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Effects of Niche Marginality on Hotter-Drought Tree Mortality in Angiosperms and Gymnosperms

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ABSTRACT

Aim: Current observations of global tree mortality events associated with drought raise concerns about climate change risks to forests' dynamics and function. It is unclear which forests are more susceptible to pulses of mortality under further changing climates. We examined whether tree mortality related to hotter droughts is predominantly occurring in edge or core populations in niche space and assessed whether mortality patterns are consistent with species' drought tolerances.

Location: Global.

Time Period: 1970–2020.

Major Taxa Studied: Angiosperm and gymnosperm trees.

Methods: We estimated species' climatic niches on the basis of global occurrences and annual time series of climate. We computed the distance to the niche core of drought mortality sites (982 observations, 44 tree species) and compared it with null models of randomly distributed tree mortality. We assessed how loss of xylem conductance and hydraulic safety margin related to populations' position in niche space and to the degree of climate anomaly during mortality.

Results: In the year of mortality, 64.3% of the sites were closer to the species' niche edge than the niche core. However, when considering long-term climate averages, both marginal and central populations experienced drought-associated pulses of mortality. Overall, tree mortality was related to populations' shifts towards the edge of species' climatic niches and, in angiosperm mortality sites, species' drought tolerances were correlated with the intensity of climatic anomalies. In gymnosperm sites, marginal populations were more affected and other processes, such as heat-induced stress or cumulative drought effects, may have affected mortality.

Main Conclusions: Both marginal and central populations, even for highly drought-tolerant species, are vulnerable to climate change. Climate anomaly magnitude, cumulative drought effects, plant physiological limits and species niche geometry help explain range-wide patterns of hotter-drought-associated tree mortality.

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1 | Introduction

Human-induced global changes in environmental conditions (Waters et al. 2016) are altering major abiotic (e.g., wind, drought, heatwave, fire) and biotic (e.g., insect outbreaks, pathogens) forest disturbances that act at large biogeographical extents (Allen et al. 2015; Biedermann et al. 2019; Hartmann et al. 2022; Moritz et al. 2012; Senf et al. 2020) and can radically change ecosystem resilience under climate change. Hotter droughts can be defined as coincident extremely dry and hot climate anomalies, where drought conditions are occurring under much warmer than typical conditions over the recent decades at a given site; such hotter drought conditions appear in globally observed pulses of Earth's forest mortality (Hammond et al. 2022). Mechanisms of this phenomenon have been an increasing focus of scientific research (Allen et al. 2010, 2015; Hartmann et al. 2022; McDowell et al. 2022), in part because tree mortality has major consequences for ecosystem functioning and dynamics (Anderegg et al. 2013; Batllori et al. 2020). Predicting which forests are more likely to suffer climate-induced mortality, including how tree mortality may affect species across the range of environmental conditions in which they occur, remains challenging (Martínez-Vilalta et al. 2023; Sanchez-Martinez et al. 2023; Trugman et al. 2021).

Within this context, the realised climatic niche (Liu, Ye, and Wiens 2020; Lloret and Kitzberger 2018) offers a framework for assessing the response of tree species and forest ecosystems to major disturbances associated with climate change (Margalef-Marrase et al. 2020) by identifying the climatic conditions that enable species viability (Soberón and Nakamura 2009). Numerous environmental factors interact to define the ecological niche of a species (Carscadden et al. 2020). The relevance of climate for plants at biogeographic extents (e.g., Schultz et al. 2022) and the accelerated pace of climatic changes, including increased frequency of extreme events, make the climatic niche useful for assessing ecological niches at large spatial scales.

Increased knowledge of how mortality and other demographic processes vary across the species' niche increases our capacity to predict biodiversity dynamics under environmental change (Buckley and Puy 2022; Pagel et al. 2020; Pironon et al. 2018). One key issue still under debate is the performance (e.g., abundance, fitness) of central and marginal populations within a species' niche space. In geographic space, the 'core-periphery hypothesis' (Brown 1984; Martínez-Meyer et al. 2013) proposes that species performance declines from an optimal part of the niche towards the niche limits. However, environmental heterogeneity across the geographical niche may decouple niche edges in geographic and climatic space (Oldfather et al. 2020). Therefore, assessing centrality and marginality in environmental rather than geographic space is recommended (Blonder et al. 2018; Sopniewski et al. 2024; Vilà-Cabrera et al. 2019). Nevertheless, differences in the evolutionary ecology and adaptive capacity of central (core) and marginal (edge) populations, together with source-sink dynamics of gene flow, dispersal limitations, species trait variability and species interactions (Jaime et al. 2022; Lloret and Kitzberger 2018; Martínez-Vilalta et al. 2023; Rehm et al. 2015;

Sexton et al. 2009) may confound the expected effect of niche position on species performance.

From a physiological perspective, drought mortality results from hydraulic failure or the loss of functionality of the plant conductive tissue (xylem) that can be coupled to reductions in carbon uptake and thus reduction of carbon pools to maintain hydraulic function and other metabolic processes (Adams et al. 2017; Hartmann et al. 2022; McDowell et al. 2022). Plant hydraulic traits have been related to observed drought-related mortality patterns in forests (Anderegg et al. 2016) and have also been useful for projecting the global climatic vulnerability of forests in the future (Sanchez-Martinez et al. 2023). Among the hydraulic traits often used to assess drought tolerance and response are the water potential causing 50% or 88% loss of xylem hydraulic conductance (P_{50} and P_{88}) and the hydraulic safety margin (HSM), which integrates stomatal and hydraulic responses (Anderegg et al. 2019). Hydraulic traits have been used to interpret biogeographical patterns of tree mortality (Anderegg et al. 2016, 2019; Peters et al. 2021). The integration of these traits with the climatic niche allows a standardised comparison among species that increases understanding of patterns of global forest mortality due to drought.

We used a global, geo-referenced database of recent tree mortality associated with hotter drought extremes (982 observations of 44 tree species; Figure 1) (Hammond et al. 2022) to assess macroecological patterns of tree mortality across species within their climatic niches. We also examined the link between mortality patterns and species' drought tolerance traits. We used null models of randomly distributed tree mortality to test whether mortality predominantly occurred in more marginal (niche edge) or more central (niche core) populations. We examined mortality patterns for both sites' long-term climate averages (1979–2018) and the conditions from 2 to 10 years preceding mortality at each site. We then assessed how species-level hydraulic traits (P_{50} , P_{88} and HSM) were related to mortality sites' niche position and to the degree of climate anomaly during mortality. We assessed patterns of tree mortality for all species and separately for angiosperms and gymnosperms.

2 | Material and Methods

2.1 | Mortality and Hydraulic Trait Data

We used 982 observations of 44 tree species (21 angiosperms and 23 gymnosperms; Figure 1, Table 1) retrieved from the database of climate-induced tree mortality ($\geq 15\%$ canopy trees standing dead) from 1970 through 2020, described in Hammond et al. (2022). We first filtered these data to plots dominated by one or two tree species (688 plots, 52.8% of the global tree mortality database). This process excluded species-rich tropical forests where complex interspecific interactions may operate. In all plots, although additional drivers (e.g., bark beetle infestation and other insect pests or pathogens) may have contributed to the observed tree mortality (Hartmann et al. 2025; Jactel et al. 2012; Jaime et al. 2023), heat, drought, or their combination were identified by the original study authors as concomitant drivers of tree mortality, and the plots'

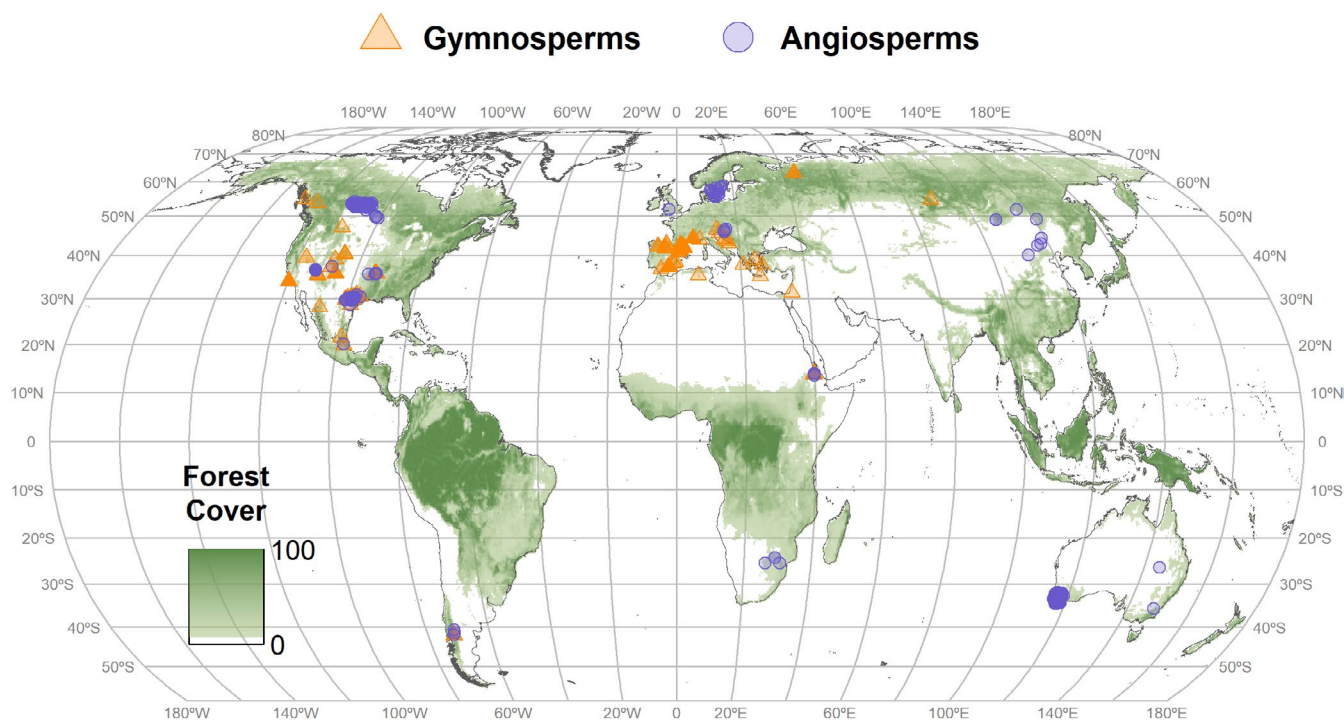


FIGURE 1 | Locations of the 982 drought-related mortality observations ($N=44$ tree species) for which the distance to the niche core and edge within the species' climatic niche was assessed. Points are semitransparent, so their colour intensity reflects overlapping observations. Mean forest cover $\pm$ standard deviation in angiosperm and gymnosperm dominated sites was $28.58\% \pm 16.24\%$ and $18.53\% \pm 21.28\%$ respectively. Global forest cover based on Global Forest Watch (<http://globalforestwatch.org>).

location with a 1 km precision was geo-referenced. For 66% of the species included in our study, the database reports mortality in multiple sites (Table 1). The data we used are limited in their taxonomic representation when compared with forests across the globe, and the number of mortality records is highly variable among species. However, these data allow the most up-to-date assessment of the patterns of drought-associated mortality for multiple tree species. We obtained hydraulic trait data, including P_{50} , P_{88} and HSM, from Sanchez-Martinez et al. (2023) and the Xylem Functional Traits Database (<https://xylemfunctionaltraits.org/>). Trait data were available for 27 of the 44 species.

2.2 | Climate Data

We obtained monthly time series of spatially gridded annual precipitation (Pr), maximum temperature (Tmax), potential evapotranspiration (Pet), vapour pressure deficit (Vpd) and climatic moisture index (precipitation minus potential evapotranspiration; Cmi) from CHESLA at 1 km² spatial resolution for each year of the period 1979–2018 (Karger et al. 2017), spanning most of the period covered by the tree mortality database. These five climatic variables are ecophysiologically meaningful predictors of relationships between plants and water in the soil or air (Sanchez-Martinez et al. 2023) that are directly related to heat and drought conditions and that have been reported to have a significant influence on forest mortality patterns at large spatial extents (Allen et al. 2015; Clifford et al. 2013; Hammond et al. 2022; Levesque and Hamann 2022; Neumann et al. 2017). Climatic variability is

key to species responses to environmental change and to modelling the species climatic niche (Broennimann et al. 2012; Pérez-Navarro et al. 2021; Zimmermann et al. 2009). We used monthly values of climate to compute at each pixel worldwide the total annual Pr; annual monthly maximum Tmax, Vpd and Pet and annual monthly minimum Cmi. Although the period of ~40 years covered by CHESLA data may not encompass all climatic variability experienced by long-lived trees in any given pixel, these data allowed us to explicitly incorporate inter-annual climate variability over the period of observed mortality.

2.3 | Species Occurrence Data

We obtained global species occurrence data for the 44 tree species from the Global Biodiversity Information Facility (GBIF.org 2025). For each species, we removed herbaria and fossil specimens, taxonomic inconsistencies and duplicate observations. The occurrence records for each species reflect past anthropogenic processes (e.g., land use) that potentially altered species' (natural) occurrence patterns in geographic space. However, in environmental space, these modifications may be buffered by the climatic redundancy of species' occurrences or can indicate the development of new populations within the species' fundamental niche. In addition, the reported rates of climatic-niche evolution in plants (Liu, Ye, and Wiens 2020) and the described niche conservatism in post-glacial colonisation and in invasive plant species (Liu, Wolter, et al. 2020; Petitpierre et al. 2012; Wasof et al. 2015) support the use of current plant species distributions to characterise their realised climatic niche.

TABLE 1 | List of species and number of observations for each species in sites with reported drought-related mortality. The total number of sites reported in the original mortality data set (All) and the number of sites with unique climatic conditions at the 1 km² resolution of the used climate data (Unique) is shown. Full information for each species and mortality site can be found in Hammond et al. (2022).

Species	N observations All/unique	Species	N observations All/unique
<i>Abies alba</i>	14/4	<i>Pinus durangensis</i>	1/1
<i>Abies lasiocarpa</i>	4/4	<i>Pinus echinata</i>	3/3
<i>Abies pinsapo</i>	2/2	<i>Pinus edulis</i>	12/12
<i>Acacia aneura</i>	1/1	<i>Pinus greggii</i>	1/1
<i>Austrocedrus chilensis</i>	4/4	<i>Pinus halepensis</i>	12/12
<i>Betula pendula</i>	1/1	<i>Pinus monophylla</i>	1/1
<i>Betula platyphylla</i>	5/5	<i>Pinus muricata</i>	79/4
<i>Cedrus atlantica</i>	1/1	<i>Pinus nigra</i>	5/5
<i>Chamaecyparis nootkatensis</i>	1/1	<i>Pinus patula</i>	1/1
<i>Corymbia calophylla</i>	248/173	<i>Pinus pinaster</i>	12/12
<i>Eucalyptus delegatensis</i>	1/1	<i>Pinus sibirica</i>	1/1
<i>Eucalyptus gomphocephala</i>	1/1	<i>Pinus sylvestris</i>	55/35
<i>Eucalyptus marginata</i>	248/173	<i>Populus tremuloides</i>	72/70
<i>Eucalyptus wandoo</i>	66/66	<i>Pterocarpus angolensis</i>	1/1
<i>Euphorbia ingens</i>	3/3	<i>Quercus affinis</i>	1/1
<i>Fagus sylvatica</i>	1/1	<i>Quercus alba</i>	3/3
<i>Juniperus ashei</i>	30/20	<i>Quercus douglasii</i>	15/12
<i>Juniperus monosperma</i>	4/4	<i>Quercus fusiformis</i>	30/20
<i>Juniperus procera</i>	4/4	<i>Quercus robur</i>	20/20
<i>Nothofagus pumilio</i>	3/3	<i>Quercus stellata</i>	1/1
<i>Olea europaea</i>	4/4	<i>Ulmus pumila</i>	2/2
<i>Picea abies</i>	6/6		
<i>Pinus contorta</i>	2/2		

2.4 | Defining Species Climatic Niche

We used information about the climatic conditions associated with species occurrences to compute the species' realised climatic niches. First, considering the 1 km² spatial resolution of the climatic data, we filtered the point-level occurrence data to retain a single observation, randomly selected, in each 1 km² pixel. Such filtering also alleviates potential biases in sampling effort over the species' distribution ranges. Second, we extracted annual values of Pr, Tmax, Vpd, Pet and Cmi for each species' selected occurrence. Third, we used the climate values associated with all 44 species (29,105,960 values, including interannual variability) to perform a principal component analysis (PCA) that defined an environmental space common to all species. Before PCA computation, we scaled the climate variables to have unit variance by subtracting their mean and dividing by their standard deviation. Fourth, to estimate the realised climatic niche for each species, we applied a kernel density function (Chacón and Duong 2018) to all annual values to determine the smoothed

density of occurrences within the axes defined by the first three PCA components (accounting for 96.5% of the variability in the original variables, see Figure S1 in Supporting Information). We estimated kernel density with a common grid of 241³ cells spanning the range defined by the three PCA components. Because defining an optimal grid size for three-dimensional kernel estimates is difficult, we also estimated the species' niches with nine additional common grids, spanning from 121³ to 301³ cells, to test whether the obtained patterns were consistent. We defined niche width for each species, and therefore niche edges, as the density kernel that included 95% of species observations in niche space. This kernel corresponds to a conservative estimate of the range of climatic values that are suitable for the different species (Wasof et al. 2015). We defined niche core, or the maximum probability of presence of a species within its realised climatic niche, by the 5% kernel. The potential occurrence of multimodal patterns of abundance justifies the use of density kernels to define niche core rather than using a centre of gravity approach to delineate the coordinates of a centroid.

2.5 | Data Analysis

We used the coordinates of the 982 observations of drought-induced mortality to extract the yearly (1979–2018) climatic values of the sites where mortality occurred (see ‘Climate data’ above). We then used yearly climatic data to compute the corresponding values in niche space (estimates of PCA components) and to define the position of the tree mortality sites within the climatic niche of the corresponding species. Given that niche properties such as shape and area can influence the values of niche metrics, we computed standardised niche metrics among species. For each study site, we computed the standardised distance to the core as $DS_{core} = D_c / (D_c + D_e)$, where D_c and D_e are the Euclidean distances to the niche core (5% density kernel) and niche edge (95% density kernel) respectively (Figure S2). We assigned a negative value to points within the niche core or outside the niche edge, so values of $DS_{core} < 0$ indicate populations within the niche core (within the 5% density kernel) and values of $DS_{core} > 1$ indicate populations outside the niche edge (outside the 95% kernel, Figure S2). We used the threshold of 0.5 in the DS_{core} metric to assess whether points were closer to the niche core ($DS_{core} < 0.5$) or niche edge ($DS_{core} > 0.5$) and the thresholds 0.25 and 0.75 as indicators of centrality ($DS_{core} < 0.25$) and marginality ($DS_{core} > 0.75$), respectively. We used yearly distances to the niche core for each study site to compute sites’ DS_{core} averages on the basis of long-term climate (1979–2018) and to consider the DS_{core} values of the years in which drought-induced mortality occurred. Additionally, we used a 10-year window preceding the year of observed mortality in each site to assess potentially lagged mortality (extreme past yearly DS_{core} values) or the cumulative impacts of less extreme climatic conditions. We assessed the cumulative influence of climate by computing the average DS_{core} in time windows from 2 to 10 years before the reported mortality. For these analyses, we used unique combinations of climatic values in PCA space for each species (703 of the initial 982 observations; Table 1) to remove potential duplicates arising from the resolution of climatic and tree mortality data, alleviating potential biases from aggregated mortality patterns and oversampling in some areas.

Given that our data were mortality-only observations and included several species without site replicates, we used null models to assess whether and where the observed mortality exceeded expectations across the environmental space (i.e., closer to the niche core or edge). We used a random sample of the entire set of GBIF observations of the 44 species to generate two null models of tree mortality in niche space, one based on long-term climate averages (1979–2018) and the other based on individual years. Therefore, the two null models incorporated the variances of climate averages (relatively low variance) and individual years (relatively high variance). First, we randomly sampled the species observations by selecting 15% of the filtered GBIF occurrence records used to define the climatic niche of each species, to a maximum of 1500 observations per species (18,735 occurrences). Second, we used the yearly climatic values of the random sample (1979–2018, $N = 3,747,000$) to compute the yearly, standardised distance to the core (DS_{core}) in the respective species’ climatic niche. Third, we used the average DS_{core} of each occurrence within the random sample to generate a null model based on long-term climate averages, and a randomly selected yearly DS_{core} for each occurrence within the random sample to

generate a null model based on individual years. We generated 10 null model replicates and constructed separate null models for angiosperm and gymnosperm species.

We compared the long-term average DS_{core} and the DS_{core} of the years of drought mortality between the study sites and the replicates of the corresponding null model. We compared the density distribution of the distances to the climatic niche core of the null models and of the drought-related mortality sites, for both long-term climate averages and for mortality year-specific conditions, with a Kolmogorov–Smirnov test and 1000 randomly selected null model observations in each case.

We assessed the relationship between species’ hydraulic traits (P_{50} and P_{88} , and the corresponding HSM) and position in niche space. First, to assess whether the degree of hydraulic vulnerability and HSM are associated with populations’ marginality during mortality, we evaluated the linear correlation between species’ hydraulic traits and the distance to niche core (DS_{core}) during the year of mortality. Second, to evaluate whether species’ drought resistance was related to the degree of climate anomaly, we assessed the relationship between hydraulic traits and the degree of climate anomaly in the year of tree mortality at each mortality site. In this analysis, we excluded *Quercus fusiformis*, which can access deep water (Johnson et al. 2018), altering the relationship with the climate anomaly, and *Juniperus communis*, the only gymnosperm species in the Cupressaceae family, because the Pinaceae and Cupressaceae families have important differences in xylem’s safety-efficiency trade-off (Gleason et al. 2016). We quantified climatic anomalies in the environmental niche space as the difference (Euclidean distance) between the estimates of PCA components for long-term climate averages (1979–2018) and mortality-year conditions in each site. Because we used mean values of hydraulic traits per species that we obtained from the open databases (see ‘Mortality and hydraulic trait data’), no acclimation or other site-dependent responses of the species can be inferred from our analyses.

We prepared and analysed data in R (R Core Team 2024). We obtained species occurrences with dismo (Hijmans et al. 2024) and conducted geospatial analyses with terra (Hijmans 2025). We estimated kernel density with ks (Duong 2025) and further processed kernel densities with misc3d (Feng and Tierney 2008). We computed distances in niche space with proxy (Meyer and Buchta 2022) and obtained the compact letter display (CLD) to illustrate the results of pairwise comparisons with biostat (Gegzna 2020). We visualised data with ggplot2 (Wickham 2016) and ggpubr (Kassambara 2023).

3 | Results

Relative to their long-term climate averages, 60.29% of the sites at which hotter droughts were associated with tree mortality were closer to the species’ climatic niche edge ($DS_{core} > 0.5$) than the niche core (Table 2, Figures 2 and S3). During the year of mortality, 64.26% of the sites were closer to the niche edge than to the niche core, and globally, there was a substantial increase in the degree of sites’ marginality in niche space during the year of tree mortality. Relative to their long-term climate averages, 13.54% of the sites had a $DS_{core} > 0.75$; during the year of

TABLE 2 | Mean distance to climatic niche core (DS_{core}) $\pm$ standard deviation (SD), and proportion of drought-related mortality sites where $DS_{core} > 0.5$, > 0.75 and > 1 (thresholds that define sites closer to niche edge than to niche core, sites close to the niche edge, and sites outside the niche edge respectively). Climate averages include years 1979–2018.

	Mean $DS_{core} \pm SD$	$DS_{core} > 0.5$	$DS_{core} > 0.75$	$DS_{core} > 1$
ALL SPECIES				
Climate averages	0.566 $\pm$ 0.198	60.29%	13.54%	1.63%
Mortality year	0.593 $\pm$ 0.314	64.25%	33.50%	8.55%
ANGIOSPERMS				
Climate averages	0.539 $\pm$ 0.184	56.12%	11.00%	0.28%
Mortality year	0.554 $\pm$ 0.317	57.36%	27.10%	8.25%
GYMNOSPERMS				
Climate averages	0.643 $\pm$ 0.214	72.16%	20.78%	5.49%
Mortality year	0.705 $\pm$ 0.277	83.92%	51.76%	9.41%

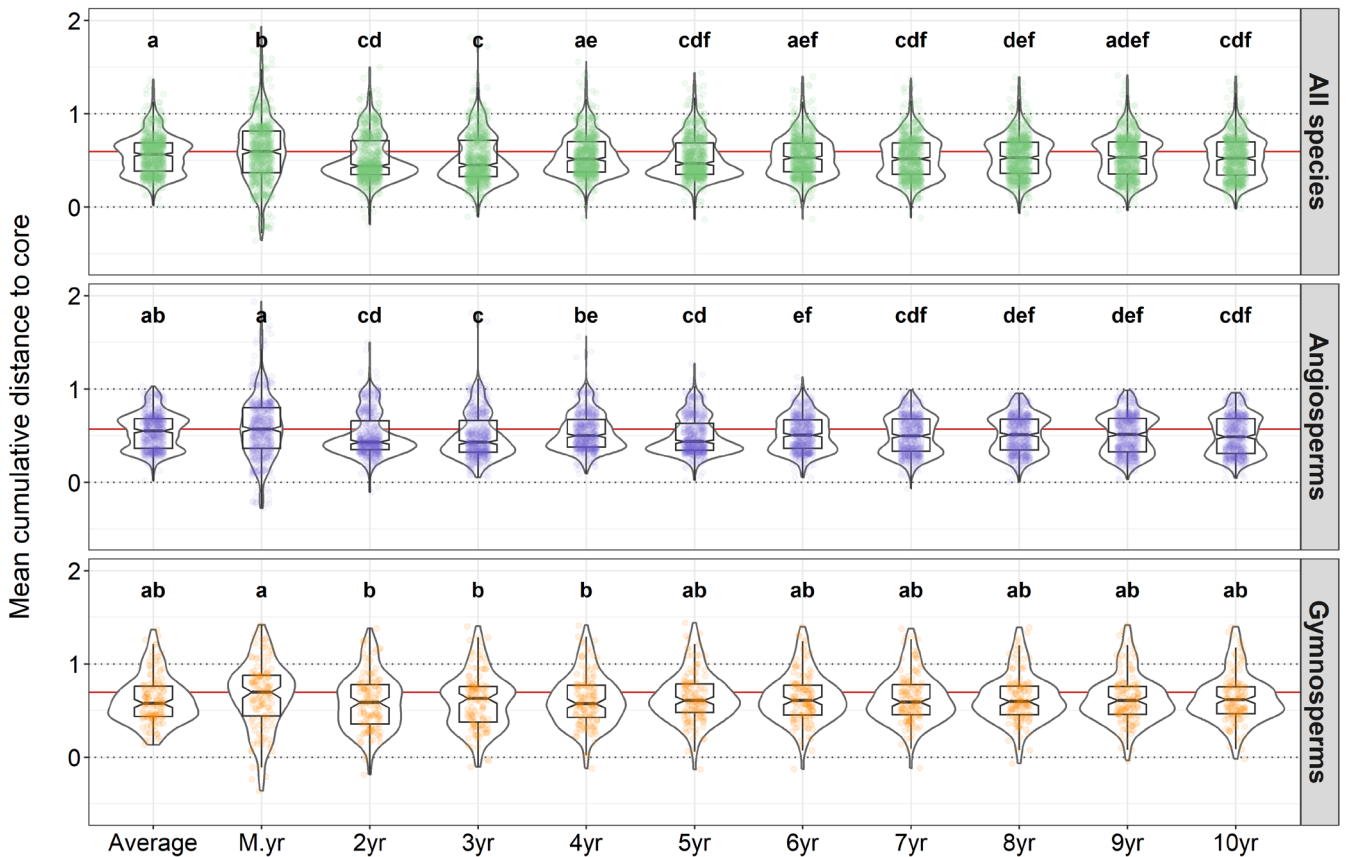


FIGURE 2 | Standardised distance to the climatic niche core in all populations that experienced drought-related mortality (all species, top; angiosperms, middle; gymnosperms, bottom) relative to site climate averages from 1979 to 2018 period (Average), climate during the year of reported tree mortality in each site (M.yr) and considering from 2 to 10 years before mortality. In each panel, different letters denote significant ($p < 0.05$) Wilcoxon rank sum differences in the distances to the core (see Table S1 for p values). The horizontal red line in each panel represents the median value of the standardised distance to the core during the year of mortality (M.yr). Horizontal, dotted lines indicate values of the distance to the core < 0 and > 1 , which correspond to populations within the niche core and outside the niche edge respectively.

mortality, this increased to 33.5%, and 8.55% of the sites were outside the niche edge ($DS_{core} > 1$; Table 2, Figure 2).

Overall, sites were significantly further from the niche core during the mortality year than on average over the 1979–2018

period (Figure 2), although the variability in DS_{core} also increased during the years of tree mortality (Figure 2, Table 2). Such mortality patterns in niche space were consistent irrespective of the grid size used to define the species' climatic niche (Figures S4 and S5). Additionally, despite year-to-year variability

(Figure S6), the distance of the sites to the niche core was greater during the year of mortality than the cumulative distances to the core (average DS_{core}) over the previous 2–10 years (Figure 2, Table S1). Therefore, general cumulative or lagged effects of previous climatic conditions did not seem prevalent in the global mortality data.

A higher proportion of gymnosperm mortality sites were closer to the niche edge than the niche core ($DS_{core} > 0.5$) than angiosperm mortality sites, for both long-term climate averages (72.16% and 56.12% respectively) and during the year of mortality (83.92% and 57.36% respectively; Table 2). The degree of marginality in niche space ($DS_{core} > 0.75$) was higher in gymnosperm than in angiosperm mortality sites for their climate averages (20.78% and 11% respectively) and for the year of mortality (51.76% and 27.1% respectively). However, the proportion of sites outside the niche edge during the year of mortality ($DS_{core} > 1$) was similar between taxonomic groups: 9.41% for gymnosperm mortality sites and 8.25% for angiosperm mortality sites (Table 2, Figure 2).

The inclusion of climate conditions up to 10 years prior to mortality did not suggest, in general, cumulative effects on gymnosperm or angiosperm mortality sites, as sites were furthest from the niche core during the year of mortality (Figure 2, Table S1). However, in both taxonomic groups, distances to core during the year of mortality were not significantly different than those during some previous years (Figure S6). Additionally, although mortality of 72.5% of the species tended to occur in sites closer to the niche edge than to the niche core, especially during the year of mortality (Figure S7), cumulative and lagged responses may have occurred in some cases. For some species (Figures S8–S11),

climate conditions within the 10-year window preceding mortality were systematically further from the niche core than the edge, and climate during some years before mortality was further from the core than during the reported year of mortality.

Comparing the niche distances of the tree mortality sites with those of the null models of tree mortality within the niche revealed different modes of angiosperm and gymnosperm mortality ($p < 0.01$, Figure 3 and Table S2). Mortality in gymnosperm sites was not significantly different from the null model for climate averages, although it exceeded the null expectations close to or within the niche core ($DS_{core} < 0$) and outside the niche edge ($DS_{core} > 1$, Figure 3c). Gymnosperm mortality exceeded null expectations ($p < 0.0001$) close to or outside the niche edge ($DS_{core} > 1$) during the mortality year (Figure 3d, Table S2). Mortality in angiosperm sites exceeded null expectations of mortality ($p < 0.0001$) in sites closer to the niche edge than the core and, to a lesser extent, close to or within the niche core for climate averages; mortality exceeded expectations ($p < 0.01$) close to or outside the niche edge during the mortality year (Figure 3a,b and Table S2).

We found no clear patterns or significant relationships between position in niche space during mortality events and hydraulic traits (Figure S12). However, in angiosperm mortality sites, the degree of climate anomaly during mortality (mortality year relative to climate averages) was significantly related to the hydraulic traits (Figure 4, Figure S13). During mortality years, climate anomalies associated with angiosperm species with less vulnerable xylem (more negative P_{88}) were significantly higher than the anomalies for more vulnerable species (Figure 4a). Similarly, climate anomalies associated with mortality in

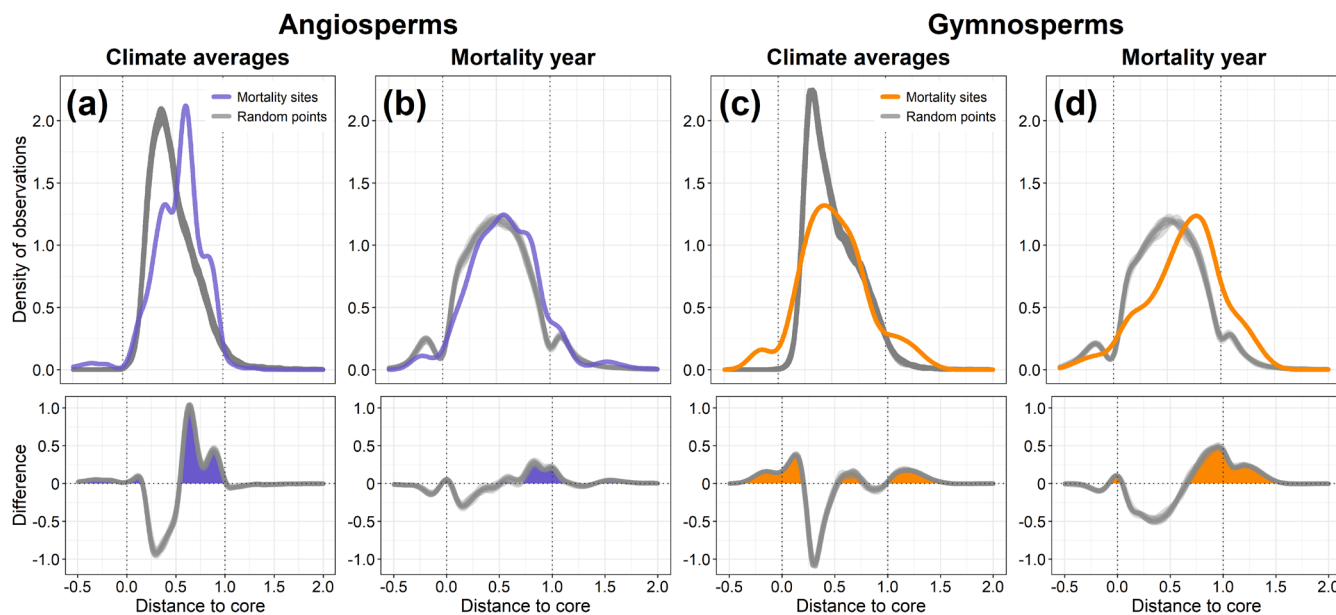


FIGURE 3 | Density distributions of the standardised distances to the climatic niche core between the tree mortality records and the 10 replicates of the null models of random tree mortality across species' niches. Angiosperm observations included 21 species and 563 sites; the null models included 9895 random points. Gymnosperm observations included 23 species and 140 sites; the null models included 8840 random points. Panels (a) and (c) show the climate averages in the null distribution and at each site (1979–2018). Panels (b) and (d) show the climate during mortality years at each site and in individual years in the null distribution. Lower panels display the difference between the distribution of the distance to the core of the study sites and the corresponding null models. Values of distance to core < 0 correspond to populations within the niche core, whereas distances to core > 1 correspond to populations outside the niche edge.

angiosperm species with high hydraulic safety margins (HSM), reflecting a lower probability of hydraulic failure, were significantly higher than in species with a low HSM (Figure 4b). The relationship between P_{88} and the degree of climate anomaly in gymnosperm mortality sites was not significant. Also, although the climate anomaly–HSM relationship in gymnosperms was the same as that in angiosperms, the relationship was not significant (Figure 4b). The relationships with the degree of climate anomaly were similar for P_{50} and the corresponding HSM (Figure S14).

4 | Discussion

Tree populations that are both central and marginal in climatic niche space are affected by climate-driven mortality, but for gymnosperms, marginal populations are affected more. The consideration of both long-term climate averages and conditions associated with mortality emerges as very important for mortality patterns in central and marginal populations. Year-specific conditions associated with climate-related tree mortality, when translated to position within the climatic niche space, shifted towards the dry limit of the species niche, significantly decreasing the distance to the niche edge of the populations experiencing mortality (marginality increase). Indeed, changes in populations' position in niche space in the years of mortality represent increasingly hot droughts: lower precipitation and higher vapour pressure deficit, potential evapotranspiration and temperature (Figures 5, S15 and S16). As such, in the years of mortality, climatic conditions may push species towards or past their physiological limits (e.g., hydraulic failure; Anderegg et al. 2016; Hammond et al. 2019; Peters et al. 2021), perhaps in combination with reduced nonstructural carbohydrates (Adams et al. 2017) and, in some cases, reflecting lagged or cumulative drought effects (Sánchez-Pinillos et al. 2022). Therefore, although the long-term climatic core of a species' climatic niche may be typically consistent with survival, extreme climate

anomalies can promote mortality events from the edge to the core of the species' range. These findings reveal that eventually, species could experience pulses of mortality across their range under intense enough climatic extremes, especially when considering plant-water relations (Reyer et al. 2013).

4.1 | Vulnerability in Central and Marginal Populations

Tree mortality close to the niche edge suggests that local adaptation in range edge populations (Bontrager et al. 2021), including hydraulic traits (Rehm et al. 2015; Peters et al. 2021, but see Alon et al. 2023), may not be sufficient for persistence under extreme climatic anomalies. Drought conditions in the years of mortality were, in fact, outside the climatic niche of ca. 10% of populations. This further emphasises the vulnerability of range-edge populations to ongoing and future drought (Anderegg et al. 2019). Mortality close to niche core supports the notion that trees in niche core populations sometimes are operating close to their hydraulic thresholds (Heilmayr et al. 2023; Peters et al. 2021). Also, the rapid development of trees and forests under more typically optimal climatic conditions at the niche core may contribute to structural overshoot, where growth during relatively cool, wet years can become a liability when followed by extremely hot droughts (Hammond et al. 2022; Jump et al. 2017).

The balance between historical and episodic conditions has best explained tree mortality in response to compound drought and bark beetle attack (Lloret and Kitzberger 2018). Our assessment reveals that such shifts towards marginality may depend on the geometry of species' climatic niches. The position of the niche core relative to the niche edges (Figure S17) may promote the displacement of core populations towards marginal positions even under low to moderate changes in climate. For instance, in angiosperm mortality sites within or close to the niche core, the degree of climate anomaly during the year of mortality was

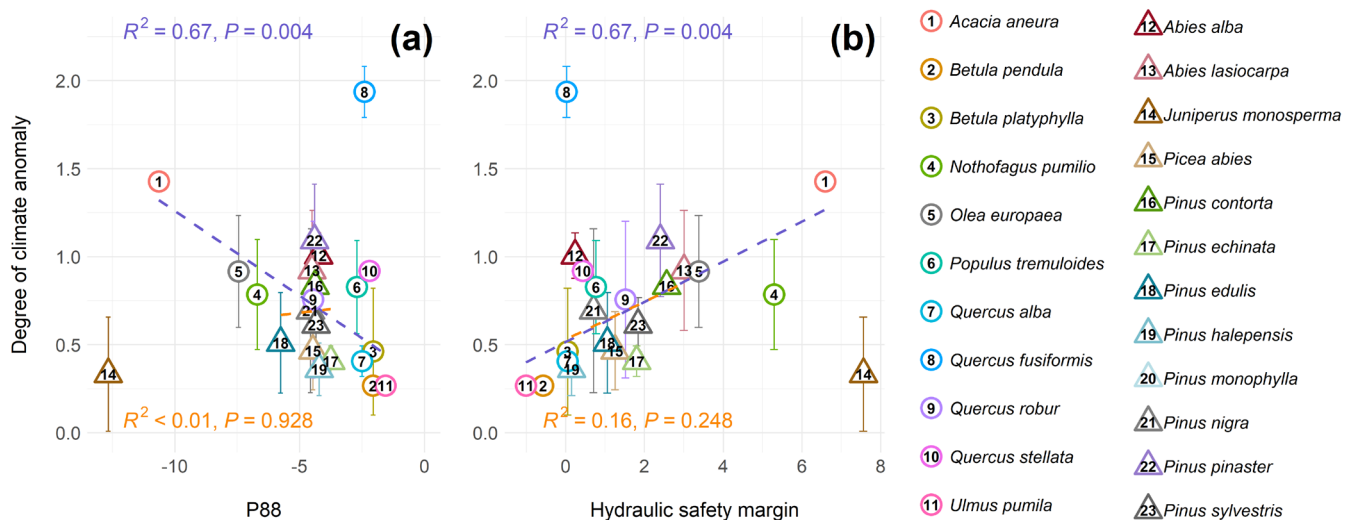


FIGURE 4 | Relationship between the degree of climate anomaly during the reported mortality year in each site relative to its climate averages (1979–2018) and (a) 88% loss of xylem hydraulic conductance (P_{88}) and (b) hydraulic safety margin. Relationships are plotted for angiosperm (circles) and gymnosperm (triangles) species together but linear regressions were computed separately for each taxonomic group (angiosperms in purple, gymnosperms in orange). The fitted linear regression excluded points for *Quercus fusiformis* and *Juniperus monosperma* (see text for details and Figure S13 for the relationships including all species).

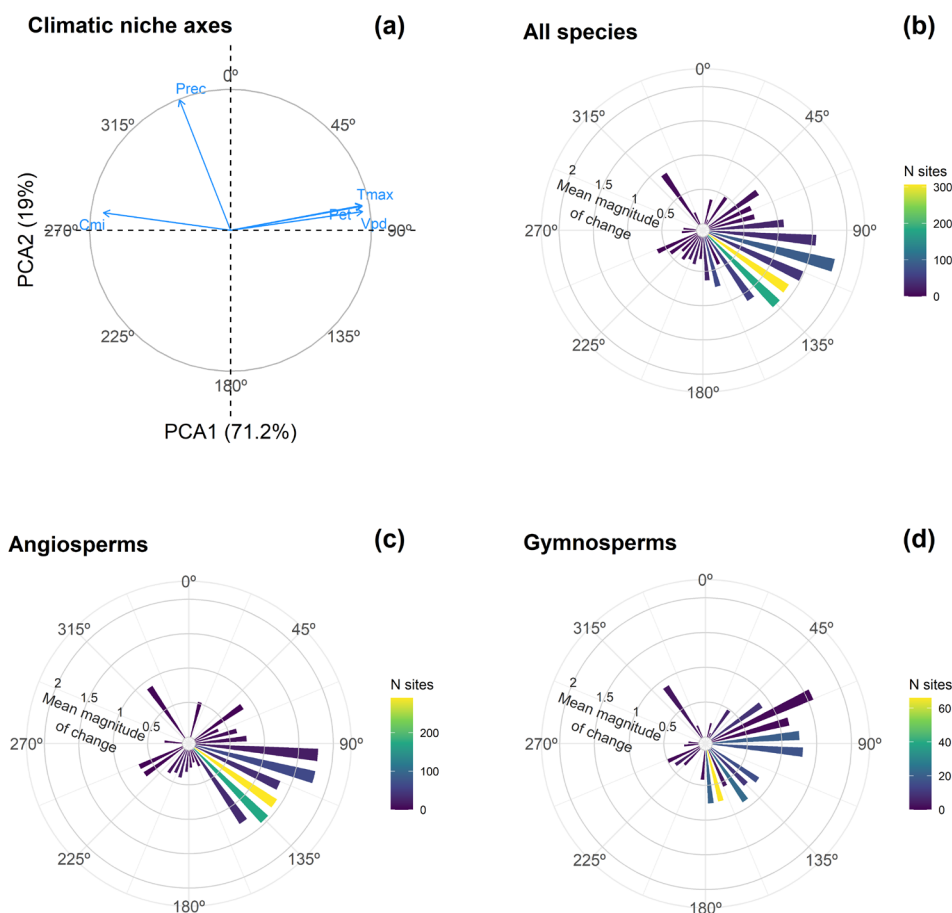


FIGURE 5 | Direction and magnitude of environmental change between sites' climate averages and conditions during the year of mortality. (a): Influence of each climatic variable in the first and second principal component axes (PCA1 and PCA2) used to define the climatic niche, where Pet=potential evapotranspiration, Prec=total precipitation, Cmi=climatic moisture index (Prec—Pet), Tmax=maximum temperature and Vpd=vapour pressure deficit. Degrees from 0° to 360° are superimposed on the correlation circle to guide directionality assessment. (b–d): Mean magnitude of environmental change, estimated through the Euclidean distance, of all tree mortality sites in each of 10° section of the PCA1-PCA2 climatic niche space. Each bar shows both the mean magnitude of environmental change and the number of tree mortality sites in which the trend in environmental change was the same during the year of mortality and relative to its climate averages. The number of sites in the colour scales varies among panels.

not high compared to the rest of the populations, but it was associated with a significant change in these sites' degree of marginality (Figure S18). However, species-specific patterns (Figures S8–S11) also suggest that lagged and cumulative effects of drought may be operating in some cases. As such, past extreme conditions or multiple years of moderate drought may lead to mortality regardless of the degree of centrality–marginality of the populations.

4.2 | Mortality Patterns in Angiosperms and Gymnosperms

We found some contrasting mortality patterns in niche space between angiosperm and gymnosperm species, although at the global scale, they are both likely to die under drought stress (Anderegg et al. 2016; Greenwood et al. 2017). Although mortality exceeded expectations close to the niche edge and core in both groups, gymnosperm species tend to conform better to the expectations of the core–periphery hypothesis: populations that experienced drought-related tree mortality tended to be closer to

their climatic niche edge than to their niche core. Among angiosperm tree species, mortality was more ubiquitous across their niche space. Such differences among major tree groups may be related to their functionally different wood anatomy, including hydraulic traits, which present medium to high levels of phylogenetic signal (Sanchez-Martinez et al. 2020). For instance, angiosperms tend to have more efficient xylem transport, which leads to higher sensitivity to vapour pressure deficit (Flo et al. 2021), although their potential for regrowth and higher amount of parenchyma also make them more capable of recovering from drought (Anderegg et al. 2016). Gymnosperms tend to have reduced non-structural carbohydrate reserves at mortality, which may reduce hydraulic function (Adams et al. 2017), and the xylem of several genera may be intrinsically vulnerable to extreme dry conditions (Martínez-Vilalta et al. 2004). Furthermore, gymnosperm trees often retain evergreen foliage for multiple years, and the relatively higher carbon cost of canopy failures may more often lead to whole-tree mortality.

Across all species, the hydraulic safety margin (HSM), the difference between typical minimum xylem water potential and

that causing xylem dysfunction, seems to be a strong predictor of mortality patterns (Anderegg et al. 2016; Peters et al. 2021). At angiosperm mortality sites, the relationship between hydraulic traits and degree of climatic anomaly during mortality emphasises that the change or anomaly relative to trait properties explains observed mortality patterns better than trait values themselves (Sanchez-Martinez et al. 2023). The lack of a significant relationship between hydraulic traits and climate anomaly in the gymnosperm mortality sites may reflect that the climate anomalies required to trigger mortality are less extreme for gymnosperms than angiosperms (Figure S16), and that other processes, such as heat-induced stress followed by mortality (Allen et al. 2015), may be occurring. Indeed, differences in precipitation between the mortality year and the sites' climate averages were lower in gymnosperm sites (Figure S16). Additionally, in several cases, gymnosperm populations' position within the niche during the years preceding mortality (Figure S10) suggests cumulative drought effects. The tightly constrained range of hydraulic traits for gymnosperm species, compared to the relatively broad range of trait values observed for angiosperms, likely contributed to the weaker, insignificant relationship for the former. Nevertheless, the degree of climate anomaly also appears to be important in explaining mortality in gymnosperm core populations (Figure S19).

Overall, our assessment suggests that the difference between long-term average climate conditions and climatic extremes may explain mortality patterns across climatic niche space and biogeographical ranges, even for drought-tolerant species. As such, drought-induced tree mortality may occur not only at the driest sites (Anderegg et al. 2019) but in sites where the climate anomaly is large enough relative to the species' drought tolerance. Additionally, the niche geometry can explain mortality patterns when the direction of climate anomaly, even if small, pushes populations towards their physiological limits. The observed range-wide vulnerability of forests reinforces the notion that mortality under future and more extreme climates (IPCC 2021) may affect species dynamics and jeopardise their persistence.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Geographical coordinates of climate-induced tree mortality are available from <https://doi.org/10.1038/s41467-022-29289-2> and are publicly available at <http://tree-mortality.net/globaltreemortalitydatabase>. Hydraulic trait data are available from <https://doi.org/10.1038/s41559-023-02180-z> and the Xylem Functional Traits Database (<https://xylem>

functionaltraits.org/). Climate data are available at <https://chelsa-climate.org/> and species occurrence data at <https://doi.org/10.15468/dd.ymx22h>. The code used for data preparation and analysis is publicly available at <https://doi.org/10.5061/dryad.tjq2bw8f>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70128-sup-0001-Supinfo.docx. Supporting Information.