and lifespan = annual), and for lifespan categories,
 281 predicted at the average of all other variables. Red symbols represent significant effects while
 282 black symbols represent non-significant correlations. (c) Estimates ($\pm CI_{95\%}$) from PGLS and
 283 LME of the effect of standardized temperature and precipitation SCI trends on occupancy
 284 trends, for each biogeographic region.

285
 286 The analysis of the correlates of species occupancy trends reveals that plant species pay a
 287 climatic debt, but only in some parts of Europe. While at the continental scale, the negative

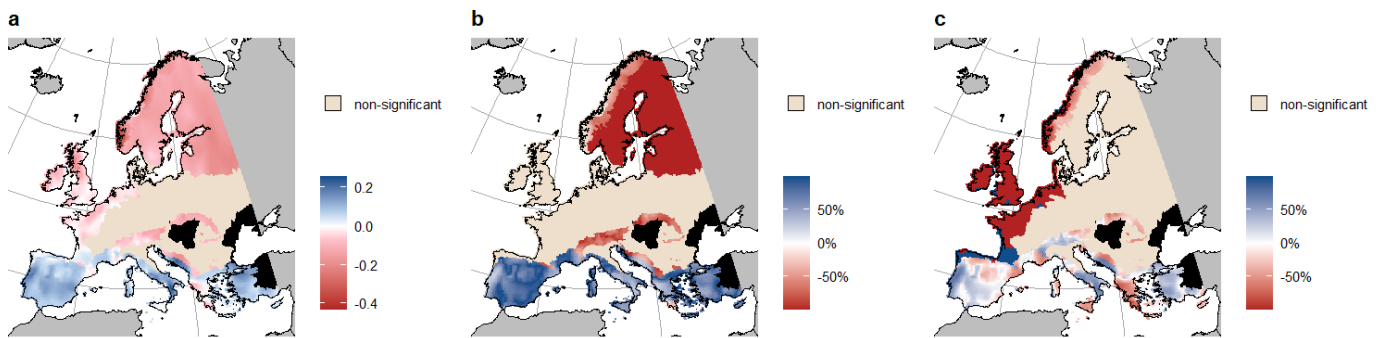
288 relationship between SCI trends and occupancy trends is not significant (Fig. 2b), analysis by
289 biogeographic regions reveals significant correlations, with a strong heterogeneity among
290 regions and across bioclimatic variables. Regarding temperature, in the two coldest
291 biogeographic regions (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.

336 **Discussion**

337 Our study of the consequences of climate change for plant species first confirms a spatial
338 lag in species responses to climate change, evidenced by an increase in both temperature and
339 precipitation SCIs (Fig.1) suggesting that species are not moving fast enough to track their
340 historical climatic conditions (i.e. to keep constant SCIs). Those SCI trends are phylogenetically
341 structured, which could be explained by the already known climatic niche conservatism in
342 plants (Prinzing Andreas *et al.* 2001; Preston & Sandve 2013; Hawkins *et al.* 2014; Liu *et al.*
343 2015) but also by the phylogenetic structure in the ability of plant species to track their optimum
344 spatially via colonization (Baeten *et al.* 2015). Furthermore, we also find that temperature and
345 precipitation exhibit contrasting temporal trends in Europe, inducing uncorrelated SCI changes
346 and possibly leading to a spatial trade-off for European plants between tracking precipitation
347 and temperature historical conditions, as has been shown along the elevation gradient
348 (Crimmins *et al.* 2011).

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

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

2019), and its significance only in the cooler parts of Europe (Fig. S8) confirms the well-known stronger effect of climate warming at higher latitudes (Parmesan 2007). Occupancy trends correlate significantly both with temperature SCI trends and temperature of the historical niche in cooler parts of Europe, suggesting that climate is an important driver of species persistence in these areas. In contrast, the surprising climatic bonus in the Mediterranean region is consistent with the absence of correlation between the historical climatic niche and occupancy trends there, suggesting that climate is currently not a strong driver of plant occupancy trends in this area, as previously shown for colonization patterns (Normand *et al.* 2011). This unexpected climatic bonus, which is generally overlooked, could be caused by changes in competitive interactions, an important driver of species responses to climate change (Alexander *et al.* 2015), although we cannot exclude a role of other types of interspecific interactions, such as facilitation or herbivory (Descombes *et al.* 2020). Plants with limited or no northward shift (i.e. plants with an increasing temperature SCI) may benefit from competitive release associated with the range shift of more mobile species, without being in competition with novel competitors from southern regions, because of the numerous geographic barriers limiting plant colonization in the Mediterranean region (Normand *et al.* 2011). These apparent benefits may however disappear when focusing on the whole Mediterranean region: here we ignored the southern margin of many Mediterranean plants, located in Northern Africa, a region with few plant records. Moreover, this climatic bonus is likely to be reversed by sustained climate change on the longer term, when climatic conditions exceed the climatic tolerance of species.

In addition to these effects of temperature, the climatic debt can also be driven by changes in precipitation, albeit to a lesser extent. When we combine the effects of temperature and precipitation SCI trends, we show that the inability of plant species to track their historical climatic conditions has been costly in the Alpine, Atlantic and Boreal regions, but beneficial in 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.

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458 **Author Contributions**

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.

462 **Competing interests**

463 The authors declare no competing interests.

464 **Data availability statement**

465 R scripts used to perform the analysis are available here: [https://github.com/f-
466 duchenne/European-plants-lagging-behind-climate-change-](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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