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Widespread Effects of Climate Change on Local Plant Diversity

Highlights

- Climate change increases local plant species richness, at least temporarily

- Empirical and modeled data suggest an increase of ~5% per decade in cool regions

- Climatic perturbation is identified as a process driving biodiversity accrual

- Uneven global coverage of field data could be obscuring other climatic effects

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In Brief

Most biodiversity metrics are declining, but there is no clear trend in local species richness over time. Here, Suggitt et al. show that negative responses of local diversity to human activity are masked by a positive response to changes in climate, particularly in cooler regions of the world, where diversity is accruing at ~5% per decade.

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Report

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Widespread Effects of Climate Change on Local Plant Diversity

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SUMMARY

Human activity has sent many measures of biodiversity into long-term decline, and there are suggestions that the sheer scale of this impact is sufficient to consider the modern era as a geological epoch of its own, known as "The Anthropocene" [1]. However, recent meta-analyses show that local alpha diversity is often stable or slightly increasing [2–4]. Here, we show that the local alpha diversity (species richness) of plants found in quadrats and transects has increased the most in cooler regions of the world that have experienced the highest *absolute* changes (i.e., changes in either direction) in climate. The greatest statistical support is for the effects of precipitation change. On average, alpha diversity declined slightly (−4.2% per decade) in the third of sites that experienced the lowest precipitation change but increased (+10.8% per decade) in the third of sites with the highest precipitation change. These results suggest that the "perturbation" of local communities during climatic transitions increases the average number of species, at least temporarily, an effect likely to remain important as climate change continues.

RESULTS AND DISCUSSION

Local plant diversity is of fundamental scientific interest to those wishing to understand why diversity varies in space and time, and it is of practical importance as we contemplate the impacts of humanity on biodiversity across the Earth's surface. For example, the local alpha diversity of plants underpins diversity in animals [5] and contributes to the functional performance of ecosystems, their resilience when the environment changes, and the provision of ecosystem services [6, 7]. Here, we find that the alpha diversity of plants has, on average, been increasing in regions of the world where the climate has been changing the most. Insofar as the sites and climates we analyze here are globally representative, this implies that (1) the Earth's (changed and changing) Anthropocene climate can support higher levels of alpha diversity in plants than previously and/or

(2) terrestrial ecosystems that are in a state of transition associated with climate change tend to contain excesses rather than deficits of species.

It is widely appreciated that many metrics of global biodiversity are declining [8], but quite how and why local alpha diversity is changing is still unclear. Major land use transitions may have been responsible for reducing local animal and plant diversity by a global average of approximately 13% over the last ~500 years [9]. However, human-associated disturbances and species introductions can, on occasion, increase local diversity [10, 11]. Thus, some anthropogenic habitats support more species than the original vegetation [12, 13], and longitudinal studies on timescales of a few decades typically find that local losses of species in some locations are balanced by species gains in others [2–4]. There is agreement that local biological communities have been changing, but no consensus has yet emerged whether the processes that are contributing to local increases in some locations are sufficient to offset losses elsewhere [14, 15].

We investigated the role of climate as a driver of local diversity change by using Vellend et al.'s [4] database of locations (Figure 1A) where plant species richness (α) had been remeasured after an interval of at least 10 years (median duration 26 years), in plot sizes of 10^{-2} to 10^{4} m^2 (median size 25 m^2). We used the estimates of local richness change for each site provided in the database, which were calculated by dividing the final measured species richness of each study by the initial measured species richness, before taking the natural logarithm of this number and subsequently dividing by the study duration (ln [SR $_{final\ year}$/SR $_{initial\ year}$] per decade). We found that richness has increased the most (Figure 1E) in the "cold" and "polar" Köppen [16] global climate regions (one-way ANOVA: F (4,413) = 4.58; p = 0.001), where rates of climate change were greatest (Figure 1D).

Considering climate and climate change as a number of continuous variables (as opposed to Köppen regions), local plant species richness increased the most in the coldest parts of the world, and also where the climate had changed the most, such that local richness *declined* by a mean rate of 4.2% per decade (raw, exponentiated rate) in the third of sites (bottom tercile) that experienced the least precipitation change but *increased* by a mean of 10.8% per decade in sites with "high" (top tercile) rates of precipitation change (Figure 2; mean for middle tercile = +3.15% per decade). Local richness also *declined* by a mean rate of 2.8% per decade in sites that experienced the
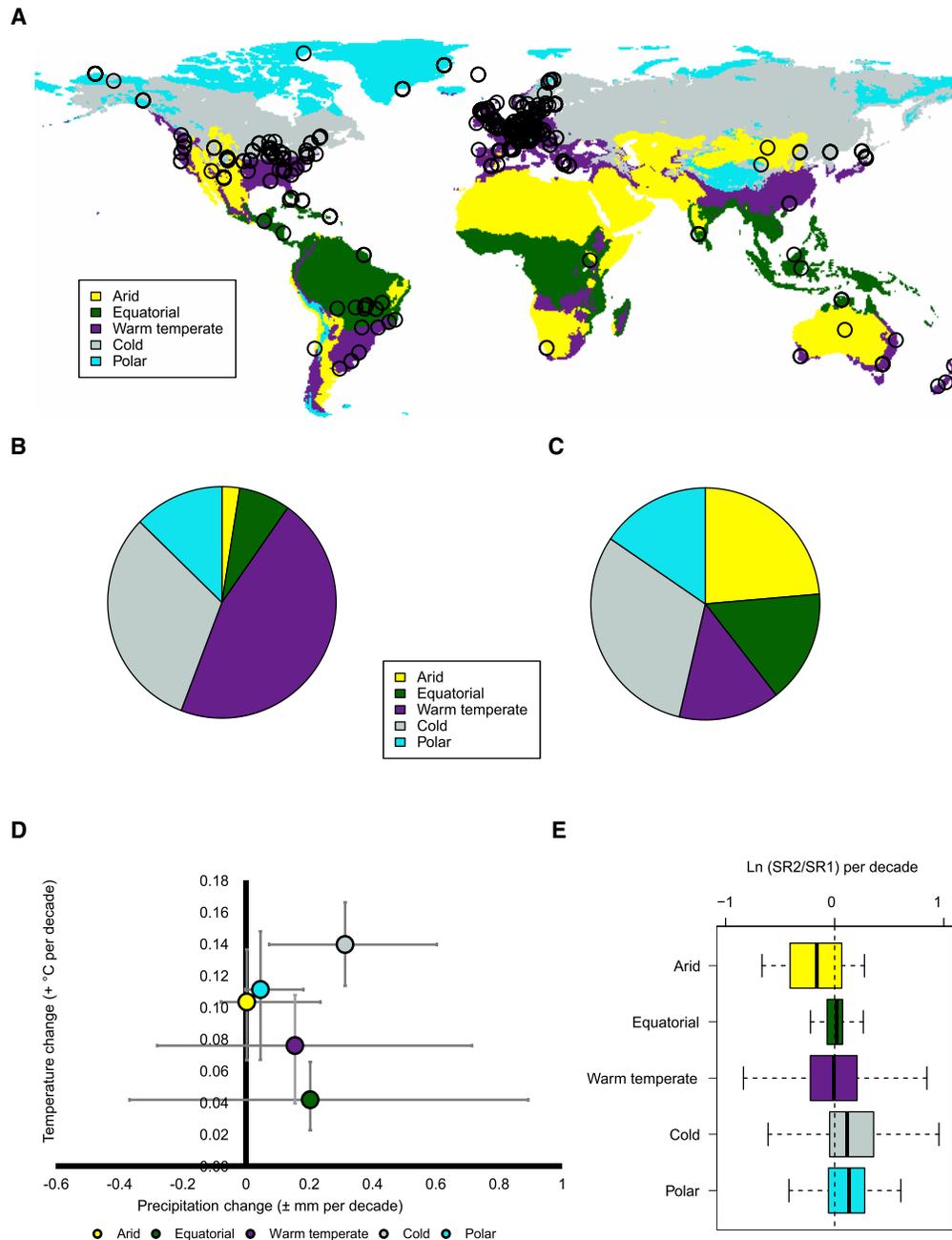
Figure 1. Climate and Climate Change at Study Sites Investigating Species Richness (α) Change

(A) The global distribution of the five major Köppen climate classifications overlain by Vellend et al. [4] study sites.

(B and C) The representation of these climate classifications in the Vellend et al. dataset (B) does not reflect the total proportion of the Earth's land surface they occupy (C; excludes Antarctica), with a particular bias toward the sampling of "warm temperate" sites.

(D and E) Median rates of climate warming have been higher in "cold" or "polar" zones (D), calculated for 1901–2013, with error bars extending to the 25th and 75th percentiles across 0.5° × 0.5° cells), where median richness has also increased (E; with hinges extending to the 25th and 75th percentiles). Because richness at warm temperate sites has shown the lowest rate of change (E), change in local diversity could be underestimated overall.

least temperature change (mean of bottom tercile), but *increased* by 9.1% per decade in sites with "high" (mean of top tercile) rates of temperature change (Figure 2; mean for middle tercile = +3.23% per decade), although there is less statistical support for the effects of temperature change (below). Note that all of these values pertain to the climatic changes and associated diversity changes for the distributions of sites with plant diversity change information (Figure 1A).

GLMM (generalized linear mixed model; STAR Methods) analyses confirmed that richness increased more in colder locations in all three of the best models (and in wetter locations for two of the three top models; Table 1). Absolute precipitation
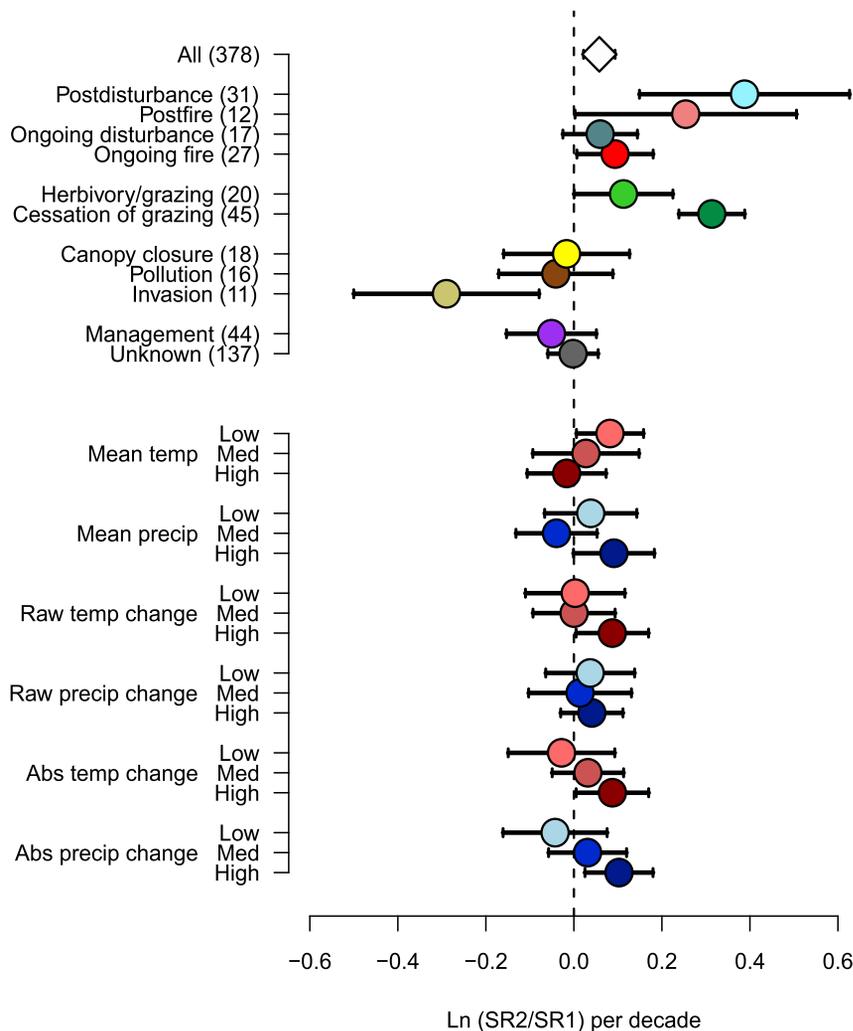
Figure 2. The Effect of Various Drivers of Species Richness (α) Change

The drivers of species richness (α) change analyzed in the Vellend et al. [4] study (above break in y axis) and the effect of climate change we analyze here. The raw mean (±2 x S.E.) richness change per decade at sites subject to each author-identified driver is shown. To illustrate the effects of climate, sites are grouped by tercile levels of each variable (low, medium, and high). Where two or more studies were conducted in the same 0.5° × 0.5° climate grid box, the mean values of climate change and diversity change for those studies were used.

with apparently stronger effects are influencing a smaller subset of sites (Figure 2).

In almost all cases, our modeling framework offered more support for the influence of absolute changes in climate (i.e., the magnitude of change in either direction, positive or negative), rather than raw, directional changes, as drivers of diversity change (Table 1). This supports the idea that climate change can act as a diversity-inducing perturbation rather than simply as the driver of a unidirectional transition toward a new state of higher local diversity (although the two are not mutually exclusive). With climate change set to accelerate, particularly in the cold and polar climate regions [18], the prominence of this climate perturbation effect is likely to increase through this century.

We tested the robustness of our conclusions by repeating the analysis in several different ways (STAR Methods). The results were similar when we removed non-climatic drivers or the autocorrelative grid box identity variables (Tables S1 and S2) or removed both (Table S3). Overall, the results were robust in that the sign and relative importance of the climate effects were similar in the top models identified by each framework, with climate explaining a similar proportion of the variation. We also used a continuous-space GEE approach to further assess the influence of spatial autocorrelation (STAR Methods). Using this approach, the slope values for the relationships between diversity change and climatic variables were very similar to those generated by the GLMMs (Figure S1).

It is important to recognize that there are "gaps" in the global database [4, 19], particularly in Africa, Asia, and the tropics, and that our results describe statistical associations for the locations for which data exist (Figure 1A). Given this geographic constraint, we applied our model-derived coefficients for climate response to a global climate dataset [20] to estimate how local species richness is likely to have changed around the world between 1981 and 2010 (Figure 3). This extrapolation suggests that a precipitation change of ±1 mm would give an increase in local diversity of approximately 5% in cold or polar Köppen climate regions and just less than 1% in "temperate" regions, depending on which top model is used (the three models with substantial

change appears in all three models with "substantial" support (Δ AIC < 2 versus top model) [17], but absolute temperature change appears in only one, so the effects of temperature *change* remain uncertain (as opposed to the consistent inclusion of *baseline* temperature conditions, as represented by the mean temperature variable). These models also revealed a statistical interaction such that richness has increased the most in cold parts of the planet that have experienced high levels of precipitation change (mean temperature × absolute precipitation change), but there was no substantial support for the other types of interaction we tested (Table 1). The 52% of variation explained by the best model (containing climatic and non-climatic variables plus the spatial autocorrelation control of grid box identity) is relatively high for a global-scale analysis, particularly considering that plant quadrats are often small (resulting in stochastic variation in measurements), that additional environmental drivers (for which data are unavailable) are also important, and that responses may depend on vegetation and floristic histories. In this best model, climatic variables alone explain 8% of the variation in diversity change. Although relatively modest, these effects of climate are taking place across the entire world surface, whereas most of the other drivers

Table 1. Candidate GLMMs, Ranked by AIC Score, where Rank No. 1 Is Best

						Baseline Climatic Conditions		Raw Trends		Absolute Trends		Interactive Effects											
Rank	AIC	Δ AIC	Conditional r-Squared	Marginal r-Squared	Intercept	Mean Temp	Mean Precip	Raw Temp Trend	Raw Precip Trend	Abs Temp Trend	Abs Precip Trend	Mean Temp: Raw Temp Trend	Mean Temp: Abs Temp Trend	Mean Temp: Raw Pecip Trend	Mean Temp: Abs Precip Trend	Mean Precip: Raw Temp Trend	Mean Precip: Abs Temp Trend	Mean Precip: Raw Precip Trend	Mean Precip: Abs Precip Trend	Raw Temp Trend: Raw Precip Trend	Abs Temp Trend: Raw Precip Trend	Raw Temp Trend: Abs Precip Trend	Abs Temp Trend: Abs Precip Trend
1	254.3		0.52	0.08	0.08	−0.0782	0.0575				0.1206				−0.0633								
2	255.7	1.4	0.51	0.05	0.07	−0.0663					0.1382				−0.0605								
3	256.0	1.7	0.52	0.08	0.08	−0.0724	0.0599			0.0159	0.1180				−0.0633								
4	256.3	2.0	0.52	0.08	0.08	−0.0795	0.0572	−0.0031			0.1210				−0.0633								
5	256.3	2.0	0.51	0.05	0.06	−0.0864	0.0544				0.0586												
6	256.4	2.1	0.52	0.07	0.07	−0.0961	0.0505			0.0396	0.0727		0.0446										
7	256.7	2.3	0.52	0.03	0.06	−0.0668	0.0684																
8	257.0	2.7	0.51	0.05	0.07	−0.0899				0.0352	0.0927		0.0487										
9	257.3	3.0	0.51	0.03	0.06	−0.0749					0.0778												
10	257.5	3.2	0.52	0.08	0.08	−0.0651	0.0555			0.0067	0.1250							−0.0730		−0.0237			

Absolute changes in temperature and precipitation have more support (using AIC) and explain more variation (marginal r-squared) than models including raw changes. Slope coefficients only appear if the variable was included in the model formula. Author-identified drivers of diversity change (from the Vellend et al. database) [4] were fitted as a random effect, in which the slope of the relationship between diversity and each climate variable was fixed (across all drivers), yet the intercept could vary. See also Figure S1 and Tables S1–S3.
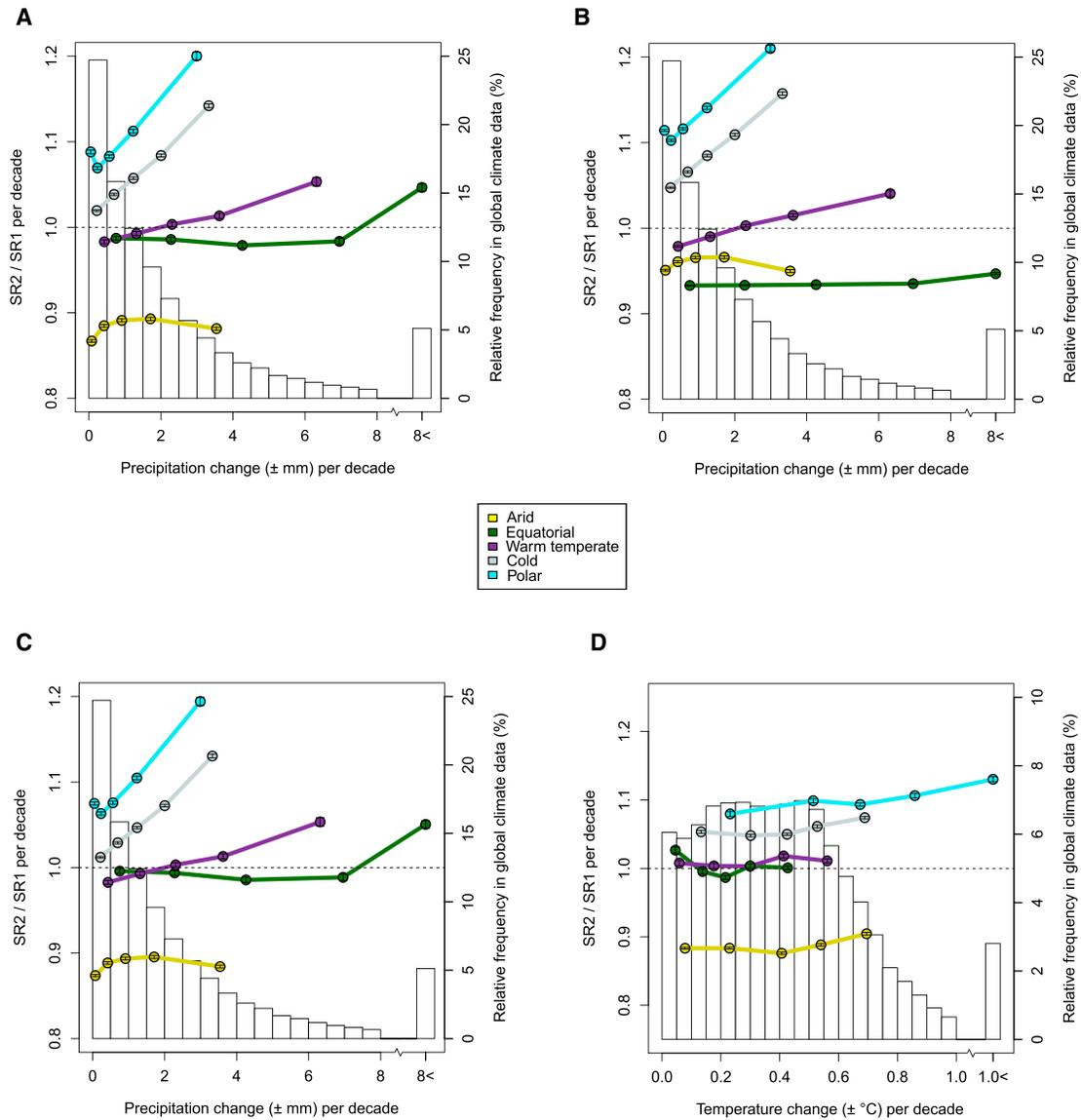
Figure 3. Model-Predicted Change in Local Species Richness in Response to Climate Change

Richness change per decade was predicted for each 0.5° × 0.5° global grid square, using observed climate data from 1981 to 2010. Predictions were first grouped by Köppen climate region (colored lines) and then ordered by exposure to the rates of absolute precipitation change (x axis in A–C) and absolute temperature change (x axis in D) within each region (low to high quintiles for each region are presented from left to right). Note that lines vary in length because levels of climate change experienced in each region differed. Absolute precipitation change was retained in all top models (model ranks 1–3 appear as A–C, respectively), and absolute temperature change was only retained in the model ranked third (D; the same model as in C). Error bars (within symbols) represent 95% confidence intervals of the means within each climate region for each level of climate change. Histograms indicate the percentage of the global land surface that has experienced each level of climate change.

support are represented by Figures 3A–3C). Any positive effects of precipitation change in the equatorial and arid regions appear not to be sufficient to counteract the negative effects of other (non-climatic) drivers of diversity change, although it remains the case that predictions for diversity change in equatorial and arid regions with highest levels of climate change are less negative than those predicted for locations with lower levels of climate change. By comparison, applying a corresponding extrapolation to absolute change in temperature reveals a more muted response, with rates of richness change seeming

to increase in most biomes once the rate of temperature change exceeds ±0.5°C per decade (Figure 3D). Although such rates of temperature change are uncommon outside of the cold, polar, and arid zones at present, they are likely to become more commonplace if climate change accelerates through this century [18].

In sum, our GLMM analyses suggest that local species richness has, on average, been increasing by ~5% per decade in cooler regions of the world (Figure 3). This is supported by the empirical estimates taken from all locations for which data are

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available (Figure 1A), which suggests that species richness has increased by 9.1% per decade and 10.8% per decade at locations where temperature and precipitation (respectively) have changed the most and by roughly 3% per decade in locations subject to medium levels of temperature or precipitation change (Figure 2). It is worth noting that even this latter estimate of 3% per decade (at medium levels of climate change) is substantially larger than Newbold et al.'s [9] global-scale estimate of a 13% decline in local diversity associated with land use change and intensification over the last 500 years, although it should be noted that heavily transformed habitats are likely to be more strongly represented in the Newbold et al. study than in the dataset [4] we use here. Despite the apparent conflict between these estimates, we believe the results are actually compatible. Vegetation quadrat studies tend to show slight declines in plant species richness in places where the climate has changed the least, which implies that, on average, non-climatic drivers of environmental change may have a slightly negative impact on local diversity (Figure 2). In contrast, the overall positive effect of climate change on local plant species richness (Figure 2) helps explain why the overall net change in local diversity is slightly positive ("all" in Figure 2), despite localized negative effects of some other drivers. As always, there are caveats associated with global analyses, and the findings reflect any geographic or taxonomic biases of the underlying studies. But nevertheless, it is entirely possible that we are witnessing an accrual of local diversity in response to modern climate change [21]. It is important not to confuse this positive effect of climate change on local-scale species richness with its heightening of global extinction risk for a substantial portion of the species on our planet [22, 23]. It will be important for future research to determine the impacts of climate change on relationships between local species richness, the turnover of species in time and space [24], and global diversity and to understand the contributions of different types of species (e.g., in relation to specialism) to changing richness patterns [25].

Our initial expectation was that local diversity might increase with a switch to warmer and wetter conditions [26], given that the global distribution of species richness increases with temperature and precipitation [27], and that poleward and upslope range shifts will tend to increase local richness in communities that receive immigrant species [14]. However, the perturbing nature of climate change may also give rise to transient effects—our results are consistent with this hypothesis. It is unlikely that the geographic distribution of species richness is in "equilibrium" with current environmental conditions, given the rapidity of ongoing climate shifts. Indeed, evidence from paleoecology increasingly suggests that equilibria may be rare [28]. The observation that terrestrial animals tend to spread polewards faster than their equatorial range boundaries retreat [29]—and our demonstration here that it is the magnitude of climatic changes per se, rather than the direction of change, that is associated with increases in local plant diversity—are consistent with the hypothesis that terrestrial ecosystems that are in a state of climatic transition tend to contain excesses rather than deficits of species [30]. These two hypotheses (higher future richness and higher transitional richness) are not mutually exclusive. Whatever the underlying cause, our results indicate that local plant species richness has tended to increase in cool parts of the world with relatively high levels of precipitation change.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2019.06.079.

AUTHOR CONTRIBUTIONS

C.D.T. and A.J.S. designed research, A.J.S. and D.G.L. performed research, A.J.S. and D.G.L. analyzed data, and all authors wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Diversity change data	[4]	https://doi.org/10.1002/ecy.1660
Climate data	[20]	http://www.cru.uea.ac.uk
Köppen climate distributions	[31]	http://koeppen-geiger.vu-wien.ac.at/present.htm
Software and Algorithms		
R (3.4.4)	[32]	https://www.r-project.org/

LEAD CONTACT AND MATERIALS AVAILABILITY

Requests for further material and resources should be directed to the lead contact, Dr Andrew Suggitt (andrew.suggitt@york.ac.uk). This study did not generate new unique reagents.

METHOD DETAILS

We used the compilation of plant diversity data plots from the Vellend et al. study [2, 4]. The stated value for α given in the Vellend et al. data is a measure of the central tendency across plots at a given site: often the mean, but sometimes median and on one occasion a prediction from a species-area relationship. We used the distribution of Köppen climate regions published in Kottek et al. [31] for the initial analyses relating plant diversity change to the climate (Figure 1).

As potential drivers of change, we used those identified by the original study authors, as documented in the Vellend et al. study [2]. We calculated climatic changes over the time period in which the studies were conducted using the high resolution (0.5° x 0.5°) CRU TS 4.01 dataset for global climate [20]. One study [33] ran from 1731 until 1992, and hence it started prior to the first year of the CRU dataset (1901); so we used climate data for 1901-1992 inclusive in this instance. We calculated temperature (°C per decade) and precipitation change (mm per decade) from the slope of the relationship between each variable and year, for the span of years from the initial to the final plant surveys. We excluded data from 85 sites where the gap between surveys was less than ten years. Because changes could operate in either direction (i.e., warming/cooling or wetting/drying trends), we tested for the effect of both raw changes (with signs retained) and absolute changes (the level of change, ignoring direction) in temperature and precipitation. We also included the mean temperature and mean precipitation at each site, to represent the general state of the climate during the study, allowing us to evaluate whether diversity changes were greater in hotter/colder or wetter/drier parts of the world.

The durations of studies were used to calculate the response variable (as per the original Vellend et al. study [2],); the natural logarithm of change in species richness (SR), divided by the study duration (i.e., ln (SR $_{Final\ year}$ /SR $_{Initial\ year}$) per decade). We did not otherwise adjust for study duration; as suggested by Gonzalez et al. [19] but rebutted by Vellend et al. [4]. Adding a study duration variable to each model constructed in the full model set (and presented in the main text) failed to generate any models with substantial support (their inclusion always resulted in models with Δ AIC > 2 versus top model in Table 1), so this variable was omitted. Logarithmic transformation ensured that our response variable was uncorrelated with species richness in the first survey (Spearman's ρ = 0.03, N = 414, p = 0.62).

QUANTIFICATION AND STATISTICAL ANALYSIS

The results in the main text are derived from GLMMs in which combinations of climate variables were included as fixed effects, with random effects for author-identified driver. The identity of the 0.5° x 0.5° climate grid box that each site was located in as a further random effect, to account for spatial autocorrelation. The intercepts for the random effects could vary, but their slopes were fixed. We do not present results from GLMMs in which the author-identified driver slopes vary because these models all had AIC value that were substantially higher than the top ten models in which the slopes were fixed. All GLMMs were fitted via Maximum Likelihood using the 'identity' link function. As per study duration (see above), the addition of a plot size variable (or a log-transformed plot size variable) failed to generate any models with substantial support (including plot size always resulted in models with Δ AIC > 2 versus top model in Table 1), so we did not include it as a covariate in our final analyses (see also Table S3 in Vellend et al. [2]). Our results can thus be interpreted as the change in species number per decade in plots of ~25 m^2, the median plot size. We also tested the sensitivity of the results to the total removal of either the author-identified driver or grid box identity variables (Tables S1 and S2), or both (Table S3). To further test for autocorrelative effects on our results, we ran analogous GLMs within the 'geepack'

package [34] in R [32], which uses generalized estimating equations to account for correlations within spatial clusters of datapoints (Figure S1). Results did not differ substantially across these approaches (Tables S1–S3; Figure S1). The signs of slopes were always the same, and the slope values, relative importance of different variables and explanatory power of climate variables was similar for all approaches, so we concentrate on those derived from the primary analyses in the main text. The main difference to note was that two of these frameworks (Tables S2 and S3) offered less consistent support for a statistical interaction between baseline temperature and absolute precipitation change (while retaining the main effects for both of these variables), and more support for an effect of temperature change.

We used the three models with 'substantial' support (Table 1, the top model and two others with Δ AIC < 2) to extrapolate the site level findings to the global level (Figure 3). Richness change was predicted for every grid box on the global climate grid using observed values of mean temperature, mean precipitation, absolute temperature change and absolute precipitation change for 1981-2010 (also calculated using the CRU TS3.10 dataset). These predicted values were grouped by Köppen climate region and subsequently ordered by their (relative) level of climate change exposure (quintiles: very low, low, medium, high, very high) to create each plot in Figure 3. The standard error for each point is calculated across all the predictions that fall into each region–change level combination (i.e., for 5 levels of climate change within each of the 5 climate regions). There are three precipitation change plots, but only one for temperature change, which only featured in one of the top three models.

DATA AND CODE AVAILABILITY

The diversity change data utilized in our paper are presented as supplementary information to the updated Vellend et al. study ([4], https://doi.org/10.1002/ecy.1660). Climate data analyzed here are available via the UEA CRU website ([20], http://www.cru.uea.ac.uk). Köppen climate distributions are available at the website of the University of Veterinary Medicine, Vienna ([31], http://koeppen-geiger.vu-wien.ac.at/present.htm). All analyses were performed in R software, version 3.4.4 ([32], https://www.r-project.org/).