Title: Precipitation drives global variation in natural selection

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One sentence summary: Global and local climate conditions predict variation in natural selection across diverse plant and animal populations.

Abstract:

Climate change has the potential to affect the ecology and evolution of every species on Earth. While the ecological consequences of climate change are increasingly well documented, the effects of climate on the key evolutionary process driving adaptation—natural selection—is largely unknown. We report that aspects of precipitation and potential evapotranspiration, along with the North Atlantic Oscillation, predicted variation in selection across plant and animal populations throughout many terrestrial biomes, whereas temperature explained little variation. By showing that selection was influenced by climate variation, our results indicate that climate change may cause widespread alterations in selection regimes, potentially shifting evolutionary trajectories at a global scale.

Main text:

Climate affects organisms in ways that ultimately shape patterns of biodiversity (*1*). Consequently, the rapid changes in Earth's recent climate impose challenges for many organisms, often reducing population fitness (*2-4*). While some species may migrate and undergo range shifts to avoid climate-induced declines and potential extinction (*5*), an alternative outcome is adaptive evolution in response to selection imposed by climate (*6*). However, we lack a general understanding of whether local and global climatic factors such as temperature, precipitation, and water availability influence selection (*2, 7*). Understanding these effects is critical for predicting the consequences of increasing droughts, heat waves, and extreme precipitation events that are expected in many regions (*8, 9*).

To quantify how climate variation influences selection, we assembled a large database of standardized directional selection gradients and differentials from spatially (mean = 4.6 ± 5.4 [standard deviation, SD] populations, range = 2 - 59 populations) and temporally (mean = 5.2 ± 6.8 [SD] years, range = 2 - 45 years) replicated selection studies (N = 168) in plant and animal populations (Table 1, Database S1). We focused on directional selection (selection that can generate increases or decreases in trait values) because it is well-characterized and is likely to drive rapid evolution (*10*) in response to variation in climatic factors. However, selection acting on trait combinations and trait variance may also be affected by climate (*7*). Selection gradients estimate the strength and direction of selection acting directly on a trait, while differentials estimate 'total selection' on a trait via both direct and indirect selection because of trait correlations (*11*). These standardized selection coefficients describe selection in terms of the relationship between relative fitness and quantitative traits measured in standard deviations, thus facilitating cross-study comparisons (*11, 12*).

Geographically, the database contains many estimates of selection from temperate, mid-latitude regions centered at 40° N (Fig. 1A). The populations in this database span many terrestrial biomes on Earth, with the exception of tundra and tropical rainforests where selection

has rarely been quantified (Fig. 1B). This exception is concerning because tundra and tropical rainforests are likely to face severe effects of climate change (*1*, *13*). Spatially and temporally replicated studies of selection in aquatic environments are also uncommon (Table 1), so our results pertain mainly to terrestrial systems. Additionally, the majority of studies are from vertebrate and plant populations, use fecundity or survival as a fitness measure, and use morphological traits (Table 1).

These data allowed us to determine whether directional selection covaries with changes in climatic factors among populations or across time within a given population. For each set of selection estimates, we geo-referenced the population and cross-referenced each population and time point with corresponding values of both local and global climatic factors (Database S2). We then used a random effects Bayesian Markov chain Monte Carlo meta-analysis to estimate the proportion of variation in selection within spatially and temporally replicated studies that was associated with climatic factors (*14*). This analysis is a hierarchical model, which separates the observation process (accounting for statistical noise in inference of individual selection coefficients because of sampling error) from a process model (modelling variation in the selection coefficients in relation to climate variables) (*14*). Under this analytical framework, we used a random regression mixed model component to model the distribution of within-study variation in the dependence of selection on climatic factors (*14*). As a measure of effect size, we present the mean and 95% credible intervals of the proportion of within-study variation in selection explained by a given climatic factor.

To investigate the role of local (0.5 x 0.5 degree cells) climatic factors, we analyzed air temperature, precipitation, and potential evapotranspiration (PET). While there is likely climate variation within a 0.5 degree grid, the populations where selection was quantified will often be spread out over this grid area, and the scale of climate variation is typically at an even larger geographic scale. We analyzed the data in two ways: with spatially and temporally replicated selection estimates both included together and treated separately. We modeled how mean annual

values of climatic factors influenced directional selection, as well as variation (the standard deviation [SD]), and the influence of extremes (minimum and maximum monthly values for a year) in these climatic factors because climate extremes frequently determine fitness and are expected to increase with climate change (*15, 16*).

When combining spatial and temporal studies, models that included temperature factors did not explain variation in selection (Fig. 2A, B). However, 20-40% of the variation in selection was associated with precipitation mean, maximum, and SD (Fig. 2C, D). Because precipitation factors are correlated (Table S1), our results collectively illustrate the potentially general importance of local precipitation as a selective force. In addition, minimum PET explained more than 20% of the variation in selection across the dataset (Fig. 2E, F). When we ran the analyses separately for spatial and temporal selection, the results largely mirrored the patterns in the combined analysis (Figs. S1-S2). However, we found that for selection gradients, but less so for differentials, precipitation factors were more strongly associated with temporal rather than spatial variation in selection (Figs. S1-S2). A multivariate model that included means and SDs of both precipitation and temperature together (*14*) supports the finding that variation in selection is most closely associated with precipitation factors (Table S2). However, given the low levels of replication typical of individual studies, we cannot unambiguously attribute a direct effect to any one of these four climate factors (Table S2).

We also explored whether within-study variation in selection associated with local climatic factors differed among subsets of major trait types, fitness components, and taxonomic groups (*14*). This analysis also indicated effects of precipitation and PET, although, there is substantial variation across the different subsets (Tables S3-S5). Among fitness components, no precipitation or PET climatic factors were consistently most associated with selection through mating success; however, selection through fecundity and survival were affected by precipitation, and survival alone was also affected by minimum PET (Table S3). Selection on morphological traits was most associated with precipitation factors, but not size or phenological

traits (Table S4). Precipitation also explained variation in selection on plants, whereas minimum PET consistently explained variation in selection among all major taxonomic groups (Table S5). While these findings are intriguing, it is important to note that the overall analysis revealed somewhat low precision in the estimates of the dependence of selection on climatic factors (Fig. 2, S1 and S2), and these subset analyses resulted in many estimates. With these important caveats in mind, we encourage a cautious interpretation of the above subset findings (*14*).

In addition to local climate variation, global climate cycles are known to be powerful agents of selection (*17*), but their capacity to operate as drivers of selection more broadly is unclear. To explore how annual global climate cycles may affect selection, we modeled the relationship between temporal variation in selection and the North Atlantic Oscillation (NAO) and the Oceanic Niño Index (ONI), which provide measures of inter-annual variability in atmospheric circulation for northern hemisphere and equatorial regions, respectively (*14*).

We found that the NAO explained between 10-30% of the variation in selection, whereas the ONI explained no appreciable variation (Fig. 3). The NAO was also most associated with selection through fecundity as a fitness component (Table S3), selection on morphological traits (Table S3), and on invertebrate and plant populations (Table S5). The overall stronger effect of the NAO (Fig. 3) relative to the ONI index is perhaps not unexpected because the ONI index would presumably be more important at equatorial latitudes (where studies of selection are rare), whereas the NAO index would be more important at northern latitudes (where selection is well documented; Fig. 1A). Indeed, although global in their reach, there are frequently correlations between large-scale climatic indices and local variation in climatic conditions that have subsequent effects on ecological and evolutionary processes (*18, 19*). Moreover, these global climate cycles are changing in response to climate change (*20*) and may therefore have cascading effects on selection at a global scale.

Previous studies have predicted the greatest fitness consequences associated with climate variation, especially related to precipitation, should occur at northern latitudes (*2*). Our results

add a further nuance to these potential climate effects and suggest that variation in fitness associated with precipitation may also influence selection (Fig. 2, S1-2). Increases in strong precipitation events that are predicted for the near future (*21*) could therefore result in considerable shifts in patterns of selection. Similarly, variation in selection was associated with variation in minimum PET—conditions when water deficits are low. While correlative, our findings do not support the idea that short-term moisture stress, as indicated by minimum precipitation or maximum PET, is a major driver of selection. Conversely, the effects of changes in mean precipitation could result from sustained drought conditions or changes in resource abundance related to water availability (*17*).

Whether climate-selection coupling will lead to local adaptation and reduce the risk of extinction is difficult to predict (*3, 6*), because adaptive evolution also depends on genetic variation in the traits under selection (*3, 11*). Moreover, if selection is strong relative to existing genetic variation, and if the rate of climate change is rapid, selection might result in population extinction faster than adaptation and evolutionary rescue (*3, 22*). Phenotypic plasticity might also therefore have a key role in promoting population persistence due to climate change (*6, 7*).

Our analysis benefits from drawing on decades of accumulated inferences about natural selection. However, we acknowledge a potential limitation: annual measures of local climate factors may not always reflect the most relevant scale underpinning selection in a population (*19*). Although annual variation at even larger geographic scales such as the NAO (Fig. 3) often have considerable predictive power for explaining variation in demographic rates (*18, 19*), short-term climatic and extreme weather events, including winter storms and heat waves, can also generate strong selection (*23*). Our finding of no effect of temperature on selection, despite case studies showing an influence of temperature (*24*), suggests that such selection may be occasionally driven by shorter-term thermal variation. The association between selection and PET is consistent with this interpretation because PET is calculated from temperature, but reflects temperature during the growing season when selection is most often studied. In contrast,

the observed relationship between precipitation and selection at the annual scale makes sense because moisture availability is determined by precipitation over longer periods. Ultimately, to more fully understand and predict the consequence of climate variation on selection we also need replicated transplant experiments across broad climate gradients in diverse systems (*6*). Transplant experiments would be especially beneficial because past selection may have eroded trait variation as populations locally adapted to a given climate regime, and such experiments would force populations to experience potentially stronger selective climate conditions, much like they could under climate change.

We have identified a signature of the effects of climate on selection in a phylogenetically diverse dataset across multiple environments. This provides evidence that local and global climate cycles are likely important drivers of selection in the wild. Thus, rather than selection being driven entirely by the local idiosyncrasies of each system, selection is partly predictable based on shared environmental features. Although ecologists and biogeographers have long recognized the importance of climate for explaining major ecological patterns, our analyses reveal a role for climate in explaining a key evolutionary process. In this era of unprecedented change to Earth's climate (*8, 9*), and as future climatic conditions are expected to become increasingly more variable (*15*), natural populations will likely have to contend with greater climate variation than they have in the recent past. Such shifting climatic conditions, particularly changing precipitation patterns (*2, 21*), may present a challenge for many organisms (*7, 16*).

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Supplementary Materials:

Materials and Methods

Figs. S1 and S2

Table S1-S5

Databases S1 and S2

References (*25-41*)

Figure legends:

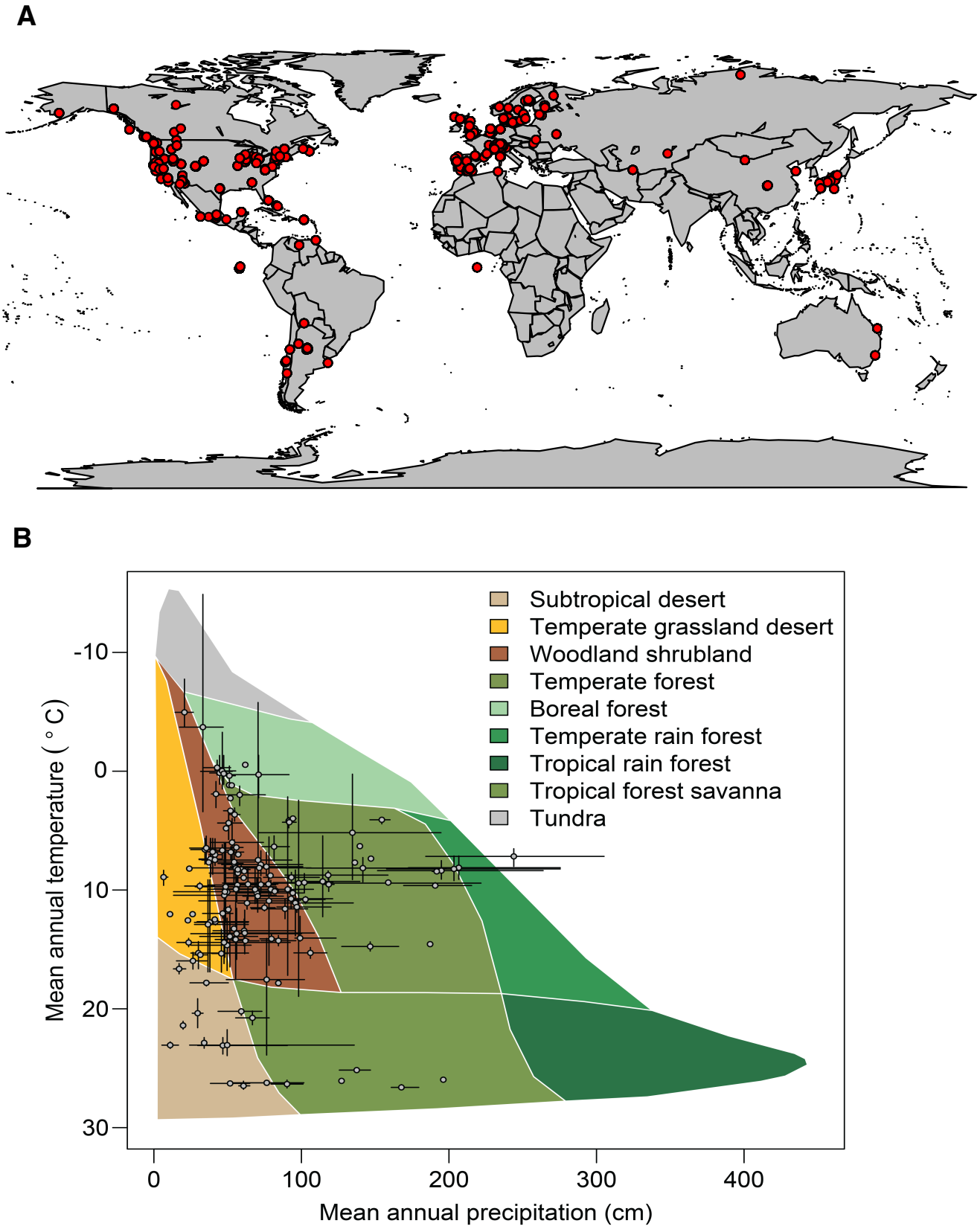
Fig. 1. Selection estimates included in this study are broadly distributed geographically and in climate space. (A) Red circles denote individual study locations of natural selection. **(B)** Shown are individual studies overlaid on Whittaker's terrestrial biome plot, which demarks biomes as a function of mean annual precipitation and temperature *(14)*. Points represent mean annual temperature and precipitation across the years of investigation for each study and lines denote the minimum and maximum across the time period of each study.

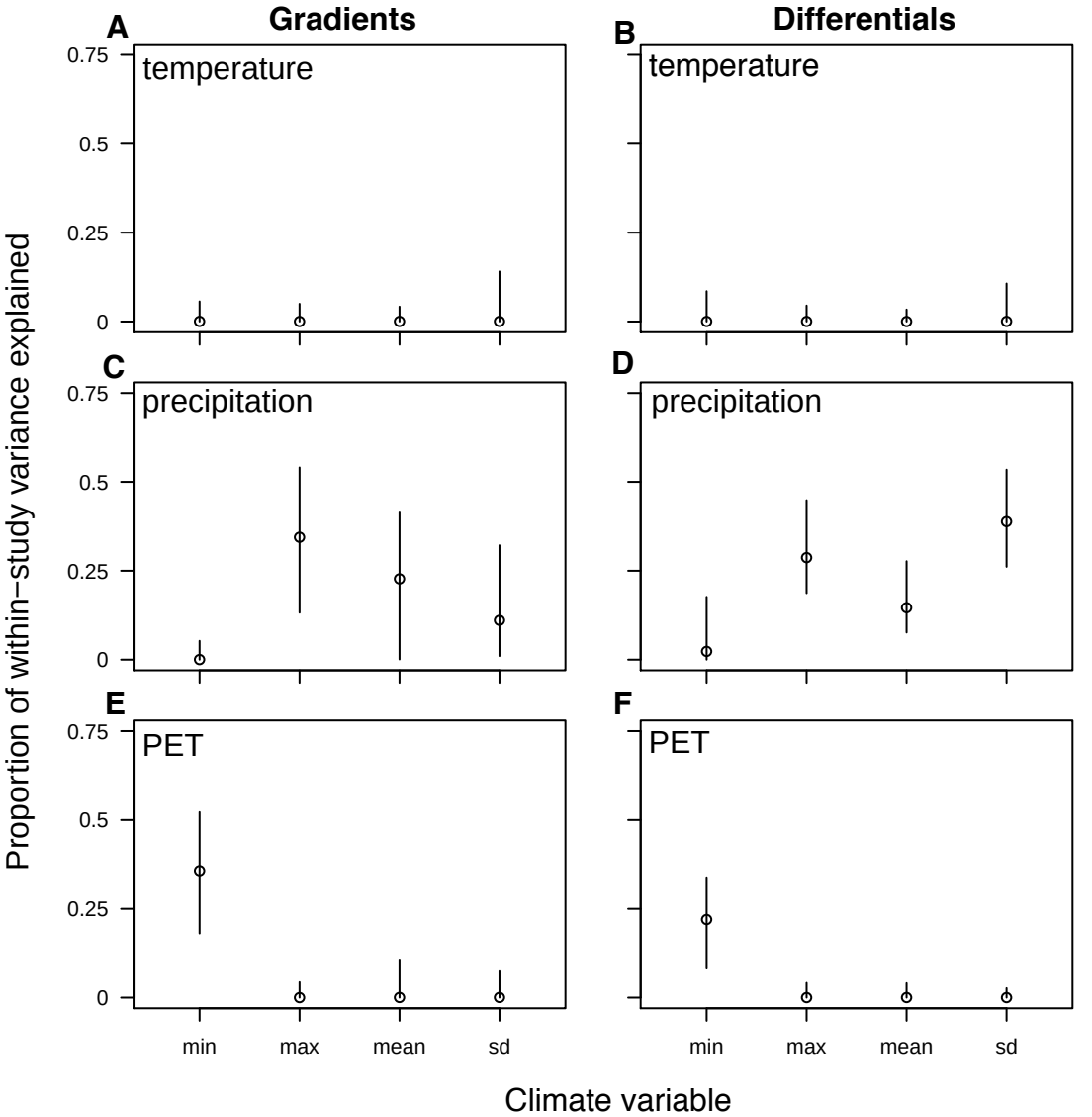
Fig. 2. Variation in selection is explained by local climate factors. Shown are mean and 95% credible intervals of the proportion of within-study variation in selection (combining temporal and spatial variation; see fig. S1 and S2 for temporal and spatial variation analyzed separately, respectively) explained by a given climatic factor. Little variation in selection gradients **(A)** and differentials **(B)** is accounted for by temperature, whereas considerable variation in gradients **(C)** and differentials **(D)** is accounted for by precipitation. Likewise, minimum PET also consistently explains variation in selection for both selection gradients **(E)** and differentials **(F)**.

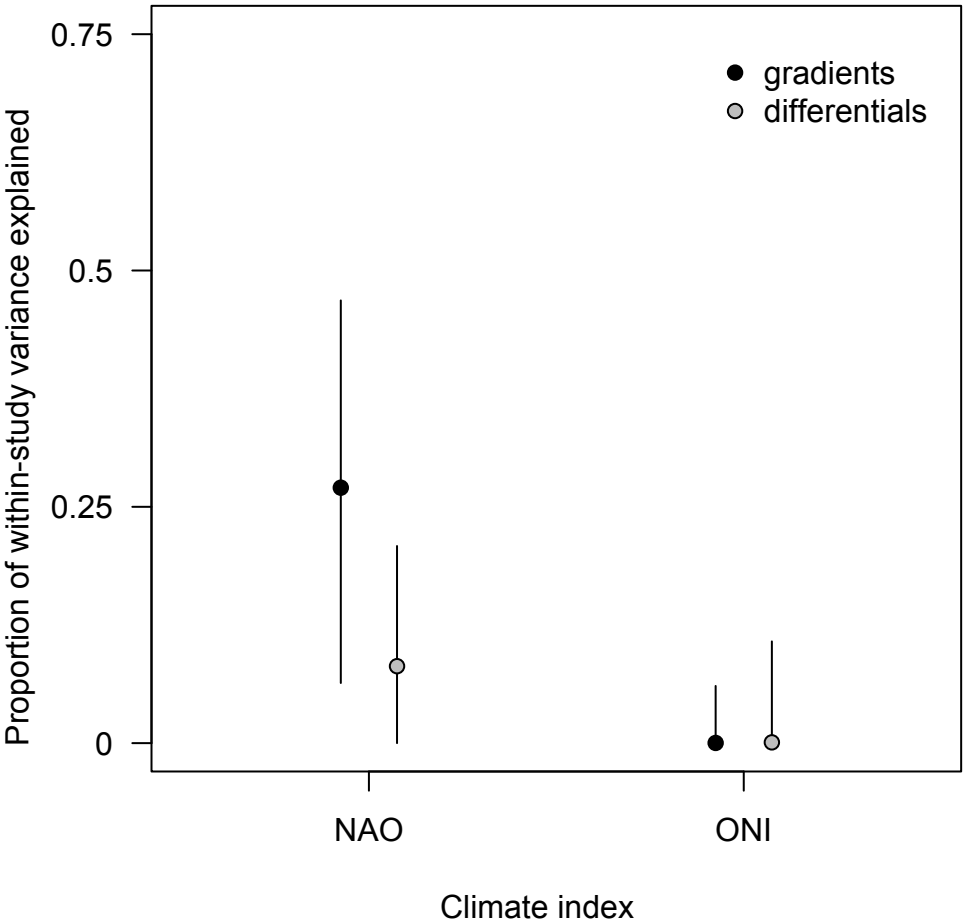
Figure 3. Variation in selection is explained by global climate indices. Shown are mean and 95% credible intervals of the proportion of within-study variation in selection gradients (black circles) and differentials (grey circles) explained by the North Atlantic Oscillation (NAO) index and the Oceanic Niño Index (ONI).

Table 1. Summary of records in the selection database.
Numbers refer to the number of items in the database.
Only those records with SE's were used in analyses (*14*).

	Replicate type	
Item	Spatial	Temporal
Studies	84	120
Selection coefficients		
Linear differentials	1608	2539
Linear gradients	2658	3120
Species	70	97
Habitat		
Terrestrial	3098	4409
Freshwater	527	713
Marine	8	73
Taxon type		
Invertebrates	1050	627
Plants	1381	1046
Vertebrates	1202	3522
Trait Type		
Behavioral	21	54
Other	126	286
Morphological	2298	1818
Life History	334	542
Principal Components	158	307
Phenology	327	1154
Size	369	1034
Fitness Component		
Fecundity/Fertility	1848	1758
Mating Success	847	863
Other	227	35
Survival	656	2481
Survival and Fecundity	16	0
Total Fitness	39	58


A
B
Subtropical desert
Temperate grassland desert
Woodland shrubland
Temperate forest
Boreal forest
Temperate rain forest
Tropical rain forest
Tropical forest savanna
Tundra
-10
0
10
20
30
Mean annual temperature (° C)
0
100
200
300
400
Mean annual precipitation (cm)


Gradients
Differentials
A
B
C
D
E
F
temperature
precipitation
PET
0.75
0.5
0.25
0
min
max
mean
sd
Proportion of within−study variance explained
Climate variable


0.75
0.5
0.25
0
Proportion of within-study variance explained
gradients
differentials
NAO
ONI
Climate index



Supplementary Materials for

Climate variation shapes natural selection in the wild

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This PDF file includes:

Materials and Methods
Figs. S1 and S2
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Captions for database S1 and S2

Other Supplementary Materials for this manuscript includes the following:

Database S1 and S2: Selection database, Climate database

Materials and Methods

Selection database construction

We assembled a database of spatially (2 or more populations) and/or temporally (2 or more annual estimates from a given population) replicated studies of phenotypic selection on quantitative traits in the wild. By and large, the data sets were either spatially or temporally replicated; only 23 % of the selection estimates included both spatial and temporal replication in the same study. The database consists of standardized measures of selection coefficients: differentials and gradients. These standardized selection coefficients reflect selection on traits in terms of the relationship between relative fitness and variation in a quantitative trait measured in standard deviation units, and are desirable because they allow for cross-study comparisons, irrespective of study organism, fitness measure, or trait studied (*11, 12*).

To begin, we combined earlier published databases that compiled studies on spatially (*25*) and temporally (*26*) replicated estimates of selection. Because the initial temporal database included studies published up until March 2008 and the spatial database studies up December 2011, we performed an additional literature search from March 2008 through December of 2012 to identify additional studies for inclusion. We reviewed the published literature for additional spatially and temporally replicated selection studies using the Web of Science indexing database system with the goal of identifying all studies estimating selection on multiple populations or multiple temporal replicates within populations. This search resulted in an additional 723 studies that we screened for inclusion in our final database. We also included two additional studies published shortly after December 2012 that we became aware of during our study.

Our inclusion requirements included criteria used in previous database compilations (*12, 25, 26*). Specifically, we only included studies that (i) focused on wild, un-manipulated populations, (ii) estimated selection on quantitative traits that showed continuous variation, (iii) presented variance standardized selection differentials and/or gradients (*11, 12*) to facilitate comparisons across studies, and (iv) estimated selection in at least two populations or two annual temporal replicates within a population. When articles reported that selection had been measured on different populations, but data from multiple populations were combined for analyses, we contacted the authors to ask for population-specific selection coefficients. These later estimates were published in the appendix of (*26*). We relied on the author's designations of populations being unique if the populations were either noted by the authors as geographically distinct, or were reported in the article to be genetically distinct. We suspect some level of dispersal might occur between some populations, but most studies lacked information (e.g., analysis of neutral genetic markers) to evaluate this possibility. Three studies estimated selection over multiple years, but presented their data averaged over the duration of their study, and so we contacted these authors directly to obtain year-specific selection coefficients. These later estimates were published in the appendix of (*25*). When data were presented in figure format, we contacted authors directly to obtain values of the selection coefficients. Each article was entered into the database by one author and error checked

by a different author. The database is available from the Dryad Digital Repository and as Database S1.

In many studies, multiple datasets existed *within* studies. These within-study datasets represent selection estimated on different subsets of data defined by species, trait, fitness component, sex, age, etc. For clarity, we use the term "dataset" to refer to each unique combination of the above within studies.

Climate variables

We obtained local climate data at a resolution of 0.5 x 0.5 degree cells from the CRU-TS 3.1 Climate Database (*27*) spanning the years of data collected in the selection database. These climate data are one of the finest scale climate databases available at a global scale and are frequently used in large scale biological analyses such as ours (*28, 29*). Although the 0.5 degree cell size changes with latitude, our use of a 0.5 degree grid was simply the mechanism that rendered the opportunity to resolve the climate and selection databases. That is, with matched projections for coordinates and climate grids, the decrease in grid cell size with increasing latitude had little bearing on the fact that we simply extracted climate data from the 0.5 x 0.5 degree cell within which each population coordinate resides.

From these data, we generated grid files reflecting annual mean, annual standard deviation, and annual monthly minimum and maximum values for precipitation, temperature, and potential evapotranspiration (PET) across the study period. PET is an informative climatic index because it integrates the effects of temperature, humidity, and radiation to quantify the overall potential moisture deficit for a location (*30*). To obtain appropriate temporal and spatial climatic information for each study location, we performed a spatial overlay of study site coordinates over each climatic grid using the function *over* in the R package *sp* (*31*). This procedure was performed to estimate climate values experienced at each study location during the year in which the data were collected for a given population. This database is available from the Dryad Digital Repository and as Database S2.

We obtained annual global climate indices (ONI and NAO) from the National Weather Service at the National Oceanic and Atmospheric Administration. These indices relate variability in atmospheric forcing of climate change in northern and southern hemisphere mid-latitude regions. We used the Oceanic Niño Index (ONI) as a measure of the El Niño Southern Oscillation retrieved from http://www.esrl.noaa.gov/psd/data/correlation/oni.data [Accessed February, 2014]. The North Atlantic Oscillation (NAO) index was retrieved from http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml [Accessed September, 2013]. For each year of study in our database we used the mean value of the monthly reported ONI and NAO indices.

We generated the Whittaker's biome plot (Fig. 1B of the main text) overlaid with selection estimates using the BIOMEplot package in R (*32*), where biomes are plotted

using annual mean cumulative precipitation and annual mean temperature that had been digitized from Ricklefs (*33*). To display the environments represented in our study samples through an overlay on Whittaker's biome plot, we used the annual mean temperature and annual cumulative precipitation generated from the CRU dataset for each location to calculate annual mean temperature and annual mean cumulative precipitation for each study across the duration of the study. Additionally, for the timeframe of each study we also calculated the lowest and highest annual mean temperature and annual mean cumulative precipitation to represent the climatic extremes experienced in each study.

Meta-analytical model and analysis

From earlier analyses, we know that there is non-trivial, detectable variation in selection in space and time (*25, 26, 34*), and progress has been made in developing meta-analytical methods to get at this variation accounting for the fact that variation in selection can be inflated by sampling error (*25, 34*). Thus, to control for sampling error we only used those records from the database that had associated standard errors with the selection coefficients (n = 2385 selection gradients and n = 946 selection differentials).

We used a random effects meta-analysis to determine the proportion of variation in selection across the entire database that could be accounted for by different climate variables after taking into account sampling error. This analysis can be most intuitively represented as a hierarchical model, separating the observation process (i.e., modelling statistical noise in inference of individual selection coefficients) and a process model (i.e., modelling variation in the underlying selection coefficients).

We model the observation process according to

$$(1) \qquad \hat{\beta}_{i,j} \sim N\left(\beta_{i,j}, SE_{i,j}^2\right),$$

where $\hat{\beta}_{i,j}$ is the ith selection coefficient (linear gradient or differential) estimate for the jth trait/study combination (that is, a given combination of phenotypic traits and/or fitness components, etc. for a given study; hereafter "trait"). Each selection gradient estimate $\hat{\beta}_{i,j}$ is assumed to be drawn from a normal distribution with a mean corresponding to the true, unobserved (i.e., latent), corresponding selection gradient $\beta_{i,j}$, and with a known variance defined by the square of the corresponding standard error $SE_{i,j}$.

We model the distribution of (latent) selection gradients according to

$$(2) \qquad \beta_{i,j} = \alpha_j + b_j \times \varepsilon_{i,j} + e_{i,j},$$

where α_j is the intercept for trait j and b_j is a trait-specific slope of the regression of the selection gradient on the climate variable $\varepsilon_{i,j}$ (e.g., precipitation, temperature, PET, NAO, etc.) for the ith selection coefficient of the jth trait, and $e_{i,j}$ is the residual (the deviation of the ith selection coefficient from its associated trait-specific regression). For all analyses, the climate variable is standardized within each dataset (as described above) to have a mean of zero and a variance of one. Under this standardization, trait-specific intercepts

are interpretable as trait-specific mean selection gradients. Note that unlike most applications of mixed models, the $e_{i,j}$ are not simply random noise, but are the variation in selection among replicates (i.e., within traits), and as such is a parameter of biological interest. We assume

$$(3) \quad e_{i,j} \sim N(0, \sigma_e^2),$$

where σ_e^2 is the estimated residual variance. The random intercepts (α_j) and random slopes (b_j) were modelled with a bivariate normal distribution with means μ_α and μ_b, and standard deviations σ_α^2 and σ_b^2, respectively, and covariance $\sigma_{\alpha,b}$

$$(4) \quad \begin{bmatrix} \alpha_j \\ b_j \end{bmatrix} \sim N\left(\begin{bmatrix} \mu_\alpha \\ \mu_b \end{bmatrix}, \begin{bmatrix} \sigma_\alpha^2 & \sigma_{\alpha,b} \\ \sigma_{\alpha,b} & \sigma_b^2 \end{bmatrix} \right),$$

where the mean intercept μ_α and slope μ_b, and their covariance matrix, are estimated parameters.

We implemented all analyses in a mixed model framework, using MCMCglmm (*35*). We used default diffuse normal priors on the fixed parameters (i.e., the overall intercept and average slope), parameter-expanded priors (*36, 37*) for the random (co)variance components (i.e., of the random slopes and intercepts), and a diffuse inverse gamma prior for the residual variance. The analysis is thus similar to the meta-analytic models of selection gradients in (*25*) and (*34*) for estimating within-study variance in selection, but with the extension to a random regression component to model the distribution of among-study variation in the dependence of selection on climate variables, via equation 4.

This model can be summarized in terms of the amount of variance in slopes (i.e., σ_b^2), but a more intuitive summary is obtained by considering how much (within-study) variance in selection coefficients is implied by the family of regressions between each climate factor ($\varepsilon_{i,j}$) and its corresponding selection estimate ($\beta_{i,j}$) that is estimated by the random regression mixed model. Given that within-study environmental covariates are standardized to mean zero and unit variance, the variance among studies is σ_α^2 (note that in a linear random regression model, the covariance of slopes and intercepts, $\sigma_{\alpha,b}$ does not enter into the among study variance). The variance within studies associated with environmental variables is σ_b^2, and the variance within studies that is not associated with the environment is the residual variance. The sum of these is the total variance in selection.

In the analyses of all replicates (combined space and time) we did not decompose the residual variance into that associated with space, time, and their interaction. These possible separate components of the residual variance are not separable because very few studies report on both temporal and spatial replicates together (only 23 % of selection

estimates). Rather, the great majority report on variation in selection only in space or in time. It is for this reason that we can conduct analyses where we combine space and time, and then analyze space and time separately as we have done. Those few studies that report both spatial and temporal replication jointly typically have very low levels of replication in both, and will therefore not contribute sufficient information to separate these different, and potentially interesting, components of variation in selection. The residual variance, in the combined analysis, is thus simply interpretable as the total variance in selection, accounting for the climate variables, across both classes of replication.

Multivariate extension

Whether individual climate-selection associations are attributable to the climate variable in question, or whether they arise largely via associations with other climate variables, is of interest. However, with the generally low level of replication in individual studies (e.g., typically 2-5 data points for any given trait within any given study) it is infeasible to include many climate variables simultaneously in a multivariate model. Thus, to target the most relevant comparisons in a multivariate analysis, we developed a model that included the means and standard deviations of both temperature and precipitation in a single model by expanding equations 2 and 4 to accommodate four, rather than one, estimates of variance in slopes.

To manage the complexity of the model, we did not estimate covariances among the random slope terms, and we applied the analysis only to selection gradients, which is the measure of selection for which we have the most data (Table 1). The variance explained by the random slopes in this model depends on the within-study correlations among variables, which varies among studies. Therefore, rather than presenting variance associated with each climate variable as a proportion of the within-study variance in selection, as done for the univariate models, we present the variances in direct effects for each climate covariate (Table S2).

Sub-set analysis of trait types, fitness components, and taxonomic groups

We also conducted analyses where we estimated how much variation in selection associated with local and global climatic factors varied among fitness components, trait types, and major taxonomic groups. These subsets are typical of meta-analyses such as ours (*12, 25, 26*). We conducted these analyses using selection gradients, and those fitness components, trait types, and taxonomic groups where we had the most substantial data (Table 1).

Results from this analysis reveal some very intriguing patterns of heterogeneity in the possible effects of climate on selection through fitness components (Table S3), trait types (Table S4) and taxonomic groups (Tables S5). However, interpretation of the results requires some caution. While the analysis benefits from drawing on a large database assembled from decades of accumulated inferences about natural selection (Table 1, Database S1) that are based on a solid theoretical framework (*11*), and the opportunity to resolve these selection inferences with detailed climate data, the somewhat

low precision of the resulting estimates of the dependence of selection on climate variables (e.g., Figs. 2 and 3, S1 and S2) requires caution because such analyses result in many estimates, and their interpretation in isolation would likely be unreliable (*38, 39*). The causes of the low precision, despite large quantities of data (Table 1 and S1) is two-fold: the imprecision of individual selection estimates (*34*) and the somewhat limited extent of temporal and spatial replication of most studies (*25, 26, 34*). It is therefore important to note that apparently significant (i.e., non-overlapping 95% credible intervals), large estimated effect sizes would be inevitable given the low precision noted above (e.g., type M errors, *38, 39, 41*). These issues highlight the need for studies with larger sample sizes, and continued long-term and spatially replicated studies for tackling longstanding questions in ecology and evolution (*40*). Additionally, experimental approaches are needed to further investigate these patterns (*6*). Importantly, though, these cautionary statements do not in any way preclude the potential biological significance of these findings.

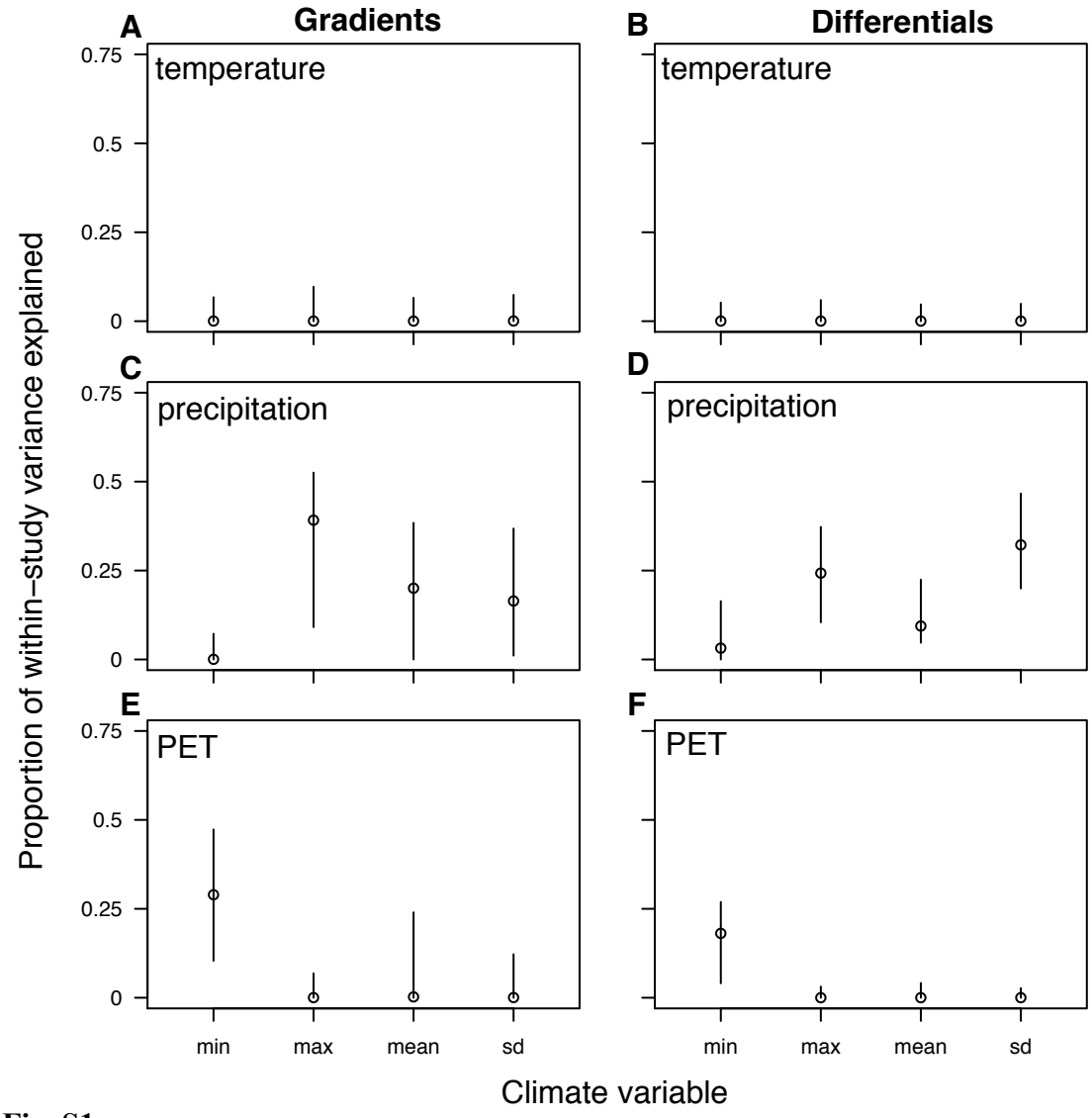


Fig. S1.

Temporal variation in selection explained by local climate factors. Shown are mean and 95% credible intervals of the proportion of within-study temporal variation in selection explained by a given climate variable ((A) and (B) temperature, (C) and (D) precipitation, and (E) and (F) PET) from a Bayesian meta-analytical model. Across all panels, the left column shows climate-selection associations with selection gradients and the right column selection differentials.

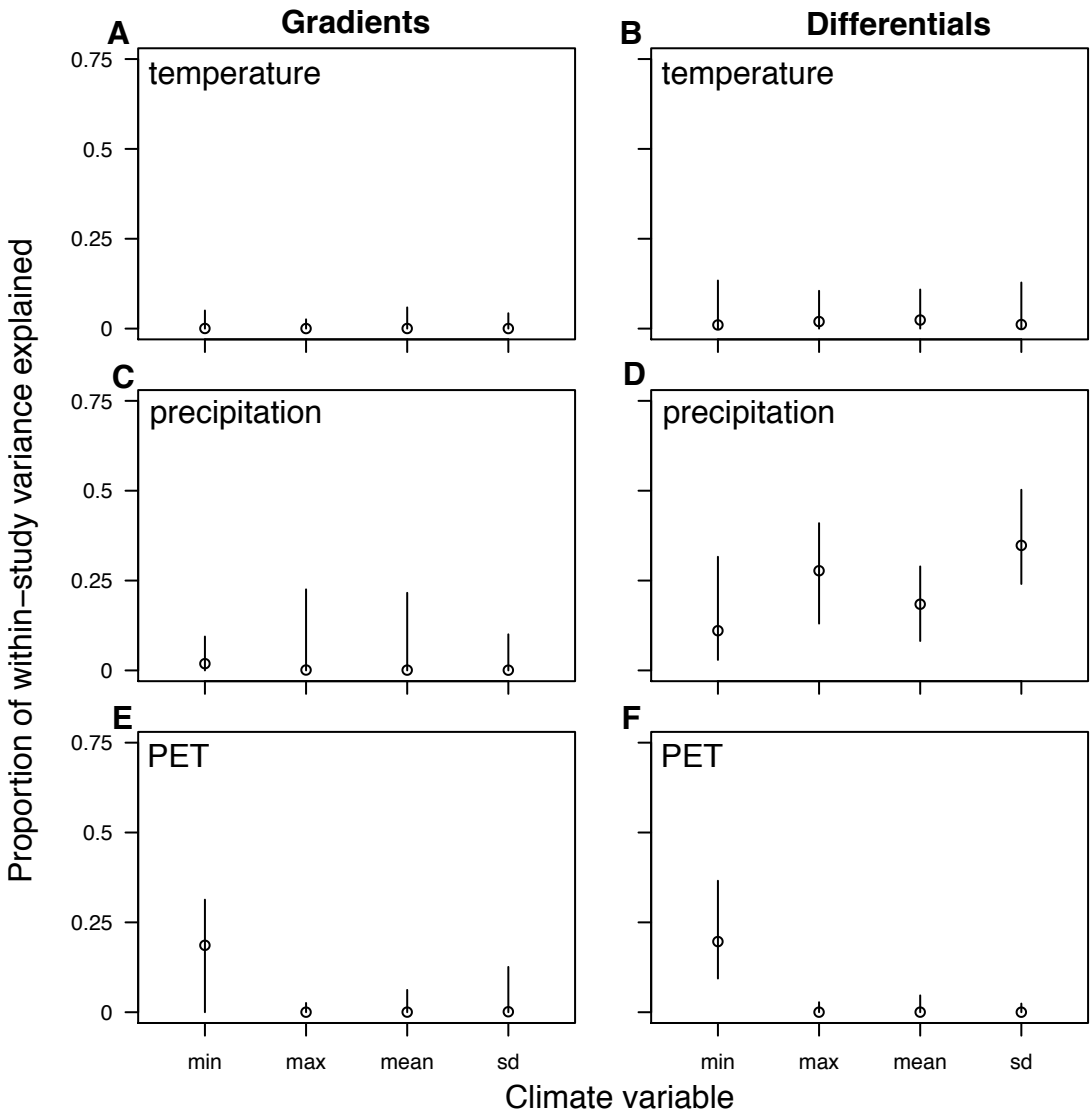


Fig. S2.

Spatial variation in selection explained by local climate factors. Shown are mean and 95% credible intervals of the proportion of within-study spatial variation in selection explained by a given climate variable ((A) and (B) temperature, (C) and (D) precipitation, and (E) and (F) PET) from a Bayesian meta-analytical model. Across all panels, the left column shows climate-selection associations with selection gradients and the right column selection differentials.

Table S1.

Correlation matrix of climate variables across studies. Min. = minimum, max. = maximum, SD = standard deviation.

	Mean temp.	Min. temp.	Max temp.	SD temp.	Mean precip.	Min. precip.	Max precip.	SD precip.	Mean PET	Min. PET	Max. PET	SD PET
Mean temp.	1.000											
Min. temp.	0.868	1.000										
Max temp.	0.666	0.280	1.000									
SD temp.	-0.575	-0.864	0.147	1.000								
Mean precip.	0.020	0.236	-0.393	-0.403	1.000							
Min. precip.	-0.135	-0.006	-0.384	-0.125	0.738	1.000						
Max precip.	0.107	0.305	-0.278	-0.451	0.890	0.530	1.000					
SD precip.	0.177	0.365	-0.211	-0.498	0.826	0.368	0.968	1.000				
Mean PET	0.701	0.395	0.878	-0.086	-0.322	-0.406	-0.157	-0.061	1.000			
Min. PET	0.865	0.686	0.666	-0.464	-0.021	-0.164	0.085	0.163	0.834	1.000		
Max. PET	0.317	0.038	0.776	0.234	-0.536	-0.575	-0.351	-0.255	0.818	0.421	1.000	
SD PET	-0.231	-0.423	0.402	0.580	-0.591	-0.527	-0.461	-0.407	0.336	-0.206	0.787	1.000

Table S2.

Results from a multivariate model simultaneously estimating the variance of slopes of regressions of selection gradients on four key climate variables (mean and SD of temperature, and mean and SD of precipitation). Shown are intercepts and slopes with their 95% credible intervals (in parentheses) from a Bayesian meta-analytical model. The variances of slopes represent the variance in the partial effects (i.e., conditioning on the other climate variables) of each climate variable across study systems. Not surprisingly, given the typically low levels of replication within studies, we cannot unambiguously attribute a direct effect to any one of the four modelled key climate variables (the slope variances of each climate factor have similarly very low lower bounds to their CIs). However, the results are consistent with patterns revealed in the univariate analyses of climate variables that variation in selection within studies tends to be most strongly associated with variation in precipitation (Fig. 1, Figs. S1 and S2). All covariates were standardized within studies to a variance of one, so fixed and random slopes are in units of changes in standardized selection gradients per standard deviation of the environmental variable.

Coefficient	Fixed intercept or slope	Random variance of intercepts or slopes
Intercept	0.053 (0.026 - 0.080)	0.042 (0.035-0.051)
Mean temp.	-2.9×10^{-4} (-6.3×10^{-3} - 6.5×10^{-3})	4.1×10^{-5} (1.6×10^{-10} – 1.6×10^{-4})
SD temp.	3.7×10^{-3} (-3.8×10^{-3} – 0.011)	2.5×10^{-4} (7.8×10^{-10} – 9.2×10^{-4})
Mean precip.	-1.9×10^{-3} (-0.012 - 7.7×10^{-3})	1.1×10^{-3} (1.6×10^{-10} – 2.4×10^{-3})
SD precip.	-1.8×10^{-3} (-0.012 - 6.4×10^{-3})	4.0×10^{-4} (6.5×10^{-10} – 1.3×10^{-3})
Residual	-	3.9×10^{-3} (3.1×10^{-3} – 4.8×10^{-3})

Table S3.

Variation in selection explained by local and global climate factors among different fitness components. We only considered those fitness components that were well-represented in the database (Table 1). Shown are mean and 95% credible intervals (in parentheses) of the proportion of within-study variation (combining both spatial and temporal replication; temporal replication only for NAO and ONI) explained by a given climatic factor from a Bayesian meta-analytical model.

Climatic factor	Fitness component		
	Fecundity	Mating	Survival
Min. temp.	0.001 (0 - 0.277)	0.001 (0 - 0.239)	0.001 (0 - 0.113)
Max. temp.	0.001 (0 - 0.16)	0 (0 - 0.121)	0.001 (0 - 0.253)
Mean temp.	0.001 (0 - 0.143)	0.001 (0 - 0.174)	0.003 (0 - 0.417)
SD temp.	0.419 (0.062 - 0.612)	0.001 (0 - 0.181)	0 (0 - 0.077)
Min. precip.	0.001 (0 - 0.209)	0.001 (0 - 0.16)	0.608 (0.069 - 0.789)
Max. precip.	0.637 (0.395 - 0.78)	0.002 (0 - 0.284)	0.132 (0 - 0.44)
Mean precip.	0.002 (0 - 0.354)	0.001 (0 - 0.271)	0.351 (0.032 - 0.652)
SD precip.	0.579 (0.33 - 0.75)	0.001 (0 - 0.303)	0.059 (0 - 0.192)
Min. PET	0.389 (0 - 0.544)	0.003 (0 - 0.578)	0.422 (0.083 - 0.645)
Max. PET	0.001 (0 - 0.14)	0.001 (0 - 0.153)	0 (0 - 0.085)
Mean PET	0 (0 - 0.14)	0.001 (0 - 0.212)	0.474 (0 - 0.643)
SD PET	0 (0 - 0.112)	0.001 (0 - 0.145)	0.004 (0 - 0.585)
NAO	0.815 (0.44 - 0.912)	0.002 (0 - 0.301)	0.002 (0 - 0.235)
ONI	0.409 (0 - 0.76)	0.001 (0 - 0.187)	0 (0 - 0.032)

Table S4.

Variation in selection explained by local and global climate factors among different trait types. We only considered those trait types that were well-represented in the database (Table 1). Shown are mean and 95% credible intervals (in parentheses) of the proportion of within-study variation (combining both spatial and temporal replication; temporal replication only for NAO and ONI) explained by a given climatic factor from a Bayesian meta-analytical model.

Climatic factor	Trait type		
	Size	Morphology	Phenology
Min. temp.	0.325 (0 - 0.662)	0.004 (0 - 0.665)	0.001 (0 - 0.195)
Max. temp.	0.005 (0 - 0.604)	0.526 (0.039 - 0.706)	0.001 (0 - 0.207)
Mean temp.	0.579 (0.099 - 0.837)	0.471 (0.019 - 0.713)	0.001 (0 - 0.162)
SD temp.	0.005 (0 - 0.649)	0.003 (0 - 0.551)	0.001 (0 - 0.1)
Min. precip.	0.003 (0 - 0.475)	0.695 (0.377 - 0.842)	0.001 (0 - 0.154)
Max. precip.	0.001 (0 - 0.44)	0.522 (0.211 - 0.693)	0.001 (0 - 0.213)
Mean precip.	0.707 (0.288 - 0.85)	0.719 (0.484 - 0.841)	0.002 (0 - 0.323)
SD precip.	0.003 (0 - 0.447)	0.486 (0.189 - 0.727)	0.001 (0 - 0.217)
Min. PET	0.004 (0 - 0.633)	0.002 (0 - 0.293)	0.174 (0.022 - 0.556)
Max. PET	0.529 (0 - 0.707)	0.169 (0.008 - 0.604)	0.001 (0 - 0.149)
Mean PET	0.003 (0 - 0.66)	0.606 (0.002 - 0.725)	0.002 (0 - 0.307)
SD PET	0.407 (0.071 - 0.75)	0.003 (0 - 0.47)	0.001 (0 - 0.192)
NAO	0.467 (0 - 0.683)	0.663 (0.424 - 0.783)	0.003 (0 - 0.5)
ONI	0.001 (0 - 0.201)	0.397 (0.159 - 0.691)	0.001 (0 - 0.199)

Table S5.

Variation in selection explained by local and global climate factors among different taxonomic groups. Shown are mean and 95% credible intervals (in parentheses) of the proportion of within-study variation (combining both spatial and temporal replication; temporal replication only for NAO and ONI) explained by a given climatic factor from a Bayesian meta-analytical model.

Climatic factor	Taxonomic group		
	Invertebrates	Plants	Vertebrates
Min. temp.	0.869 (0.352 - 0.974)	0.003 (0 - 0.424)	0 (0 - 0.05)
Max. temp.	0.005 (0 - 0.814)	0.001 (0 - 0.188)	0 (0 - 0.061)
Mean temp.	0.958 (0.659 - 0.996)	0.002 (0 - 0.245)	0 (0 - 0.044)
SD temp.	0.765 (0 - 0.927)	0.561 (0.208 - 0.712)	0 (0 - 0.061)
Min. precip.	0.745 (0.243 - 0.966)	0.002 (0 - 0.402)	0 (0 - 0.061)
Max. precip.	0.004 (0 - 0.719)	0.666 (0.503 - 0.829)	0.001 (0 - 0.188)
Mean precip.	0.005 (0 - 0.715)	0.006 (0 - 0.466)	0.092 (0 - 0.384)
SD precip.	0.003 (0 - 0.627)	0.708 (0.47 - 0.811)	0 (0 - 0.094)
Min. PET	0.959 (0.184 - 0.996)	0.462 (0.114 - 0.725)	0.229 (0.051 - 0.456)
Max. PET	0.003 (0 - 0.618)	0.003 (0 - 0.396)	0 (0 - 0.048)
Mean PET	0.855 (0.219 - 0.981)	0.006 (0 - 0.426)	0 (0 - 0.084)
SD PET	0.003 (0 - 0.471)	0.001 (0 - 0.254)	0.001 (0 - 0.129)
NAO	0.629 (0.227 - 0.97)	0.896 (0.344 - 0.983)	0.001 (0 - 0.202)
ONI	0.002 (0 - 0.325)	0.789 (0.053 - 0.96)	0 (0 - 0.023)

Database S1 (separate file)

Database of selection coefficients for spatially and temporally replicated studies of selection.

Database S2 (separate file)

Database of local climate factors cross-referenced for each selection estimate in Database S1.