Title

Rapid shifts in grassland communities driven by climate change

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Publication Date

2024-10-16

DOI

10.1038/s41559-024-02552-z

Grassland communities rapidly respond to climate change to settle climatic debts

Compositional shifts in forest communities are known to not keep pace with climate change, which leads to accumulating 'climatic debts'. We show that grassland communities in California are transforming rapidly, at a pace similar to that of climate warming and drying, and are paying off their climatic debts continuously.

This is a summary of:
Zhu, K. et al. Rapid shifts in grassland communities driven by climate change. *Nat. Ecol. Evol*. https://doi.org/10.1038/s41559-024-02552-z (2024).

Published online: 16 October 2024

The problem

Climate change is expected to alter species distributions, which poses considerable risks to biodiversity and ecosystem functioning. To date, evidence from forests indicates that plant communities might be lagged in their responses to changing climate, as shown by the slow shifts in community composition compared with the pace of climate change[1,2]. Such disequilibrium between plant communities and climate creates climatic debts that must be paid off with future community reshuffling[1]. However, we hypothesized that not all plant communities are accumulating climatic debts. For example, grassland communities might be more responsive than other communities to climate change, as they are dominated by short-lived species, are more directly exposed to macroclimate change[3] and are often heavily invaded by non-native plant species. Identifying such highly responsive communities is important for detecting and predicting the effects of climate change. We therefore examined changes in the composition of grassland communities in the California Floristic Province (CFP), a global biodiversity hotspot with a Mediterranean climate[4].

The discovery

To examine long-term changes in community composition and the effects of climate change treatments, we compiled a dataset of the relative species abundance in communities at 12 observational sites in the CFP and in three global change experiments (involving manipulation of temperature and precipitation). We estimated the climate niches (the climatic conditions in which species can occur) of all species in the dataset using occurrence records in the Global Biodiversity Information Facility (GBIF) (Fig. 1a). Using the relative abundance and climate niche centroids of species in communities, we calculated how much communities shifted toward species associated with warmer and drier locations, referred to as thermophilization and xerophilization[2], respectively (Fig. 1b). This approach places species and communities in the climate space defined by temperature and precipitation niches, and thus quantifies community responses in dimensions directly linked to climate change (which reveals signals that are not evident when focusing on species guilds).

We found that grassland communities at long-term observational sites experienced statistically significant shifts toward species associated with warmer and drier locations at rates comparable to the pace of climate warming and drying at these sites. Similarly, experimental manipulation of temperature and precipitation drove community compositional shifts in the climate space in time periods as short as one year. The species that experience significant change in relative abundance vary by site. However, the directions of thermophilization and xerophilization, as well as their ratio, of communities were similar across observations and experiments (Fig. 1b). These findings suggest that CFP grassland communities respond rapidly and consistently to climate change.

The implications

Our findings provide compelling evidence that grassland communities track climate change more closely than forest communities. Forest communities are considered to accumulate climatic debt, whereas some communities (such as grasslands) settle climatic debts continuously — although this does not imply that grasslands are free of risks. Instead, it highlights unique risks: first, the unequivocal effects of climate change on communities predict changes in biodiversity and species interactions[4]. For grasslands, such changes are happening now; for forests, we might expect abrupt changes in the future. Second, given that shifts in community composition are constrained by the available species' niche space (Fig. 1a), communities might be limited in the capacity to track climate change that takes place in multiple dimensions (for example, temperature and precipitation) in unprecedented ways.

Our study did not account for species' local adaptation or evolution in climate niches. Data on variations in species' climate niches, among individuals or over time, could enable a better understanding of how communities track climate change. We were not able to completely disentangle the individual effects of warming and drying within this composite climate change driver, which might be resolved by future global change experiments or as we observe novel combinations of climatic variables.

Bigger questions can be answered when situating this study in the broader field of ecological acclimation (reducing climate disequilibrium)[5]. In our study, we report responses in the structure of communities, but it is interesting to examine how the structure and function of communities acclimate to climate change. Furthermore, when considering grasslands and forest communities on a continuous spectrum, we are curious to know whether we can predict the acclimation of communities on the basis of their properties.

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EXPERT OPINION

"This is a very important study, which provides valuable insights on biodiversity responses to climate changes when compared with forest ecosystems and in light of microclimatic processes. The striking difference in the speed at which grassland plant communities are reshuffling in response to warmer and drier conditions, as opposed to the lagging dynamics in the response of forest plant communities, makes this very novel and important for a broad audience." **Jonathan Lenoir, Centre National de la Recherche Scientifique (CNRS), Amiens, France.**

FIGURE

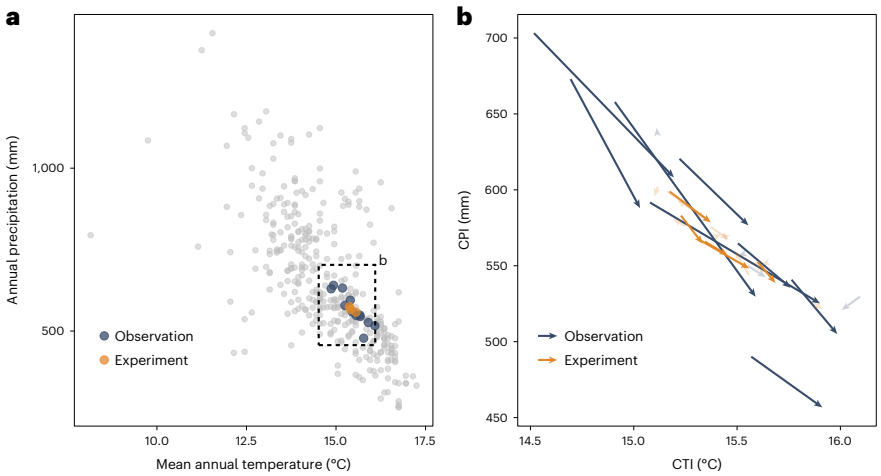

Fig. 1 | Shifts in grassland community composition in the CFP. a, Community composition was characterized at 12 observational sites (blue) and one of the three experimental sites (orange) by the median community temperature index (CTI) (°C) and community precipitation index (CPI) (mm), positioned in estimated species' climate niche centroids (median, grey). The inset indicates the area in **b**. **b**, Community shifts in the dimensions of temperature and precipitation are consistent in direction, both for observations (blue arrows pointing from the start to the end of the sampling period) and experiments (orange arrows pointing from ambient to warming treatments). Non-significant relationships in either CTI or CPI (two-sided *t*-test, $P > 0.05$) are indicated with semi-transparent arrows.

BEHIND THE PAPER

A common confusion while we prepared this manuscript was that the rapid community thermophilization and xerophilization at rates comparable to climate change were considered to be adaptations. This is risky, as it could lead to overly optimistic views of the trajectory of grassland communities and diminish potential conservation efforts in these ecologically important, vulnerable habitats. To avoid confusion, we used neutral terms such as 'response' instead of value-laden terms such as 'adaptation'. We also showed that community compositional shifts were driven by species establishment or increase as well as by species extirpation or decrease. In fact, many species that increased in abundance under climate change are non-native species. Finally, we articulated that grassland communities suffer from threats to biodiversity and species interactions, albeit different from those for forest communities. More studies that assess the ecological consequences might help to evaluate whether the observed community responses can be considered adaptations. **Y.S.**

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FROM THE EDITOR

"This study combines a considerable amount of data from both manipulative field experiments and observational datasets. It identifies a strong signal of climate-driven community shifts in a biodiversity hotspot. The inclusion of a CPI, in addition to the most widely used CTI, is a notable element of the analysis." **Editorial Team, *Nature Ecology & Evolution*.**