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Climate change is projected to outpace rates of niche change in grasses

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Climate change may soon threaten much of global biodiversity, especially if species cannot adapt to changing climatic conditions quickly enough. A critical question is how quickly climatic niches change, and if this speed is sufficient to prevent extinction as climates warm. Here, we address this question in the grass family (Poaceae). Grasses are fundamental to one of Earth's most widespread biomes (grasslands), and provide roughly half of all calories consumed by humans (including wheat, rice, corn and sorghum). We estimate rates of climatic niche change in 236 species and compare these with rates of projected climate change by 2070. Our results show that projected climate change is consistently faster than rates of niche change in grasses, typically by more than 5000-fold for temperature-related variables. Although these results do not show directly what will happen under global warming, they have troubling implications for a major biome and for human food resources.

1. Introduction

Climate change may soon threaten much of global biodiversity [1], especially if species cannot adapt to changing conditions quickly enough. These biodiversity losses may have very different implications for humans, depending on the species. For example, the loss (or even local declines) of just a few species of grasses (Poaceae) might cause widespread starvation. Here, we address how quickly climatic niches change in grasses, and the potential implications under global climate change.

The grasses (Poaceae) are a diverse (more than 11 000 species; [2]) and broadly important plant family. Natural grasslands cover approximately 25% of Earth's land area [3], and are habitats for many endemic plant and animal species (e.g. the Brazilian Cerrado biodiversity hotspot; [4]). Further, many crucial crop species belong to Poaceae [5]. For example, wheat, maize, rice and sorghum are grasses that together occupy over half of global arable land [6]. Cereals (grasses) provide approximately 49% of total calories consumed worldwide, and are especially important in developing countries [6]. Thus, if climate change has strong negative impacts on grasses, there might be significant consequences for both global biodiversity and for humans.

The rate of climatic niche change in grass species may be critically important for understanding their responses to future climate change. A species' realized climatic niche is the set of large-scale temperature and precipitation conditions where it occurs, and may be shaped by physiological tolerances, plasticity, biotic interactions and access to different climatic conditions [7]. Given rapid climate change, a species' present climatic niche may no longer occur within its current geographical range. Under this scenario, three outcomes are likely for the species: (i) shifting its geographical range to remain within its climatic niche (e.g. moving to higher elevations and latitudes), (ii) shifting its climatic niche to encompass the new conditions (e.g. through evolutionary and/or plastic responses) or (iii) extinction [8,9]. Estimated dispersal rates in many plants may be too slow to allow tracking their niches as climate changes, including grassland species [10]. Even if dispersal were fast enough, it may be limited by numerous factors (e.g. species confined to mountaintops, specialized

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habitats, or islands), but especially human habitat modification. Therefore, survival for many species may depend on how quickly their climatic niches can shift (and niche shifts may be the only option for survival of local populations). Analyses in vertebrates suggest that projected rates of climate change exceed rates of climatic niche change by approximately 100 000-fold [11], but it is unclear if rate differences are similar in plants.

Here, we compare rates of niche change and future climate change in grasses (Poaceae). We use climatic data and time-calibrated phylogenies to assess past rates of change in realized climatic niches and compare these with projected rates of anthropogenic climate change (using methods similar to [11]).

2. Material and methods

Detailed methods are given in the Dryad Digital Repository, appendix S1 (see also figure S1, appendices S2–S10 and tables S1–17 in the Dryad Digital Repository [12]). A brief summary is given here. We used three time-calibrated molecular phylogenies to identify sister species and estimate rates of niche change. We used a phylogeny of 1230 grass species (Tree 2010 hereafter; [13]) and two phylogenies of 3595 grass species (Trees 2014–1, 2014–2; [2]). All trees were estimated from both chloroplast and nuclear sequences, but were calibrated differently.

To reduce the effects of incomplete taxon sampling on rate estimates, we estimated rates only for closely related species pairs [11]. Thus, we selected the youngest sister species pair in each genus for which climatic data were available (from [13]). Using these criteria, we selected 85 pairs (170 species from eight subfamilies) from Tree 2010, including 155 species unique to this tree. We selected 31 and 30 species pairs (62 and 60 species) from Trees 2014–1 and 2014–2, including seven subfamilies. A total of 236 species were included across all three trees, representing 95 genera and nine subfamilies.

Climatic data were previously obtained from georeferenced localities from herbarium collections [13]. The median number of localities per species was 95.5 (range 10–35 339). We analysed four variables: mean annual temperature (Bio1), maximum annual temperature (Bio5), minimum annual temperature (Bio6) and mean annual precipitation (Bio12). These are standard variables for describing climatic niches and climate change [11]. We used the mean value across localities to represent each species for each variable.

To estimate past rates of climatic niche shifts, we first determined the best-fitting model of evolution for each climatic variable for each subfamily in each tree. We then reconstructed ancestral values of each climatic variable for the ancestor of each species under the best-fitting model. The niche shift was the absolute difference between the estimated value of each species pair's most recent common ancestor and the current climatic value for each species. We then divided the niche shift by the age of each species to determine the rate of niche change.

To determine projected rates of climate change, we examined a range of climate scenarios to find scenarios representing minimum, maximum, and intermediate levels of future change. We selected from four greenhouse gas scenarios and eight standard global climate models for a total of 32 possible climate scenarios. Climatic data were from the WorldClim database, v. 1.4 (release 3) [14]. We selected the projections that most frequently predicted the minimum, median and maximum levels of climate change across the distributions of two representative temperate and tropical grass species. Then, for each climatic variable and climate change scenario in each species, the future rates

of climate change were estimated as the difference between 'current' conditions (mean from 1950–2000, midpoint 1975) and projected climate conditions (for 2070) at each locality, divided by 95 years (2070–1975). The final value was the mean of these rates across localities for each species.

3. Results

Projected rates of climate change are dramatically faster than past rates of realized climatic niche change in grass species (figure 1). Exact values depend on the climatic variable, trees, species and future climate models (summary in the Dryad Digital Repository, table S1 [12]). Overall, rates of niche change in temperature variables are typically approximately 1–8°C per million years, whereas rates of future change are approximately 0.02°C per year (median climate model), and approximately 3000–20 000 times faster than median niche rates. Niche rates in temperature variables can be faster in some species, but the difference between past and future rates is always at least 20-fold or greater.

Rates of niche change in precipitation are typically approximately 200–600 mm per million years, and median rates are approximately 800–1700 times slower than projected change (median climate model). However, some species do approach the future rates. This may occur (in part) because some regions are projected to have little change in precipitation patterns.

4. Discussion

In this paper, we show that past rates of climatic niche change in grasses are much slower than rates of future projected climate change, suggesting that extinctions might occur in many species and/or local populations. This has several troubling implications, for both global biodiversity and human welfare. First, grasslands are one of Earth's most widespread biomes, with many endemic plant and animal species. Second, grasses are an important food source for humans (especially rice, wheat and corn). Evolutionary adaptation seems particularly unlikely for domesticated species (given reduced genetic variation), and even local declines may be devastating for some human populations. Strong reductions in crop yields are already predicted [15]. Third, the wild relatives of domesticated grass species may also be endangered by climate change, and yet these wild relatives may be crucial for helping maintain crop species in changing climates [16]. Fourth, non-domesticated grass species may provide important food for livestock.

We acknowledge that predicting the effects of climate change on species and populations is a very difficult problem, and rates of past niche change are only one of many components that should be considered. Our results cannot show directly what will happen in the future (a limitation also shared with experimental and modelling studies). There are several additional sources of uncertainty that might influence our conclusions. First, our estimates are based on past rates, and faster rates might still occur in the future. What our results can show is that such rapid rates would not only be atypical, but unprecedented based on the hundreds of species analysed here. Second, our rate estimates implicitly assume that niche change is constant over time. However, more rapid changes might occur over shorter
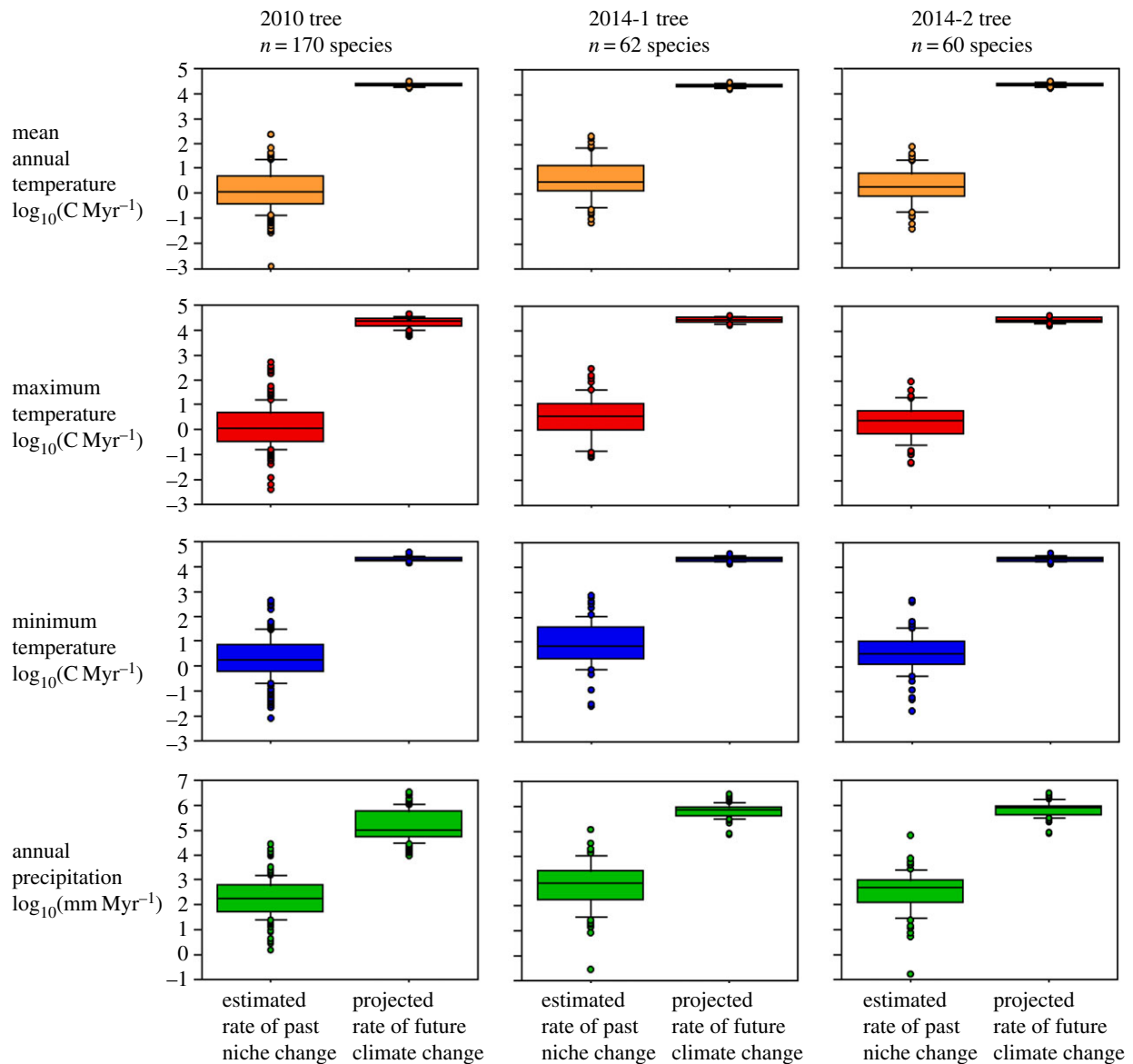
Figure 1. Comparison of rates of past niche change and future climate change in grass species, using three phylogenies and three sets of species (indicating median, quartiles, 10th and 90th percentiles, and outliers). Rates of niche change are based on the best-fitting model. Rates of future climate change are from the intermediate model (note: rate differences are identical using years or millions of years (Myr) for time units). Full results are provided in tables S5–S7 in the Dryad Digital Repository [12].

timescales. Indeed, younger grass species do have faster rates (table S8 in the Dryad Digital Repository [12]). A critical question is whether these fast rates can be sustained to yield the magnitude of niche changes needed to keep pace with climate change. Simply comparing niche divergence between sister species in our study shows that many pairs differ by less than the magnitude of expected climate change, suggesting that niche changes that have accumulated over thousands or millions of years are still less than projected climate change (table S9 in the Dryad Digital Repository [12]). There are many other potential sources of error in our rate estimates. However, our results are largely robust to different trees, divergence dates, and models of evolution. The accuracy of our ancestral climate reconstructions should have little impact, because niche rates estimated here should depend mainly on differences in climatic distributions of sister species (and species ages). Furthermore, our estimates are based on realized rather than fundamental niches [7]. However, physiological tolerances alone (i.e. fundamental niches) may be less important than the outcome of both abiotic and biotic factors (i.e. realized

niches). Species interactions are demonstrably important for climate change impacts on species in general [17], and for grassland plants in particular [18].

Finally, we note that our results are concordant with other lines of evidence indicating that niche shifts might be too slow to save local populations (and species) from extinction under climate change. For example, transplant experiments with a grassland plant suggested that adaptation will be too slow to keep pace with climate change [19]. Most importantly, studies of plant communities on elevational gradients over time have documented local extinctions at lower elevations associated with climate change [20–22]. These results support our inferences from grasses that niche shifts may generally be too slow to save populations from rapid anthropogenic climate change.

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