

REPORT

ADAPTATION

Precipitation drives global variation in natural selection

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Climate change has the potential to affect the ecology and evolution of every species on Earth. Although the ecological consequences of climate change are increasingly well documented, the effects of climate on the key evolutionary process driving adaptation—natural selection—are 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.

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). Although 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 in-

creasing 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 (SD) populations, range = 2 to 59 populations] and temporally [mean = 5.2 ± 6.8 (SD) years, range = 2 to 45 years] replicated selection studies ($N = 168$) in plant and animal populations (Table 1 and database S1). We focused on directional 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, whereas 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 ter-

restrial 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 georeferenced 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 (modeling 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

Table 1. Summary of records in the selection database. Numbers refer to the number of records in the database. Only those records with SEs were used in analyses (14).

Item	Replicate type	
	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 and fertility	1848	1758
Mating success	847	863
Other	227	35
Survival	656	2481
Survival and fecundity	16	0
Total fitness	39	58

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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° by 0.5° cells) climatic factors, we analyzed air temperature, precipitation, and potential evapotranspiration (PET). Although there is likely to be climate variation within a 0.5° grid, the populations for which 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 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 spatial and temporal studies were combined, models that included temperature factors did not explain variation in selection (Fig. 2, A and B). However, 20 to 40% of the variation in selection was associated with precipitation mean, maximum, and SD (Fig. 2, C and 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 data set (Fig. 2, E and F). When we ran the analyses separately for spatial and temporal selection, the results largely

mirrored the patterns in the combined analysis (figs. S1 and 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 and 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 climatic 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 to 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). Although 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 and figs. 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 interannual variability in atmospheric circulation for Northern Hemisphere and equatorial regions, respectively (14).

We found that the NAO explained between 10 and 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 S4), and selection 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.

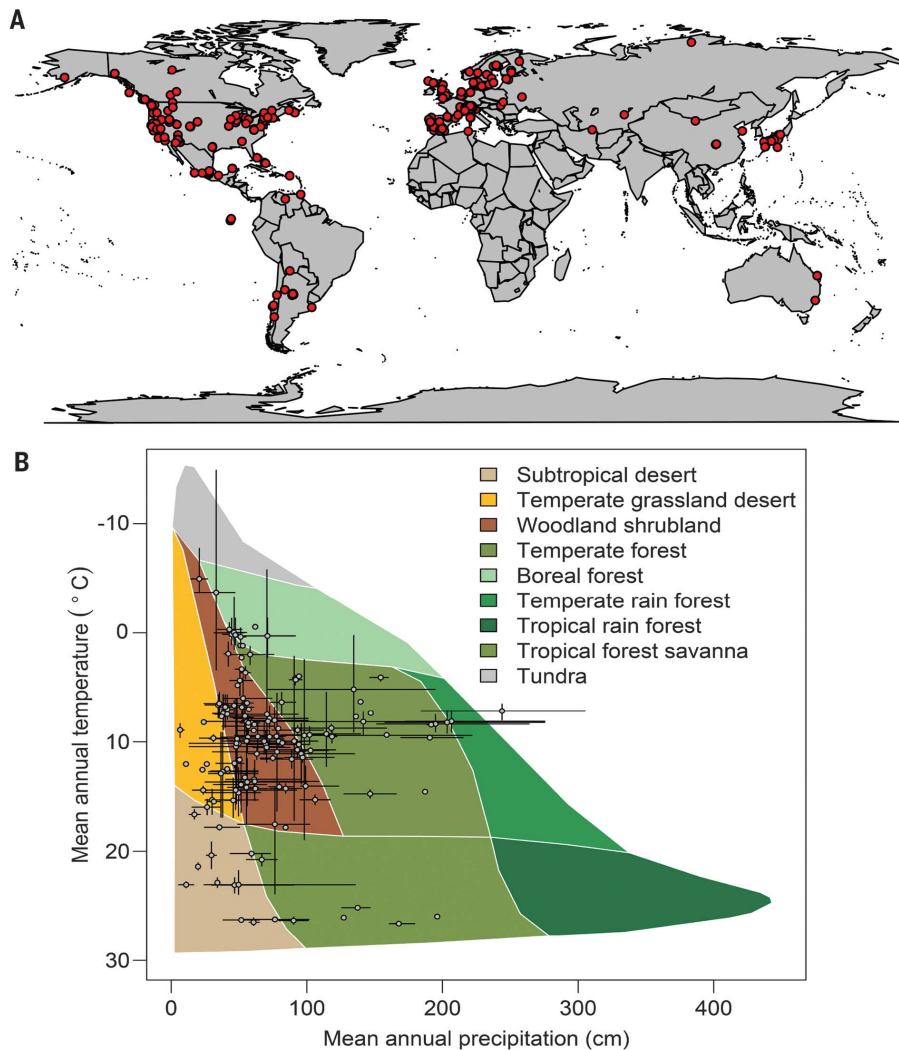


Fig. 1. Selection estimates included in this study are broadly distributed geographically and in climate space. (A) Red circles denote individual study locations of natural selection. (B) Shown are individual studies overlaid on Whittaker's terrestrial biome plot, which demarks biomes as a function of 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.

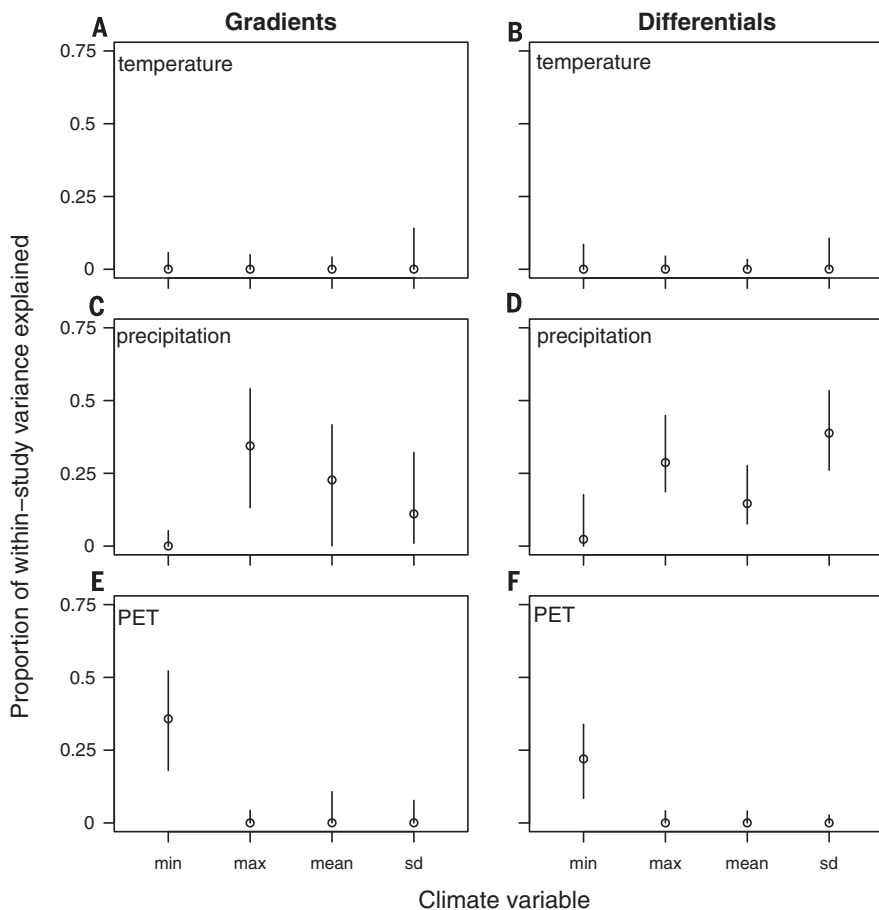


Fig. 2. Variation in selection is explained by local climate factors. Shown are mean and 95% credible intervals of the proportion of within-study variation in selection (combining temporal and spatial variation; see figs. S1 and S2 for temporal and spatial variation analyzed separately, respectively) 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).

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 that 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 and figs. S1 and S2). 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. Although 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 rather than evolutionary rescue through adaptive evolution (3, 22). Therefore, phenotypic plasticity might also 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 var-

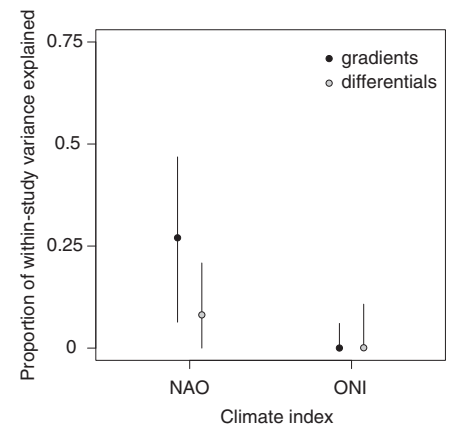


Fig. 3. Variation in selection is explained by global climate indices. Shown are mean and 95% credible intervals of the proportion of within-study variation in selection gradients (black circles) and differentials (gray circles) explained by the NAO index and the ONI.

iation at even larger geographic scales such as the NAO (Fig. 3) often has 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 as they could under climate change.

We have identified a signature of the effects of climate on selection in a phylogenetically diverse data set 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—natural selection. 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

www.sciencemag.org/content/355/6328/959/suppl/DC1
Materials and Methods
Figs. S1 and S2
Tables S1 to S5
Databases S1 and S2
References (25–41)

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Editor's Summary

Climate-driven selection

Climate change will fundamentally alter many aspects of the natural world. To understand how species may adapt to this change, we must understand which aspects of the changing climate exert the most powerful selective forces. Siepielski *et al.* looked at studies of selection across species and regions and found that, across biomes, the strongest sources of selection were precipitation and transpiration changes. Importantly, local and regional climate change explained patterns of selection much more than did global change.

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