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Climate-driven changes in the composition of New World plant communities

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Climate change is altering the distributions of species, which in turn causes shifts in the composition of plant communities. Specifically, rising temperatures should cause increasing relative abundances of heat-loving or heat-tolerant species (that is, 'thermophilization') and changes in precipitation should cause altered abundances of water-demanding species. We analysed millions of records of thousands of species and found that the plant communities in most ecoregions in North, Central and South America have experienced thermophilization over the past four decades (1970–2011). Thermophilization was fastest in ecoregions with intermediate temperatures and was positively correlated with warming rates within many biomes. Changes in the relative abundances of water-demanding species were less consistent and were not correlated with changes in precipitation, meaning that the drought sensitivity of some ecoregions may be increasing despite decreasing rainfall and increasing probabilities of drought. Climate-driven changes in plant community composition will affect the function and stability of New World ecoregions.

Climate change is altering the abundances and distributions of plant species worldwide[1–3]. Specifically, rising temperatures can lead to reduced fitness, and hence abundances, of species in the hotter portions of their ranges and increased fitness/abundance of species in the colder portions of their ranges. In some cases, these differential changes in abundance may lead to range shifts, contractions or expansions as some species die back from the areas that become 'too hot' and/or invade areas that were previously 'too cold'[4–15]. Changes in other climate variables, such as precipitation and water availability, may likewise cause changes in species' range limits as well as abundance distributions within the species' ranges[14,16–18]. Collectively, these shifts in species distributions should cause widespread and directional changes in the composition of plant communities over time. In accordance with predictions, several studies have documented directional changes in local plant communities such that most have increasing relative abundances of heat-tolerant or heat-loving (thermophilic) species concurrent with rising temperatures (a process referred to as thermophilization)[19–25]. Other studies have documented shifts in composition due to changes in precipitation. For example, some lowland Amazonian forests are shifting in composition towards increased relative abundances of dry-affiliated species concurrent with an increasing frequency of droughts and decreasing water availability[26]. However, it remains unknown how these changes in local community composition manifest at larger scales. In other words, is climate change causing broad-scale changes in the composition of regional plant communities? If so, what are the most important factors in determining the direction and pace of change?

To address these questions, we analysed changes in the floristic compositions of nearly 200 New World (North, Central and South America) ecoregions over the past 40 yr (1970–2011) using an expansive online database of plant collections and observation records (>20 million usable records after filtering for data quality and sample size criteria; see Methods and Supplementary Fig. 1). On the basis of collection locations, we estimated the optimal

mean annual temperature (MAT_{opt}) and the optimal total annual precipitation (TAP_{opt}) of >17,000 'well-collected' New World plant species[23]. We next characterized the plant community composition of each ecoregion in each year by calculating the community temperature index (CTI) and community precipitation index (CPI)[23] which reflect the relative abundances of thermophilic and mesophilic species (after correcting for collection biases; see Methods), respectively. CTI was strongly correlated with the ecoregions' current mean annual temperature (MAT; Pearson's $R = 0.98$; 95% confidence interval (CI) $= 0.98–0.99$; $t = 72.14$; d.f. $= 189$; $P < 0.0001$; Fig. 1a), CPI was strongly correlated with the ecoregions' total annual precipitation (TAP; Pearson's $R = 0.87$; 95% CI $= 0.83–0.90$; $t = 24.59$; d.f. $= 189$; $P < 0.0001$; Fig. 1b) and CTI and CPI were strongly positively correlated with each other (Pearson's $R = 0.72$; 95% CI $= 0.64–0.78$ $t = 14.04$; d.f. $= 189$; $P < 0.0001$; Extended Data Fig. 1). These results reflect the availability of different climates (correlation between ecoregion MAT and TAP: Pearson's $R = 0.58$; 95% CI $= 0.48–0.67$; $t = 9.85$; d.f. $= 189$; $P < 0.0001$) and show that both CTI and CPI can accurately characterize the climatic compositions of ecoregion plant communities (Fig. 1 and Extended Data Fig. 1).

Once we had estimated CTI and CPI for each ecoregion in each year, we then tested for changes in these metrics over time as indicators of shifts in plant species composition. For each of the ecoregions that had >10 yr of CTI and CPI estimates, we calculated the thermophilization rate (TR) and the mesophilization rate (MR). A positive TR indicates increasing CTI due to increasing relative abundances of species with hotter MAT_{opt} (that is, more-thermophilic species) and positive MR indicates increasing CPI due to increasing relative abundances of species with wetter TAP_{opt} (that is, more-mesophilic species). As a separate measure of compositional changes over time, we compared each ecoregion's initial versus final CTI/CPI as calculated using the combined collections from the first and last 15 yr, respectively. We also identified the species that had been lost from the collection record of each ecoregion between these initial and

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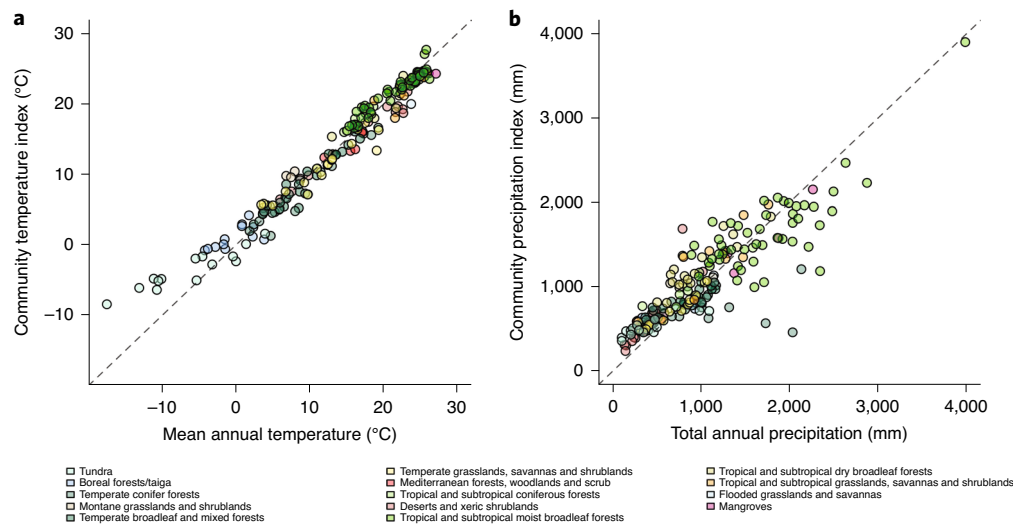
Fig. 1 | The relationships between climate and floristic composition of New World ecoregions. a,b, The correlations of the ecoregions' CTI (°C) and their mean MAT (°C; Pearson's $R = 0.98$; d.f. $= 189$; $P < 0.0001$) (**a**) and CPI (mm) and mean TAP (mm; Pearson's $R = 0.87$; d.f. $= 189$; $P < 0.0001$) (**b**). Each point represents an ecoregion and points are coloured according to their biome designation.
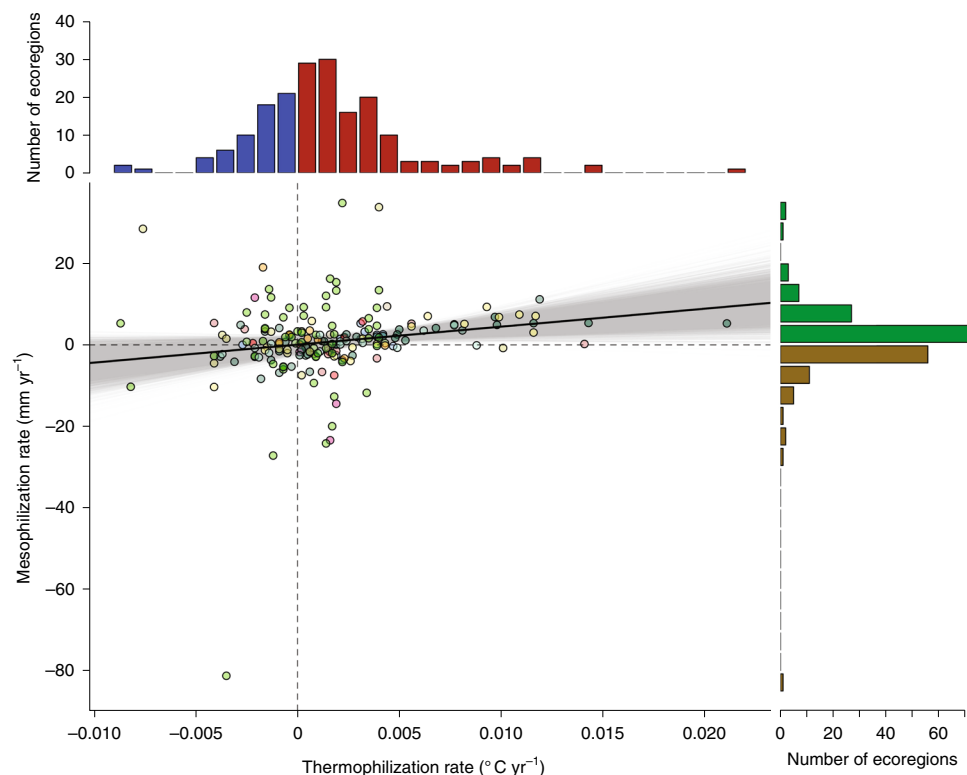
Fig. 2 | The thermophilization and mesophilization rates of 191 New World ecoregion plant communities. The main panel shows the correlation (black line, Pearson's $R = 0.19$; d.f. $= 189$; $P = 0.0095$; grey lines show 5,000 bootstrapped correlations) between TR (°C yr^{-1}) and MR (mm yr^{-1}). Each point represents an ecoregion and the points are coloured by their biome designations (see Fig. 1). The top and side histograms show the distributions of TR and MR, respectively. Of the ecoregions, 68% (binomial $P < 0.0001$) had positive TR (mean $= 0.017$ °C yr^{-1}; 95% CI $= 0.011$–0.023 °C yr^{-1}) and 60% ($P = 0.004$) had positive MR (mean $= 0.81$ mm yr^{-1}; 95% CI $= -0.55$–2.17 mm yr^{-1}).

final time periods, had recruited into ecoregions over the study period or that occurred in ecoregions at both the start and end of the study period. We then calculated the CTI and CPI of the communities of lost, recruiting and persisting/surviving species in each ecoregion and compared them to each other (see Methods).

Most ecoregions (68%, binomial $P < 0.0001$) had a positive change in their CTI over the four-decade study period (that is, they had positive TR indicating increasing relative abundances of more-thermophilic species; Figs. 2 and 3). The mean TR across all ecoregions was 0.017 °C yr^{-1} and was significantly greater than
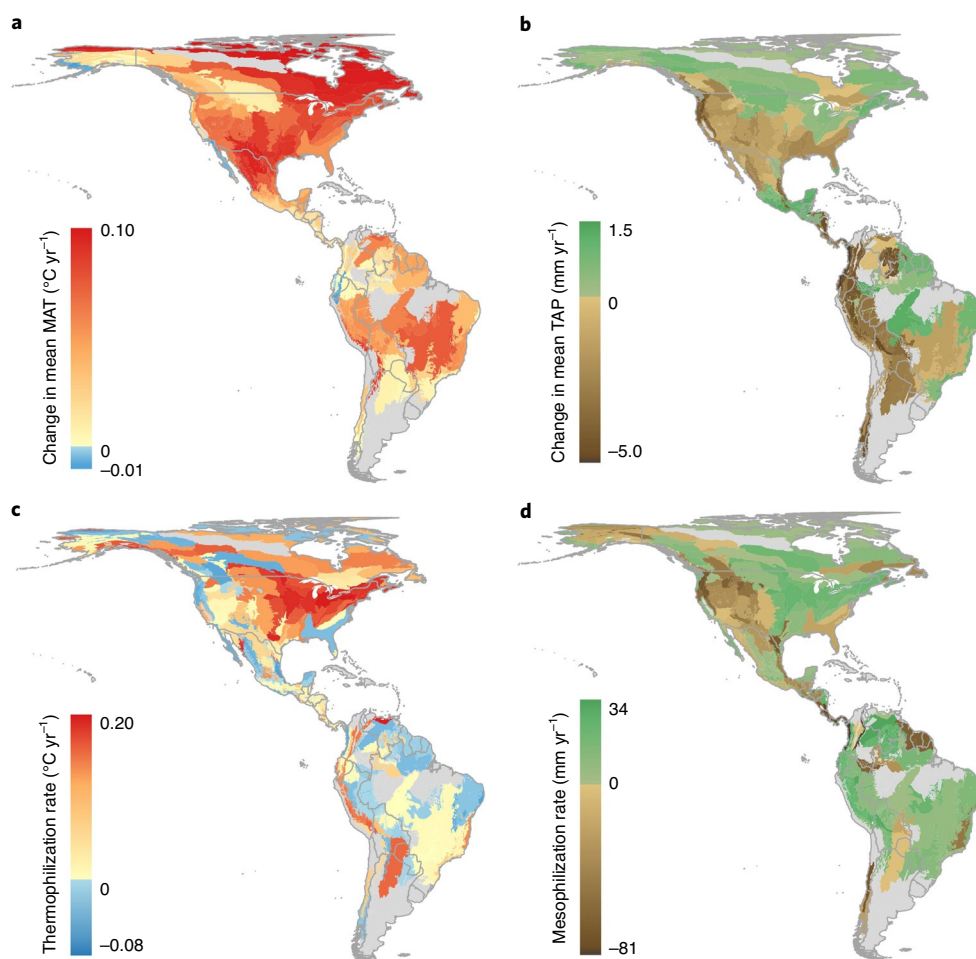
Fig. 3 | Maps showing the geographic patterns in climate change and changes in plant community composition. a–d, Warming rates as annualized changes in mean MAT (°C yr^{-1}) (**a**), annualized changes in mean TAP (mm yr^{-1}) (**b**), TR (°C yr^{-1}) (**c**) and MR (mm yr^{-1}) (**d**) within the different New World ecoregions (World Cylindrical Equal Area projection). Ecoregions that are shaded grey were not included in the analyses due to insufficient collections data.

zero (95% CI = 0.011–0.023 °C yr^{-1}, $t = 5.84$, d.f. = 190, $P < 0.0001$). The widespread increase in CTI held true whether we looked at the annual changes or if we just compared the initial and final CTI estimates (that is, in 66% of ecoregions (binomial $P < 0.0001$), final CTI > initial CTI; Supplementary Fig. 2). In accordance with this finding, in 64% of ecoregions (binomial $P < 0.0001$), the groups of species that were lost from the collection records between the initial and final periods had lower CTI than the recruiting species (mean difference = −0.96 °C; 95% CI = −0.13 to −0.63 °C). In 69% of ecoregions (binomial $P < 0.0001$), the lost species had lower CTI than the surviving species (mean difference = −0.80 °C; 95% CI = −1.06 to −0.54 °C). In contrast, the CTI of the recruiting species were not significantly different from those of surviving species (mean difference = 0.16 °C; 95% CI = −0.15–0.47 °C; Fig. 4).

TR and MR were positively correlated (Pearson's $R = 0.19$; 95% CI = 0.05–0.32; $t = 2.62$; d.f. = 189; $P = 0.0095$). More than half of ecoregions (60%, binomial $P = 0.0045$) had positive MR indicating increasing relative abundances of more-mesophilic species, but the mean MR across ecoregions was not significantly different from zero (mean = 0.81 mm yr^{-1}; 95% CI = −0.55–2.17 mm yr^{-1}; Fig. 2). In 62% of ecoregions (binomial $P < 0.0001$), the groups of species that were lost from the collection records between the initial and final periods had lower CPI than the groups of recruiting species (mean difference = −56.45 mm; 95% CI = −86.49 to −26.40 mm). In 58% of ecoregions (binomial $P = 0.0298$), the groups of lost
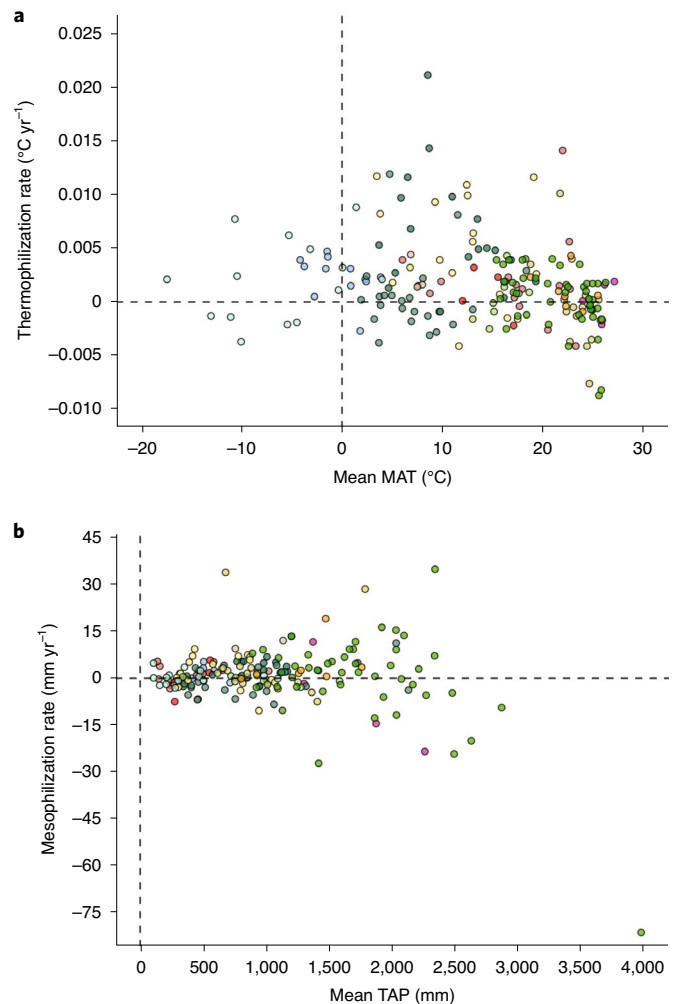
species had lower CPI than the surviving species but this difference was not significantly less than zero (mean difference = −3.83 mm; 95% CI = −29.57–21.92 mm). Recruiting species had greater CPI than surviving species in 64% of ecoregions (binomial $P < 0.0001$) and the difference was significant (mean difference = 68.75 mm; 95% CI = 33.53–103.97 mm; Fig. 4).

The observed rates of compositional change (TR and MR) varied greatly between ecoregions and biomes (Fig. 3). The fastest TR occurred in ecoregions with intermediate MATs (Fig. 5). These quickly changing plant communities include those of the 'temperate broadleaf and mixed forests' (mean TR = 0.063 °C yr^{-1}; 95% CI = 0.037–0.091 °C yr^{-1}) and 'temperate grasslands, savannas and shrublands' (mean TR = 0.048 °C yr^{-1}; 95% CI = 0.022–0.073 °C yr^{-1}). In contrast, TR were slowest in the lowland tropics. Indeed, many of these areas, including ecoregions of the 'tropical and subtropical dry broadleaf forests' (mean TR = −0.0042 °C yr^{-1}; 95% CI = −0.025–0.017 °C yr^{-1}) and 'tropical and subtropical moist broadleaf forests' (mean TR = 0.0035 °C yr^{-1}; 95% CI = −0.0044–0.011 °C yr^{-1}), have stable CTI or even negative TR (Fig. 5a). The low TR of these 'hot' lowland tropical areas may be caused by niche truncations that limit our ability to accurately characterize species' preferred climates and hence the ecoregion TR. Specifically, thermal niche truncation due to the absence of any hotter areas will cause underestimates of some species' MAT$_{opt}$, meaning that these species may be able to tolerate hotter
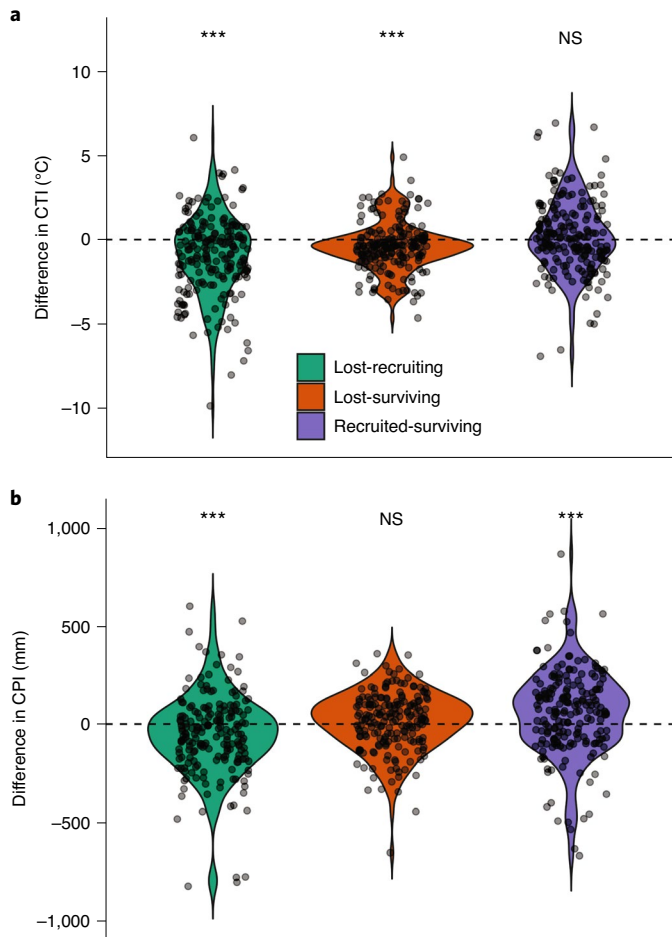
Fig. 4 | Differences in the climate compositions of lost, recruiting and surviving species. a, In 64% of ecoregions (binomial $P < 0.0001$), the groups of lost species had lower CTI (°C) than recruiting species (mean difference = −0.96 °C; 95% CI = −0.13 to −0.63 °C) and in 69% ($P < 0.0001$) of ecoregions, the lost species had lower CTI than surviving species (mean difference = −0.80 °C; 95% CI = −1.06 to −0.54 °C). The CTI of recruiting species were not significantly (NS) different from surviving species (mean difference = 0.16 °C; 95% CI = −0.15–0.47 °C). **b**, In 62% of ecoregions ($P < 0.0001$), the groups of lost species had lower CPI (mm) than recruiting species (mean difference = −56.45 mm; 95% CI = −86.49– 26.40 mm). In 58% ($P = 0.0298$) of ecoregions, lost species had lower CPI than surviving species but the difference was not significantly less than zero (mean difference = −3.83; 95% CI = −29.57–21.92 mm). Recruiting species had greater CPI than surviving species in 64% of ecoregions ($P < 0.0001$) and the difference was significant (mean difference = 68.75 mm; 95% CI = 33.53–103.97 mm). ***$P < 0.0005$.

Fig. 5 | The relationships between changes in the floristic composition of 191 New World ecoregions and their climate. a,b, The relationships between the TR (°C yr^{-1}) and mean MAT (°C) (**a**) and MR (mm yr^{-1}) and mean TAP (mm) (**b**) of ecoregions. Each point represents an ecoregion and the points are coloured by their biome designations (see Fig. 1).

temperatures and persist longer than expected under warming[27]. In addition, since the lowland tropical ecoregions are already in some of the hottest places on Earth, there are fewer potential immigrant species with higher thermal optima. Other New World plant communities with low or negative TR include some of the coldest ecoregions of the 'tundra' and 'boreal forests/taiga' biomes. These areas are also probably affected by niche truncation since the absence of colder areas will cause overestimates in species' MAT_{opt} and thereby reduce the measurable impact of losing cold-specialist species. Indeed, a simulation of TR due to warming and 'perfect' species migration but with niche truncation, produces a qualitatively similar pattern of TR being slowest in hot and cold areas and fastest in areas with intermediate

temperatures (see Supplementary Fig. 3 for simulation code and output). In other words, the slower TR observed in these ecoregions may not necessarily imply a reduced impact of climate change but rather might reflect a limited ability of our methods to detect changes in extremely hot and cold communities.

Several ecoregions of the 'mangroves' and 'deserts and xeric shrublands' biomes also had relatively low TR. In these cases, low TR may also be attributable to niche truncation since many of these ecoregions occur in very hot areas. Alternatively, the extreme edaphic and hydrologic conditions that characterize these systems may be preventing the incursion of new species.

While there are clearly many factors that can affect the stability versus dynamism of plant communities, it is possible that the observed differences in TR between ecoregions, and especially within the biomes, are explained in part by differences in the actual rates of warming (MAT_{ch}). Linear mixed-effects models indicated that there was no significant overall effect of warming rates on TR (TR = 0.01 °C + 0.38 × MAT_{ch}; parametric bootstrap 95% CI for MAT_{ch} = −0.07–0.81; marginal $R^2 = 0.03$; conditional $R^2 = 0.20$; $F = 2.8739$; Fig. 6a) and that the relationship between TR and MAT_{ch} varied significantly between biomes (Supplementary Fig. 4). However, the relationships between
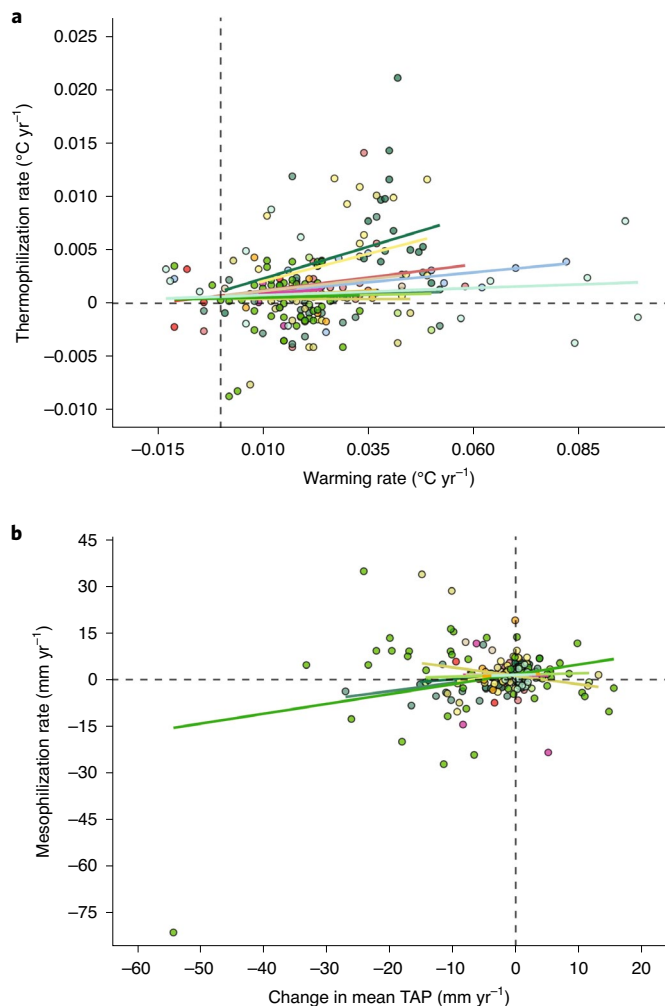
Fig. 6 | The relationships between changes in the floristic composition of 191 New World ecoregions and changes in climate. a,b, The relationships between TR (°C yr⁻¹) and observed rates of warming (°C yr⁻¹) (**a**) and MR (mm yr⁻¹) and changes in annual precipitation (mm yr⁻¹) (**b**). The lines show the biome-specific relationships predicted under the linear mixed models (best linear unbiased prediction). Each point represents an ecoregion and the points and lines are coloured by their biome designations (see Fig. 1). Biome intercepts and slopes are indicated in Supplementary Fig. 4.

thermophilization and warming rates were positive for all biomes, being particularly strong for the 'temperate broadleaf and mixed forests', 'temperate grasslands, savannas and shrublands', 'deserts and xeric shrublands', 'montane grasslands and shrublands' and 'boreal forests/taiga' biomes (Fig. 6a and Supplementary Fig. 4). Overall, the intercept of the relationship between TR and MAT_{ch} was not significantly different from zero (95% CI for intercept = −0.01–0.02), indicating that the CTI of New World ecoregions would be stable through time in the absence of global warming.

As with TR, there was no significant overall effect of changes in annual precipitation (TAP_{ch}) on MR (MR = 1.46 mm + 0.78 × TAP_{ch}; 95% CI for TAP_{ch} = −2.55–4.41; marginal R^2 = 0.004; conditional R^2 = 0.079; F = 0.215; Fig. 6b). The relationship between TAP_{ch} and MR was positive in 80% of biomes but only significantly so in 'tropical and subtropical moist broadleaf forests' and 'temperate conifer forests' (Supplementary Fig. 4).

For over half the ecoregions (60%; binomial P = 0.0029), TR have been slower than concurrent warming rates (mean MAT_{ch} − TR = 0.007 °C yr⁻¹; 95% CI = 0.0018–0.013 °C yr⁻¹). Consequently,

many communities are potentially falling out of equilibrium with temperature as differences between CTI and actual ecoregion temperatures get larger over time. Given that temperatures have been increasing since well before the 1970s, many communities may have already been out of equilibrium before the start of our study period[19].

The disequilibrium between community composition and climate is potentially of even greater concern in relation to precipitation since changes in CPI are less consistent and are less associated with observed changes in climate (Fig. 6). This is perhaps not surprising given the complexities of quantifying water availability and changes[28] and the many ways that plant species can respond to changes in water availability (that is, through drought avoidance or drought tolerance[29]). One possible explanation is that changes in CPI are being driven at least in part by changes in CTI due to the strong relationship between temperature and rainfall and the consequent positive relationship between species' MAT_{opt} and TAP_{opt} (Pearson's R = 0.55; 95% CI = 0.54–0.56; t = 85.897; d.f. = 17,241; P < 0.0001; Extended Data Fig. 1). Because of this relationship, thermophilization may potentially cause concomitant mesophilization. For example, of the 116 ecoregions where annual precipitation is decreasing through time, approximately half (56%) exhibited positive MRs and the mean TR of these ecoregions was significantly greater than zero (mean TR = 0.018 °C yr⁻¹; 95% CI = 0.0085–0.028 °C yr⁻¹). In contrast, in ecoregions where MR was decreasing as predicted due to decreasing rainfall, mean TR was significantly less (Welch's t-test, t = −2.04, d.f. = 112.8, P = 0.0438) and was not different from zero (mean TR = 0.0055 °C yr⁻¹; 95% CI = −0.0022–0.013 °C yr⁻¹). This suggests that rapid thermophilization may cause plant communities to have greater water demands and hence to become more drought-sensitive regardless of changes in precipitation and water availability (Fig. 3). If this is the case, the potential stresses caused by future droughts will be exacerbated, especially if the frequency and/or magnitude of droughts increases as is predicted for many parts of the New World[30–32].

In this study, we tested for changes in plant community composition at the hemispheric-scale over nearly a half century. Working at such large spatial and temporal scales with multiple collated and extrapolated databases obviously introduces many potential sources of error that can obfuscate important underlying factors. Despite using correction procedures to account for collection biases, it is certainly possible that the collections we analysed do not accurately represent the climatic compositions of ecoregions or the changes in composition of ecoregions through time. For example, our filters excluded plant species with few available samples and hence it is likely that rare and endemic species were underrepresented in our characterizations of community composition. Also, our dataset and methods may not distinguish the effects of urban heating versus global warming. Specifically, if records came increasingly from 'urban heat islands' (for example, due to collector biases or expanding urban areas) then the composition of collections could shift towards a greater representation of more-thermophilic species over time even in the absence of global warming. Alternatively, the observed changes in plant community composition may reflect the effects of changes in land use (for example, deforestation, forest recovery, fires and so on) or altered biotic interactions (for example, introduced pests or changes in herbivore pressure). More detailed studies are needed to determine the specific factors driving changes in the abundances and ranges of individual species through time.

Despite the many complexities and limitations inherent in large-scale studies, our results show a clear pattern of thermophilization in most New World ecoregions that is consistent with a priori expectations based on concurrent changes in temperature and the decreasing relative abundance of species in ecoregions that are becoming 'too hot'. These changes in plant community composition may in turn have important implications for the persistence of

species under ongoing climate change (for example, due to changes in population sizes and/or altered drought sensitivity), as well as for ecosystem functioning[33] and the many vital services that these species and ecoregions provide.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-020-0873-2.

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Methods

To investigate changes through time in the composition of New World plant communities, we used an expansive online database of plant collections and observation records to characterize the plant assemblages, or floras, of ecoregions[34,35] at annual timesteps from 1970 to 2011. We then tested for directional changes in the floristic composition of the ecoregions over time. Specifically, we downloaded all the georeferenced plant location records that are publically available through the Botanical Information and Ecology Network (BIEN) database[36–45] (v.4.1.1, accessed in November 2018 via the BIEN R package[42]) for the New World (North America, Central America and South America but excluding the Caribbean islands). The BIEN database provides collated observation and collection data from multiple sources such as the Global Biodiversity Information Facility (GBIF), Tropical Ecology Assessment and Monitoring (TEAM), SpeciesLink and the US Forest Inventory and Analysis (FIA) programme and provides a base level of data cleaning and standardization[40,46]. We used BIEN's default download settings that excluded records of known introduced species and cultivated individuals. We further filtered the records to include only those that were identified to species, were georeferenced and that listed the year of collection/observation as being between 1970 and 2011 (years prior and subsequent to this period had substantially fewer collection records available through BIEN). This resulted in >20 million usable records for >100,000 species in 267 ecoregions and 14 biomes (see Supplementary Data and Fig. 1).

To estimate the MAT_{opt} and the TAP_{opt} of the New World plant species[23], we extracted the estimated MAT (BIOCLIM1) and TAP (BIOCLIM12) at all of the recorded collection coordinates from the CHELSA v.1.2 raster of 'current' (that is, mean of 1979–2012) climate at 30-arcsec resolution[47]. We then estimated the MAT_{opt} and TAP_{opt} of each species as the mean MAT and TAP of all collections from 1970 to 1985, respectively. We only used the collection locations from this initial 15-yr period to minimize mischaracterizations that could potentially arise if species' ranges are in fact shifting over time. We also tried alternative metrics of water availability besides TAP including the 'climatological moisture index' and the 'Thornthwaite aridity index'[28] but we found that TAP was the best predictor of the plant community composition. We also tried alternative measures of estimating MAT_{opt} and TAP_{opt} (for example, median or modal collection MAT/TAP) but these did not change our overall results (Supplementary Figs. 5–7). We excluded species with fewer than 20 records for the period 1970–1985 from subsequent analysis, leaving us with >17,000 New World plant species represented by about 17 million georeferenced and dated collection records. Given the purported connection between the number of collections available in BIEN and species commonness[48], our filters probably disproportionately eliminated rarer species. As such, our results should be interpreted as pertaining primarily to well-collected or common plant species.

We next used the collection records to characterize the composition of the floristic communities in each of the New World ecoregions in each calendar year from 1970 to 2011 as the mean MAT_{opt} and TAP_{opt} (estimated from species' initial distributions) for all constituent species weighted by the number of collections per species that year in the ecoregion of interest. We refer to the resultant metrics as the ecoregion's CTI and the CPI, respectively[23]. We calculated each ecoregion's CTI and CPI in each year for which there were ≥50 total records of all species combined (Supplementary Data).

Preliminary analyses raised concerns that CTI and CPI can be affected by shifting collecting patterns or collector biases, especially when weighting by the number of occurrences. Specifically, if collections came predominantly from hotter portions of an ecoregion (that is, typically at lower elevations or latitudes) in a given year, estimates of CTI would be elevated. Likewise, if collections came predominantly from dryer portions of an ecoregion, estimates of CPI would be down-shifted. If these biases change directionally through time (for example, towards hotter and hotter, or dryer and dryer, locations through time) then it could create a false impression of directional shifts in community composition even in the absence of real changes. To account for this possibility, we applied a correction by calculating CTI and CPI for each ecoregion in each year on the basis of the differences between each plant species' MAT_{opt} or TAP_{opt} and the MAT or TAP, respectively, at the corresponding collection locations (as originally estimated from the CHELSA raster of 'current' climate). The resultant estimates of CTI and CPI therefore represent deviations, or anomalies, between the collected plant communities' climatic compositions and the expected values based on the baseline conditions where the collections were made and assuming no change in climate through time. In other words, positive CTI anomalies indicate that the species collected from a given ecoregion in a given year were more-thermophilic on average than expected on the basis of the baseline temperatures at the corresponding collection locations, and negative CTI anomalies indicate that species were less-thermophilic on average than expected on the basis of the baseline temperatures at their collection locations (likewise for anomalies in CPI with respect to TAP). To convert back to corrected measures of CTI and CPI in units of absolute temperature (°C) and precipitation (mm), we then added the anomalies back to the overall mean MAT and TAP, respectively, of each ecoregion as originally estimated from the CHELSA climate raster (see Supplementary Fig. 8 for an expanded explanation of the correction procedure). Simulations indicate that this correction procedure is effective. Specifically, the correction (1) has little

or no impact on results when collection locations are unbiased (that is, when collections are random with regards to MAT and TAP), (2) fully eliminates any false signal of directional changes in CTI caused by biased sampling and (3) does not obscure any changes in CTI due to compositional change (see Supplementary Fig. 9 for simulation code and output).

As an alternative means of minimizing the effects of collection biases, we also calculated each ecoregion's annual CTI and CPI on the basis of just the presence versus absence of species (in other words, when calculating CTI and CPI, we did not weight the species by their number of occurrence records in that year). The annual estimates of CTI and CPI per ecoregion and the ecoregion-level results based on the presence–absence data are presented in the Supplementary Data. In the main text, we present the results of our analyses using the weighted and corrected CTI and CPI values since this metric (1) incorporates the different contributions of rare versus common species on community composition, (2) is less sensitive to georeferencing or taxonomic errors and (3) incorporates changes in species' abundances rather than just local extinctions and immigrations when used for looking at compositional changes over time. In other words, accounting for differences in the number of collection records between species (while correcting for changing collection intensities) provides a better depiction of plant communities and should be more sensitive to changes of composition. Furthermore, while the choice of CTI and CPI metrics does influence estimates of specific rates and values, the overall pattern of directional changes in composition are robust. For example, 68% of ecoregions had positive TR (see below) when CTI values were calculated from species abundances, while 74% of ecoregions had positive TR when CTI values were calculated based on presence–absence data (likewise, 60% of ecoregions had positive MR when CPI values were calculated using abundance data versus 66% when CPI was calculated using presence–absence data).

Community mean traits, such as CTI and CPI, have been widely used to characterize plant communities and to test for the effects of climate change (both postglacial warming and modern anthropogenic climate change) on the functional composition of local plots and ecosystems over time[21–24,49–53]. However, we are not aware of any previous studies that have calculated these metrics over regional or ecoregion scales. As such, it was important to validate their use in characterizing community composition. To test if CTI and CPI can accurately characterize the composition of ecoregions, we compared the predicted CTI and CPI values for 1970 to the overall mean MAT and TAP, respectively, within each ecoregion. Ecoregion CTI and MAT were very strongly correlated (Fig. 1a), as were CPI and TAP (Fig. 1b). In other words, variation in the composition of plant species collected from different ecoregions is strongly associated with differences in climate. Ecoregions with similar MAT have similar CTI and ecoregions with similar TAP have similar CPI, even if those ecoregions occur in different continents and/or biomes and have little or no compositional overlap. For example, the 'Appalachian–Blue Ridge forests', 'California montane chaparral and woodlands' and 'Mid-Atlantic US coastal savannas' ecoregions all have nearly identical MAT and CTI values despite being widely separated geographically and in different biomes ('temperate broadleaf and mixed forests', 'Mediterranean forests, woodlands and scrub' and 'temperate grasslands, savannas and shrublands', respectively).

Once we had estimated CTI and CPI for each ecoregion, we then tested for changes in species composition over time. For each of the 191 ecoregions that had >10 yr of CTI and CPI estimates, we calculated the TR and the MR as the slope of the linear least-square regression between CTI and CPI, respectively, and calendar year weighted by the log_{10} of total number of collections per ecoregion per year. A positive TR indicates increasing CTI due to increasing relative abundances of species with hotter MAT_{opt} and positive MR indicates increasing CPI due to increasing relative abundances of species with wetter TAP_{opt}. Because of the corrections applied to estimates of CTI and CPI, TR and MR should reflect changes in the composition of the communities due to changes in species' local abundances independent of within-ecoregion shifts in collection patterns.

As a separate measure of plant compositional changes over time, we compared each ecoregion's initial versus final CTI/CPI as calculated using the combined collections from January 1970 to December 1985 (initial) versus the combined collections from January 1996 to December 2011 (final). We also identified which species had been lost from the collection record of each ecoregion between these initial and final time periods (that is, 'lost' species were those that were collected in an ecoregion during 1970–1985 but that were not collected from that ecoregion during 1996–2011) as well as species that recruited into ecoregions between these time periods (that is, 'recruiting' species were those that were not collected in an ecoregion during 1970–1985 but were collected from that ecoregion during 1996–2011) and surviving species (that is, 'surviving' species were those species that were collected in an ecoregion during both 1970–1985 and 1996–2011). We then calculated the CTI and CPI of the groups of lost, recruiting and surviving species in each ecoregion and compared them to each other (lost species were weighted by their abundances in the initial time period; recruiting species were weighted by their abundances in the final time period; surviving species were weighted by their abundances in the initial time period for comparisons with lost species and by their final abundances for comparisons with recruiting species).

For assessing how changes in climatic composition (that is, TR and MR) relate to climate change, we calculated the mean annual change in MAT and TAP in

each ecoregion over the study period. To estimate rates of change in these climate variables, we randomly selected 2,000 unique pixels (30-arcsec resolution) in each ecoregion (for any ecoregions with fewer than 2,000 pixels, we used all pixels). Then we extracted the CHELSA estimates of monthly mean and maximum temperatures and precipitation in each of these pixels and calculated the mean value for each ecoregion for each month during 1979–2012. We then fitted linear regressions to the monthly values and used the slope of these relationships as our estimates of annualized change rates for MAT and TAP (MAT_{ch} and TAP_{ch}, respectively; Fig. 3). We also calculated and analysed changes in the monthly mean maximum temperatures of each ecoregion through time but results were not qualitatively distinct from those based on MAT_{ch}.

To test the relationships between rates of compositional change (TR and MR) and rates of climate change (MAT_{ch} and TAP_{ch}, respectively), we performed linear mixed-effects models fit using the lme4 package in R (refs. [54,55]) with random intercepts and slopes for the 14 biomes. We quantified the proportion of variance explained by the linear mixed-effects models with the marginal R^2 (for the fixed-effects) and the conditional R^2 (for the fixed and random effects combined) using the MuMIn package in R (ref. [56]). The 95% CIs were estimated on the basis of parametric bootstrapping with 1,000 sampling iterations. We performed all analyses in R v.3.6.1 (ref. [54]).

Data availability

The project was based entirely on data that are publicly available through CHELSA (http://chelsa-climate.org/), Ecoregions2017 (https://ecoregions2017.appspot.com/) and BIEN (http://bien.nceas.ucsb.edu/bien/). A list of data providers contributing plant collection and observation records to BIEN is included in the Supplementary Information.

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Author contributions

K.J.F. conceived and designed the project and led manuscript writing. K.J.F., C.B., B.F., T.M.P. and D.Z. analysed the data and interpreted results. K.J.F. led manuscript writing and preparation. C.B., B.F., T.M.P. and D.Z. assisted in manuscript writing and preparation.

Competing interests

The authors declare no competing interests.
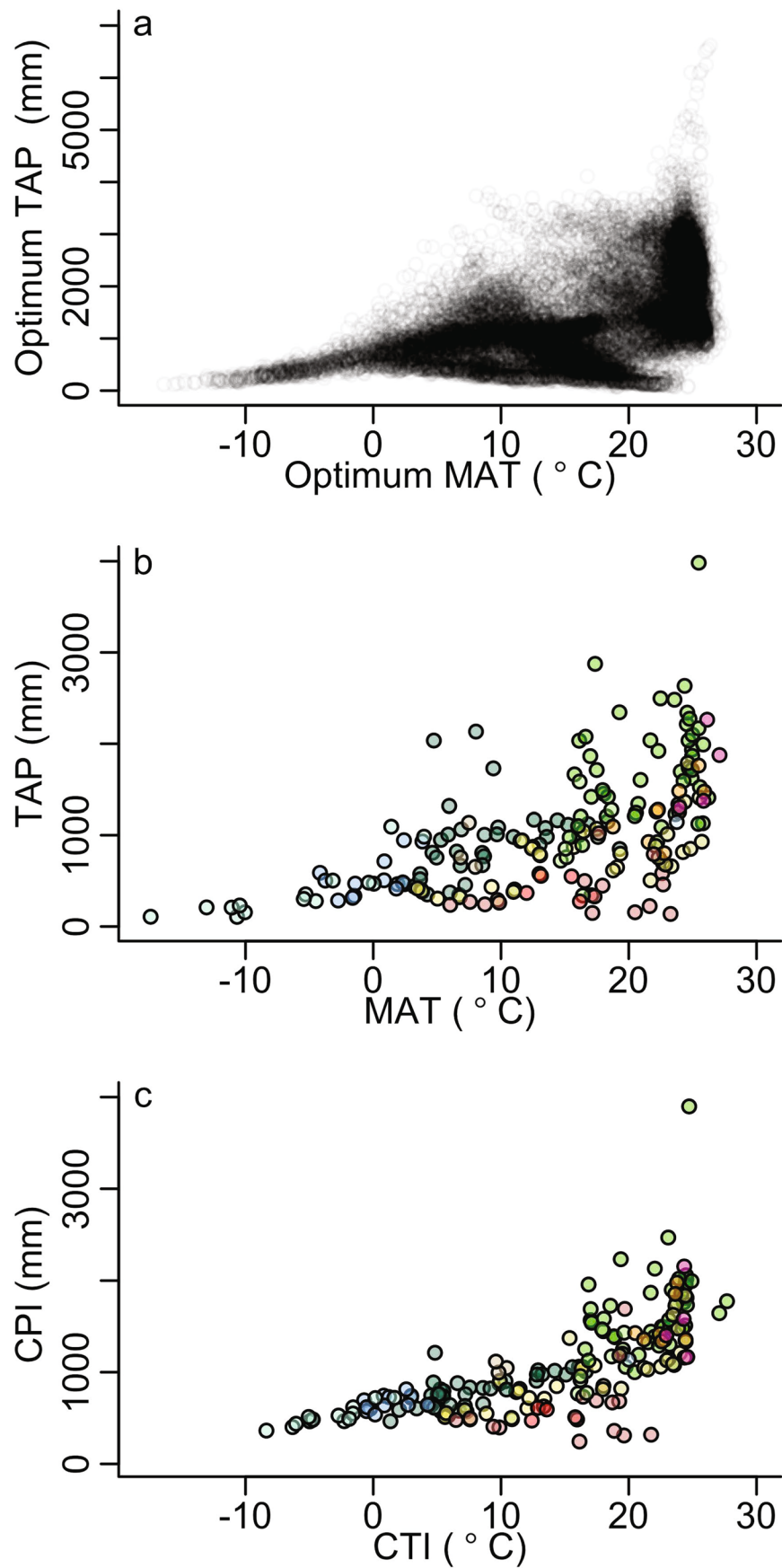
Additional information

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Extended Data Fig. 1 | See next page for caption.

Extended Data Fig. 1 | The relationships between temperature and precipitation at the species, ecosystem and community levels. The relationships between **a**, species' optimal temperature (MAT_{opt}, °C) and optimal precipitation (TAP_{opt}, mm) as based on the distribution of observation records from 1970–1985 (Pearson's R = 0.55; d.f. = 17241; P < 0.0001), **b**, the average Mean Annual Temperature (MAT, °C) and Total Annual Precipitation (TAP, mm) of ecoregions from 1979–2012 (Pearson's correlation, R = 0.58; d.f. = 189; P < 0.0001), and **c**) the initial (1970–1985) Community Temperature Index (CTI, °C) and Community Precipitation Index (CPI, mm) of ecoregions (Pearson's R = 0.72; d.f. = 189; P < 0.0001). In a, each point represents a species; in b and c, each point represents an ecoregion and points are coloured according to their biome designation (see Fig. 1).