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

François Duchenne, Gabrielle Martin, Emmanuelle Porcher

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Short title: Climatic debts and bonuses in European plants

François Duchenne*[1,2,3], Gabrielle Martin[2,3] & Emmanuelle Porcher[2,3]

Affiliations:

[1]Institute of Ecology and Environmental Sciences of Paris, (Sorbonne Université, CNRS, Université Paris Est Créteil, INRA, IRD), Paris, France, [2]Centre d'Ecologie et des Sciences de la Conservation, (Muséum national d'Histoire naturelle, CNRS, Sorbonne Université), Paris, France, [3]Laboratoire Cogitamus, Paris, France

*: corresponding author, François Duchenne, francois.duchenne@mnhn.fr

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Abstract:

For many species, climate change leads to range shifts that are detectable, but often insufficient to track historical climatic conditions. These lags of species range shifts behind climatic conditions are often coined "climatic debts", but the demographic costs entailed by the word "debt" have not been demonstrated. Here we used opportunistic distribution data for ~4,000 European plant species to estimate the temporal shifts in climatic conditions experienced by these species and their occupancy trends, over the last 65 years. The resulting negative relationship observed between these two variables provides the first piece of evidence that European plants are already paying a climatic debt in Alpine, Atlantic and Boreal regions. In contrast, plants appear to benefit from a surprising "climatic bonus" in the Mediterranean. We also find that among multiple pressures faced by plants, climate change is now on par with other known drivers of occupancy trends, 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 species face additional threats beyond climate change, e.g. habitat loss or pollution, which may be the dominant drivers of current species loss (Maxwell *et al.* 2016). Thus, a climatic debt, should it exist, might be of little consequence for population trends compared to other drivers. However, few studies so far have compared quantitatively the impact of different drivers across a large number of species, and none has included the climatic debt.

Costs associated with the putative climatic debt remain poorly investigated likely because the climatic debt concept has been developed at the community level mostly (Bertrand *et al.* 2011; Devictor *et al.* 2012), while cost estimation is easier at species level, e.g. via an assessment of species persistence. By shifting the concept of climatic debt from community to species level, one can correlate delayed spatial responses (i.e. temporal trends in SCIs) with species persistence. Under climate warming, if both species movements and adaptive responses are insufficient, we expect (1) an increase in the temperature SCI of a given species over time (limited spatial response) and (2) a negative relationship between the temporal trend in SCI for temperature and the species persistence (limited adaptive response, Radchuk *et al.* 2019). The latter observation only is suggestive of costs at individual and population levels, i.e. a climatic debt. Alternatively, uncorrelated SCI trends and species persistence would indicate an absence of climatic debt, which could be explained by adaptive responses buffering limited spatial responses or by species insensitivity to temperature (Rodríguez-Sánchez *et al.* 2012). This logic applies similarly to other climatic variables beyond temperature, such as precipitation.

Here we examine the temporal shifts in the climatic conditions experienced by a species throughout its range, as measured by SCI trends, and occupancy trends, for more than 4,000 European plant species over the last 65 years, using a large dataset of opportunistic distribution records. These two elements allowed us to verify the existence of a climatic debt, which we estimate via the relationship between occupancy and SCI trends, and to compare its strength to 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, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest month, and precipitation of the driest month. These bioclimatic variables are the same as in Worldclim (bio1, 5, 6, 12, 13, 14) but with annual data. For computational reasons we aggregated 1kmx1km raster cells, which decreased spatial resolution from 1 to about 100km² (~10km×10km).

Calculation of annual species climatic indices and their temporal trends

Species climatic indices (SCIs) are often calculated as the average of a climatic variable, e.g. temperature, across a species range (Devictor *et al.* 2012). However, the heterogeneity of opportunistic datasets can bias this index (Loiselle *et al.* 2008; Beck *et al.* 2014). Because we are interested in inter-annual comparisons, we corrected a temporal bias in the spatial distribution of sampling pressure: the average latitude and longitude of the GBIF records both decrease significantly with time. To reduce such bias we defined annual SCI as the mean climatic variable of all 100km² cells occupied by a given species, while weighting the contribution of each cell by the ratio of the number of records of this species on the number of records of all plant species for the given year and grid cell. Such method enables estimations of the SCIs that are more independent from the sampling pressure than a weighting by the number of records of the given species only (Fig. S2).

Following the method above, we calculated one SCI for each bioclimatic variable, species and year. We then assessed the temporal trend in each SCI and species separately, using the following linear model:

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

where SCI_k is the species climatic index of year k, μ is the grand mean (intercept), β is the year effect and ε_k is an error term (independent and identically distributed, following $N(0,\sigma^2)$). Observations (SCI_k) are weighted by the square root of the number of grid cells included in their calculation for each year, which gives greater weight to years with more data. We finally estimated the phylogenetic signal in SCI trends (Supplementary Methods).

Occupancy trends

To model the temporal occupancy trends, we first discretized the dataset spatially and temporally, to define areas occupied or not by a species for a given time period. Such discretization then allowed us to estimate variation in occupancy probability among time periods by taking the sampling pressure into account. As for SCI calculation, we used a grid cell of about 10km×10km to discretize the dataset spatially, and we aggregated records temporally by years. For each year, a grid cell is considered as visited by at least an observer if it contains at least one plant species record. Non-visited cells are discarded. A visited cell is considered as occupied by a species if it contains at least one record of the given species in the given year, and unoccupied otherwise. We obtained a dataset composed of annual presences and pseudo-absences in each 10km×10km grid cell.

Before analyzing the data, we discarded all grid cells visited only one year, to improve occupancy estimations by decreasing the confusion between grid cell and year effects (Isaac *et al.* 2014). To save computing time, for each species we removed non-informative grid cells, i.e. cells with no record of the species over the whole study period. Finally, to estimate a yearly occupancy probability (p), we explained remaining presences and pseudo-absences for each species separately using the following binomial generalized linear model with a logit link:

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

Where p_{ik} is the occupancy probability of grid cell *i* for year *k*, μ is the intercept of the model, β_1 is the year effect (i.e. the occupancy trend), and φ_i a random grid cell effect. Finally, β_2 is the effect of the logarithm of the species list length (SL_{ik}, i.e. the number of species observed in a given grid cell and year), used as a proxy for the sampling pressure (Isaac *et al.* 2014).

Those models were implemented using the R package *glmmTMB* (Brooks *et al.* 2017). We estimated occupancy trends for all 4,120 native and naturalized species, as well as for the 58 invasive species. This latter step allowed us to verify that occupancy trend estimates were large and positive for invasive species (Fig. S3), confirming that the data and statistical methods to estimate occupancy trends yield results consistent with known species trends. As for SCI trends, we estimated the phylogenetic signal in occupancy trends (Supplementary Methods).

Additional potential drivers of occupancy trends

To compare the strength of the climatic debt with that of other potential drivers of occupancy trends, we tried to include all additional drivers in the analysis of the relationship between occupancy trends and SCI trends (see below). We used the plant and global change literature to identify potential drivers of plant trends, which we took into account via species traits: historical climatic niche (Martin *et al.* 2019), lifespan (Martin *et al.* 2019), habitat affinity (Aronson *et al.* 2014; Buse *et al.* 2015), nitrophily (Sala *et al.* 2000; Bobbink *et al.* 2016), moisture preferences (Moeslund *et al.* 2013) and pollinator dependency (Biesmeijer *et al.* 2006). We detail all calculations for these traits in Supplementary Methods.

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

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

Analysis at continental scale

As explained above, a climatic debt can be revealed by a negative relationship between species occupancy trends and SCI trends. To assess this relationship between SCI trends and occupancy trends, while controlling for the species traits cited above, we used linear models. We first checked the correlations among the six SCI trends and six historical climatic niche indices. We noticed high correlations (*r*>0.7) among historical temperature indices, among historical precipitation indices, among SCI trends related to temperature and among SCI trends related to precipitation (Fig. S4). In order to avoid multicollinearity issues, we retained only the two most used and integrative bioclimatic variables, both for the historical climatic niche and for SCI trends: annual mean temperature and annual precipitation.

In summary, we considered the following correlates of occupancy trends: SCI trends related to annual mean temperature and annual precipitation, historical climatic index related to annual mean temperature and annual precipitation, nitrophily and moisture Ellenberg indicator values, pollinator dependency, habitat affinity and lifespan. To be able to compare the strength of relations across explanatory variables, we scaled them before using the Phylogenetic Generalized Least Squares regression, except for habitat affinity and lifespan, as we wanted to extract the effect on the intercept for the first and as the second is a qualitative variable. We used the *caper* R package (Orme *et al.* 2013) to implement models controlling for phylogenetic signal in the residuals:

$$\Delta O_{sj} = \mu + \beta_1 \times \Delta SCI_{bio1_s} + \beta_2 \times \Delta SCI_{bio12_s} + \beta_3 \times BCI_{bio1_s} + \beta_4 \times BCI_{bio12_s} + \beta_5 \times ME_s + \beta_6 \times NE_s + \beta_7 \times Poll_s + \theta_j + \sum_{i=1}^{h} \beta_{habitat_i} \times Habitat_i + \varepsilon_{sj} \qquad (3)$$

Where ΔO_{sj} is the occupancy trend of species *s* with lifespan class *j*, μ is the grand mean (intercept), $\beta_1$and β_2 are the slopes of SCI trends, β_3 and β_4 are the effects of historical climatic niche indices, BCI_{bio1} and BCI_{bio12}, related to annual mean temperature and annual precipitation respectively. β_5 and β_6 are the effects of Ellenberg indicator values for moisture and nitrogen respectively. β_7 is the effect of pollinator dependency, θ_j is the qualitative lifespan effect and $\beta_{habitat_i}$ is the effect of affinity to habitat *i*, with six habitat classes (*h* = 6, Table S2), woodland being the reference habitat. Finally, ε_{sj} is an error term, after correction by Pagel's λ value at the likelihood maximum.

This model included all species matching the phylogeny and with full trait data (*n* = 2,013). To add the 67 species that were not in the phylogeny but for which all traits were available, we also performed a linear mixed-effect model similar to the phylogenetic regression but including random taxonomic effects of class (φ_c) and of family nested in class (φ_f) instead of a phylogeny:

$$\Delta O_{sjcf} = \mu + \beta_1 \times \Delta SCI_{bio1_s} + \beta_2 \times \Delta SCI_{bio12_s} + \beta_3 \times BCI_{bio1_s} + \beta_4 \times BCI_{bio12_s} + \beta_5 \times ME_s + \beta_6 \times NE_s + \beta_7 \times Poll_s + \theta_j + \sum_{i=1}^{h} \beta_{habitat_i} \times Habitat_i + \varphi_c + \varphi_f + \varepsilon_{sjcf} \quad (4)$$

This linear mixed-effect model was weighted by the inverse of the standard errors associated with the occupancy trends.

Analysis by biogeographic region and time period

To examine the spatial variation in climatic debt, we also conducted the same analysis within biogeographic regions. We focused on the five biogeographic regions with at least 1,000 species: Alpine, Atlantic, Boreal, Continental and Mediterranean regions. For each region, as for the main analysis, we retained only species with at least 20 years of data.

We re-calculated SCI and occupancy trends within each region independently, using the same method as above, but including only plant records from the focal biogeographic region. With these new estimates, we assessed regional climatic debts as the relationship between SCI and occupancy trends, using the same models as in the European analysis (equations (3) and (4)) but removing the random effect of taxonomic class φ_c, to avoid singularities. While SCI and occupancy trends were calculated within biogeographic regions, we considered other species traits as constant throughout Europe.

Finally, to confirm that the costs of the shifts in experienced climatic conditions occur only after the acceleration of climate change (1980-2000, Fig. S5) we performed the same set of analyses on the earliest data, as detailed in Supplementary Methods. Results are shown in Fig. S6.

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

To combine the effects of annual precipitation and temperature SCI trends on occupancy trends for each biogeographic region, we multiplied each unscaled effect of SCI trends by the observed change in the corresponding climatic indices. This yielded a measure of the effective cost/bonus due to a given SCI trend, i.e. to the lag of species behind climate change. For each region, we then summed the values of effective cost/bonus for temperature and precipitation to measure the overall climatic debt/bonus over the study period. We also calculated the relative contribution of precipitation and temperature SCI trends to the overall debt/bonus by dividing each by the sum of the absolute values of both.

Results

Temporal trends in Species Climatic Indices

During the study period (1951-2014), all SCIs change significantly, in direct relation with climate change. All bioclimatic variables related to temperature and precipitation increase on average over the study area, but with substantial spatial heterogeneity for precipitation (Fig. S5). Consistently with the trends in bioclimatic variables related to temperature, we show that the temperature SCIs increase over time for a large majority of species (Fig. 1). Precipitation SCIs also increase over time on average (Fig. 1, Table S3), but the distribution of precipitation SCI trends is closer to zero, with more numerous negative trends than for temperature SCIs. Temperature and precipitation SCI trends are not significantly correlated (Fig. S4), probably due to the fact that annual precipitation and temperature trends exhibit contrasting spatial distributions (Fig. S5c-d). We also find a significant phylogenetic signal in all SCI trends (Fig. S7).

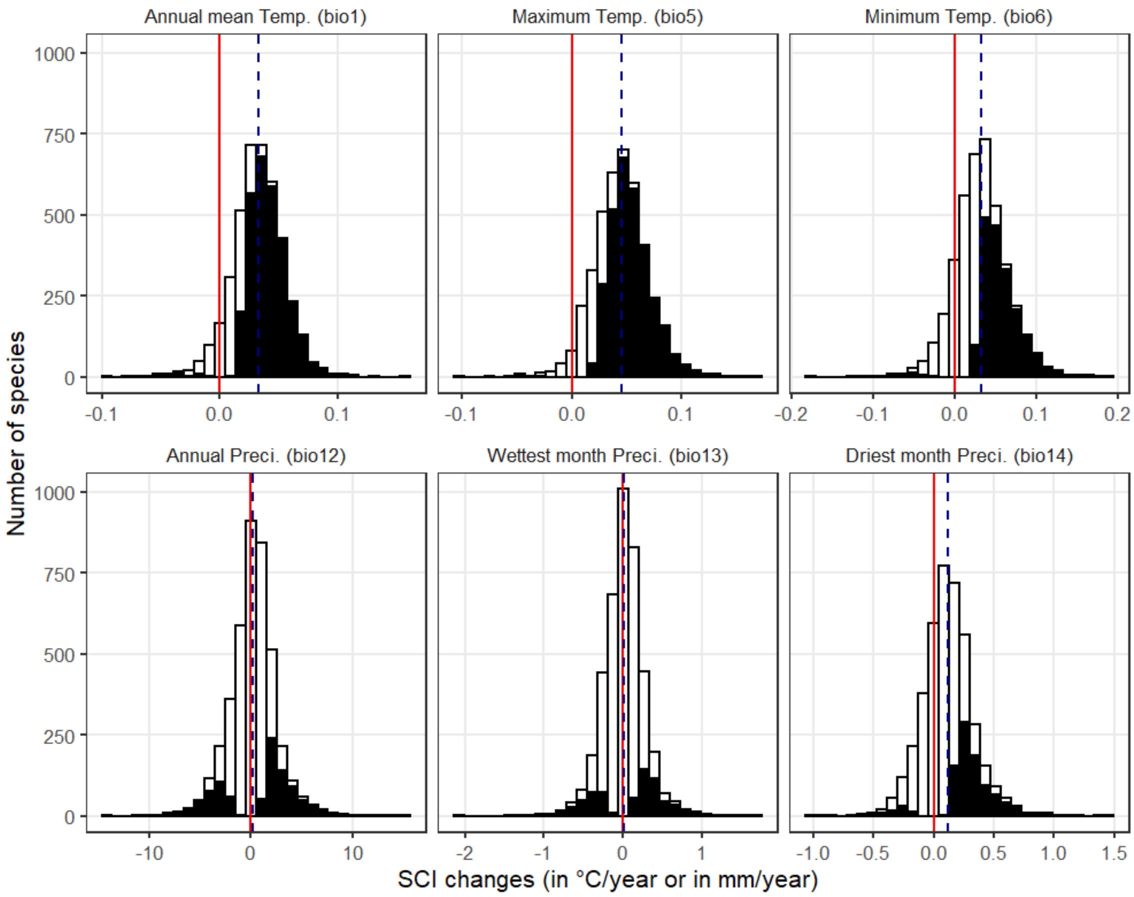
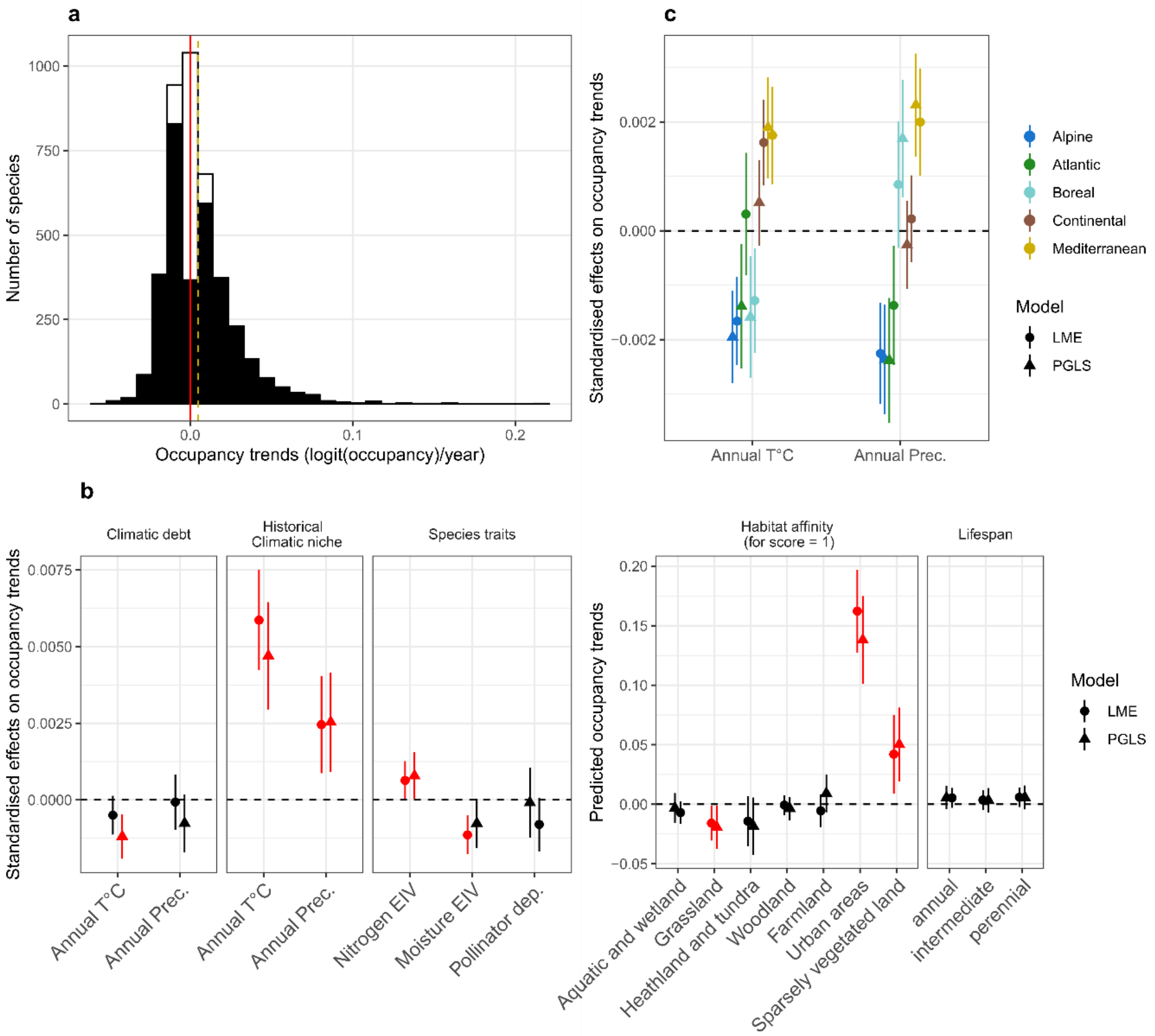


Figure 1: ***Linear trends in species climatic indices (SCIs) for all species (n=4,120).*** *The first row shows the trends in temperature SCIs and the second row the trends in precipitation SCIs over time. The WorldClim abbreviation for bioclimatic variables is indicated in parentheses atop each panel. 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 ± 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 $\lambda = 0.62$, p-value<0.01; *n*=2,785) and after (Pagel's $\lambda = 0.45$, $CI_{95\%} = [0.32,0.57]$; *n*=2,013) considering species traits.



<u>Figure 2:</u> 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.*

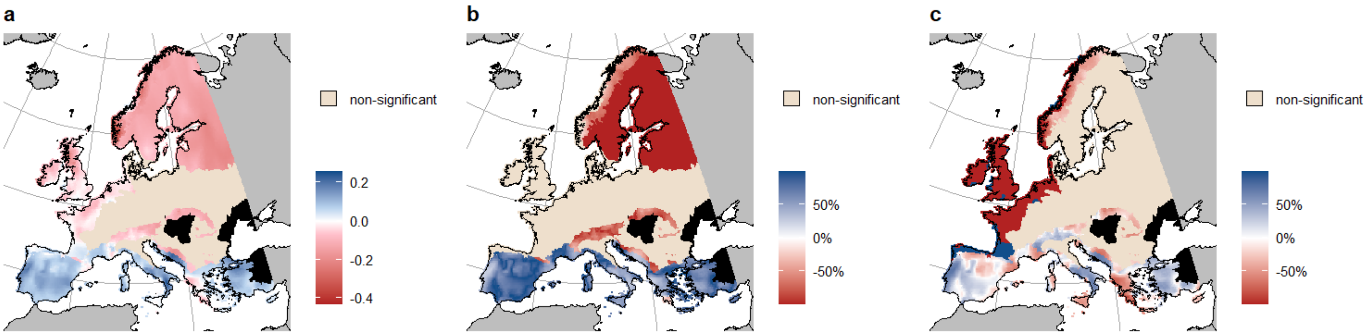
The analysis of the correlates of species occupancy trends reveals that plant species pay a climatic debt, but only in some parts of Europe. While at the continental scale, the negative relationship between SCI trends and occupancy trends is not significant (Fig. 2b), analysis by biogeographic regions reveals significant correlations, with a strong heterogeneity among regions and across bioclimatic variables. Regarding temperature, in the two coldest biogeographic regions (i.e. Boreal and Alpine regions), a temporal increase in temperature throughout a species range, a consequence of an insufficient range shift to keep pace with historical climatic conditions, is associated with more negative occupancy trends over time (Fig. 2c). Surprisingly, in the warmest Mediterranean region, the opposite pattern is observed: species that have experienced a temperature increase throughout their range tend to increase (Fig. 2c), suggesting that climate change elicits a bonus instead of a debt in this area. Regarding precipitation, plant species occupancy trends are negatively related with precipitation SCI trends in the Alpine and Atlantic regions with the highest rainfall, while this relationship tends to be positive in the drier Boreal, Mediterranean and Continental regions (Fig. 2c).

These contrasting consequences of lagging behind climate change come in addition to expected effects of the historical climatic niche (Fig. 2b), that however vary in space. At the continental scale, species from rainy and warm historical niches exhibit higher occupancy trends. However, within biogeographic regions, the advantage of warm historical niches was observed only in cooler parts of Europe (Boreal, Atlantic and Alpine regions, Fig. S8). Similarly, the benefit of rainy niches is seen in Boreal and Continental regions only (Fig. S8), where rainfall has increased the most (Fig. S5), while species with dry niches seem to be favored in the Alpine region with decreasing precipitation (Fig. S8).

The overall consequences of climate change, combining both temperature and precipitation variables, are a climatic debt in Alpine, Atlantic and Boreal regions (Fig. 3a), but a climatic bonus in the Mediterranean (Fig. 3a), driven mostly by temperature changes but with a significant contribution of precipitation locally (Fig. 3b,c). In the Continental region the observed lags in range shifts did not have any overall significant effect on plant persistence

(Fig. 3a), although when combining all the non-significant effects, lags in range shifts tended to benefit plants there, similarly to the Mediterranean region (Fig. S9). The examination of the relative contributions of temperature and precipitation SCI trends to the climatic debt/bonus shows that temperature is generally the major driver (Fig 3c), except in the Atlantic region, where precipitation shifts are the only significant driver of estimated climatic costs. Importantly, SCI and occupancy trends are not significantly related during 1951-1990 (Fig. S6), when climate was relatively stable.

Finally, plant occupancy trends are also expectedly related to other drivers beyond climate change. At a continental scale, nitrophily and urban affinity are significant correlates of plant occupancy trends (Fig. 2b). We also find a negative but non-significant effect of pollinator dependency on occupancy trends (Fig. 2b). A majority of the remaining variables, such as most habitat affinities except urban affinity and moisture preferences, have contrasting effects on occupancy trends across biogeographic regions (Fig. S8).



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

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 former areas, and confirm the climatic bonus in the Mediterranean, although lags behind climate are most often interpreted as a climatic debt there (Bertrand *et al.* 2016). The effects of lagging behind changing precipitation are variable however. In relatively dry biogeographic regions, a decrease in the annual precipitation SCI of plant species over the past decades is associated with negative, or less positive, occupancy trends, which suggests that climate change causes water-deficit stress with detrimental consequences for plant population dynamics, a well-known phenomenon (Breshears *et al.* 2005; Allen *et al.* 2010; Zhao & Running 2010). This applies to the Mediterranean region, in which precipitation shifts can be as important a driver as temperature changes, although it is widely overlooked in climatic debt assessments.

In contrast, in relatively wet areas, plant occupancy trends seem to be hindered by an increase in annual precipitation SCI, which suggests water-excess stress, via e.g. waterlogging. Such consequence of climate change, via an increase in precipitation, is less documented but has been shown to drive downhill shifts in plant species elevation against temperature changes in mountain areas (Crimmins *et al.* 2011). Their general contribution to the climatic debt relative to temperature is however moderate, except in the Atlantic region.

Beyond the effects of climate change, our results also strongly suggest that nitrogen deposition and urbanization are important disturbances for plants (Aronson *et al.* 2014; Bobbink *et al.* 2016). However, while nitrogen deposition is sometimes cited as the first driver of changes in plant species composition (Bobbink *et al.* 2016), our results challenge this statement: by assessing response traits simultaneously, we find stronger links of occupancy trends with historical climatic niche or urban affinity than with nitrophily. Hence, our results are consistent with the recent acceleration of climate change in Europe and suggest that climate warming has caught up with urbanization and nitrogen deposition to become an important driver of plant persistence. We thus provide further evidence that biodiversity is often affected by multiple global change drivers rather than by single threats (Brooks *et al.* 2017). Consistent with previous results and with the pollinator decline (Biesmeijer *et al.* 2006), we find a negative effect of pollinator dependency on occupancy trends, but the latter is non-significant. This lack of signal for an effect of pollinator loss on plant occupancy trends may be attributable to contrasting plant trends depending on the group of pollinators (Biesmeijer *et al.* 2006).

Here we show that plants are under multiple pressures from global change, and that plant occupancy trends exhibit a strong phylogenetic signal, which entails a risk of important evolutionary history losses associated with the forecasted extinctions. In particular, in some regions plant persistence is already affected by climate change and the resulting climatic debt/bonus, while these climate-related costs/benefits are often considered long-term. The climatic debt/bonus evident here is an integrative measure of all ecological and evolutionary costs/benefits associated with climate change, which we are not able to partition. For example, the costs we observe in Northern Europe could be due to insufficient adaptive response to buffer a spatial lag, to the arrival of novel competitors (Alexander *et al.* 2015), and/or to the demographic cost of an ongoing adaptive response (Lynch & Lande 1993) buffering the spatial lag. As plant adaptation to climate change opens the door to a possible evolutionary rescue for species that track their climatic optimum poorly in space (Gonzalez *et al.* 2013), assessing the contribution of ecological and evolutionary mechanisms of the climatic debt or bonus is a remaining key challenge to predict future effects of climate change on plants.

Although this study tackled two dimensions of the species climatic niches simultaneously, our estimation of the climatic debt faces some limitations. First, we examined average climatic conditions only, thereby probably underestimating the cost of climate change, which also includes changes in variability, such as in the frequency of extreme events. Moreover, other environmental conditions beyond climate have changed during the last decades, such that their effects are difficult to unravel. Our climatic debt/bonus measure is thus integrative, likely including costs related to interactions between climate change and other drivers. For example landscape alteration can hinder species tracking of their historical climatic conditions (Bertrand *et al.* 2016; Gaüzère *et al.* 2017). We used a correlative approach on the basis of species traits, while taking phylogeny into account: the remaining phylogenetic signal in plant occupancy trends points to a likely omission either of some drivers or of synergistic effects among drivers. These could be investigated through local studies.

Finally, we present the first overview of plant occupancy trends at continental scale. This was made possible by the use of opportunistic data, which are often the only data source to obtain long time-series at large spatial extent (Biesmeijer *et al.* 2006; Bartomeus *et al.* 2019), together with statistical methods aiming to correct the potential biases associated with those data (Isaac *et al.* 2014). The fact that we find strong positive trends for invasive species suggests that trends estimated from GBIF data provide an accurate picture of actual changes in species occupancy. However, finding independent datasets and methods that allow turning the clock back and studying past effects of global change on biodiversity is a major challenge to confirm our results and anticipate future threats for biodiversity.

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Author Contributions

FD designed the study, extracted the data and performed all the statistical analyses. GM and FD extracted and compiled species traits. FD and EP wrote the paper with contributions from GM.

Competing interests

The authors declare no competing interests.

Data availability statement

R scrips used to perform the analysis are available here: https://github.com/f-duchenne/European-plants-lagging-behind-climate-change-. All data supporting the analysis, excepting row data from the GBIF, can be downloaded here: http://doi.org/10.5281/zenodo.4550500.

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