

Extinction debt and delayed colonization have had comparable but unique effects on plant community–climate lags since the Last Glacial Maximum

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Abstract

Aim: Plant communities typically exhibit lagged responses to climate change due to poorly understood effects of colonization and local extinction. Here, we quantify rates of change in mean cold tolerances, and contributions of colonization and local extinction to those rates, recorded in plant macrofossil assemblages from North American hot deserts over the last 30,000 years.

Location: Mojave, Sonoran and Chihuahuan Deserts.

Time period: 30–0 thousand years before present (kybp).

Major taxa studied: Vascular plants.

Methods: Colonization and local extinction dates for 269 plant species were approximated from macrofossils in 15 packrat (*Neotoma*) midden series. Cold tolerances estimated from contemporary climate were used to quantify assemblage-mean cold tolerances through time. Rates of colonization and local extinction, and their effects on rates of change in assemblage-mean cold tolerances, were estimated for 30–20 kybp (Late Pleistocene, no directional warming), 20–10 kybp (deglaciation, rapid warming) and 10–0 kybp (Holocene, no directional warming).

Results: Rates of change in all metrics were negligible during the Late Pleistocene. Rates of change in assemblage-mean cold tolerances (mean $1.0^{\circ}\text{C} \times 10^{-4}/\text{yr}$) lagged behind warming during deglaciation, and continued at similar rates ($1.2^{\circ}\text{C} \times 10^{-4}/\text{yr}$) throughout the Holocene. Colonization and local extinction contributed equally to delayed responses to warming, but their dynamics differed through time: Colonization by warm-adapted species predominated during deglaciation, while the most heat-adapted species exhibited long delays in colonization. Only the most cold-adapted species went locally extinct during deglaciation, followed by slow repayment of the extinction debt of cool-adapted species during the Holocene.

Main conclusions: Responses to rapid warming can persist for millennia, even after cessation of warming. Consistent patterns from different midden series across the region support a metacommunity model in which dispersal interacts with environmental filters and buffers against local extinction to drive community–climate disequilibrium during and after periods of warming.

KEYWORDS

climate change, climate niche, community assembly, dispersal limitation, extinction debt, palaeoecology

1 | INTRODUCTION

A diverse array of plant and animal taxa worldwide have exhibited lagged responses to both contemporary (Dullinger et al., 2012; Menendez et al., 2006; La Sorte & Jetz, 2012; Steinbauer et al., 2018) and historical (Cole, 1985) climate changes. Colonization of suitable habitat can be delayed by dispersal limitation (Lyford, Jackson, Betancourt, & Gray, 2003), and local extinction can be deferred through demographic resistance to decreasing habitat suitability (Dullinger et al., 2012; Kuussaari et al., 2009), both of which can contribute to community–climate disequilibrium (Blonder et al., 2015, 2018). Dynamics of colonization and local extinction are fundamental to understanding drivers of biodiversity patterns, such as community saturation (Mateo, Mokany, & Guisan, 2017), priority effects (Fukami, 2015) and metacommunity dynamics (Leibold et al., 2004). The tempo and mode of colonization and local extinction during periods of climate change also inform the need and potential efficacy of different management interventions, including conservation of relict populations, refugia or biodiversity hotspots (Hampe & Petit, 2005); and the maintenance of dispersal corridors or active relocation efforts (Williams, Jackson, & Kutzbach, 2007). Few studies, however, have quantified the relative contributions of colonization and local extinction to changes in community composition during periods of profound global and regional climate change.

The change in occupied niche space associated with colonization and local extinction, rather than simply the number of taxa gained or lost, is one way to assess the relative contributions of these processes to community–climate disequilibrium (Blonder et al., 2018). If communities track climate perfectly, the community-mean tolerance of a climatic factor will match the local level of that factor (Butterfield & Munson, 2016). Thus, as climate conditions shift during periods of change, so too should community-mean climate tolerances. This approach permits estimation of rates of change in community warming response in units of degrees per year, allowing quantitative comparisons to observed warming rates. It also facilitates analogies to modern community assembly theory, specifically the roles of dispersal and environmental filters, in mediating climate change responses (McGill, Enquist, Weiher, & Westoby, 2006).

Community dynamics can be affected by species-specific life-history strategies that blur the effects of generalized assembly filters, and that leave distinct signals in the occupied climate niche of communities. Assuming that all species have similar dispersal abilities, the velocity of climate change (Loarie et al., 2009) dictates which species can disperse to and colonize a focal habitat,

such that species from distant, more disparate environments are less likely to colonize than those from closer, more environmentally similar habitats. The dispersal filter is thus tied to spatial and temporal autocorrelation in environmental filters across a landscape. For example, during a period of warming, this form of universal dispersal limitation would result in most of the newly colonizing species arriving from nearby, slightly warmer habitats rather than from more distant, hotter habitats. As a result, the colonists will have only moderately higher temperature tolerances than the resident species within a recipient community. On the other hand, species-specific dispersal limitation would result in colonization by species with varied temperature tolerances due to colonization by some species with greater dispersal ability from more distant, hotter habitats and limited colonization from nearby, slightly warmer habitats. In an analogous fashion, local extinction dictated solely by environmental filtering will result in consistent loss of the most cold-tolerant species within a community during warming. Species-specific variation in life-history traits related to local extinction risk, such as the longevity of the mature phase of the life cycle or persistence in the seed bank, would result in species with more varied temperature tolerances going locally extinct.

Changes in the composition of plant assemblages over the latter half of the last glacial–interglacial cycle represent an opportunity to assess the dynamics of colonization and local extinction during periods of relative climatic stasis and rapid warming. The last c. 30 thousand years can effectively be separated into three broad periods. The end of the last glacial period [c. 30–20 thousand years before present (kybp)] was one of relatively cold average temperatures—the Last Glacial Maximum. This was followed by rapid warming from approximately 20–10 kybp during which global temperatures increased by 6–7°C. The most recent c. 10 thousand years—most of the Holocene—have been warmer with no directional trends in annual temperature. Palaeobotanical records from around the world demonstrate not only strong responses in composition and structure to this transitional warming period (Nolan et al., 2018), but also dramatic changes in community composition throughout the Holocene. These continued changes in community composition may reflect lagged responses to past warming, as well as responses to other environmental changes during the Holocene, including shifts in temperature seasonality and precipitation during the Holocene (Giesecke et al., 2011; Prentice, Bartlein, & Webb, 1991).

Desert plant communities in the south-western USA and northern Mexico represent excellent systems in which to assess colonization and extinction dynamics over the last c. 30,000 years, due to these systems' strong responses to climate variability and the wide

availability of macrofossil records with high taxonomic resolution in the region. Contemporary plant communities from across the region have been shown to be strongly structured by low temperatures (Butterfield, 2015). Despite water being the primary limiting factor for biological activity in this dryland region (Noy-Meir, 1973), Butterfield and Munson (2016) found that local temperatures explained half the variance in assemblage-mean (AM) cold tolerances from over 1,000 sites and nearly 800 species from across the southwestern USA, whereas precipitation only explained about 10% of the variance in precipitation tolerances. The standardized range of temperature tolerances within each assemblage was also on average much narrower than that of precipitation tolerances, indicating stronger filtering of species based on temperature. Furthermore, variability and change over time in temperature is more spatially coherent at regional to subcontinental scales than for precipitation, especially in the cool half of the year. As such, regional patterns of local extinction and colonization during the Holocene were most likely to track large-scale changes in temperature affecting all three hot deserts similarly. In addition to the detailed understanding of the role that low temperatures play in structuring extant communities, another advantage of this region is the wealth of palaeoecological data from packrat (*Neotoma* sp.) middens. Plant macrofossil assemblages from middens have been catalogued and dated across the three hot deserts (Mojave, Sonoran and Chihuahuan) of the region, with many plant remains identified to species. This species-level taxonomic resolution is critical for deriving reasonable estimates of low temperature tolerances for individual taxa that can be scaled up to assess community-level responses to past climate warming and stasis.

Using 15 comparable midden series from across the Mojave, Sonoran and Chihuahuan Deserts, we analysed responses of plant assemblages to variation in temperature from 30,000 years ago to the present. In particular, we focus on the independent and additive effects of colonization and local extinction processes on the rate of change in AM cold tolerances during the Late Pleistocene, deglaciation and the Holocene. We then provide a general model of meta-community reassembly during and after periods of climate warming based on our results.

2 | METHODS

2.1 | Macrofossil series

Packrats are generalist consumers and hoarders of plant materials, collecting those materials from within c. 30 m or less of their dens, typically in rock shelters (Finley Jr., 1990). Plant material in middens usually become embedded and preserved in solidified packrat urine. A midden series represents a compilation of individual middens sampled from the same or nearby rock formations (i.e., similar environmental settings) but that were deposited at different times, as determined by ^{14}C dating. Plant assemblages in individual middens are unusually rich in species, but do not perfectly census local vegetation at a given time due to packrat selective bias (Dial & Czaplewski, 1990), the complexities of depositional duration and

time-averaging in middens (Spaulding, Betancourt, Croft, & Cole, 1990), or other factors. As a consequence, false absences are likely to occur in midden records, making it difficult to assess variation in abundance through time and associated phenomena such as resilience to environmental variability. Thus, we used species' first and last occurrences within a site as conservative estimates of colonization and local extinction times.

Fifteen midden series were selected across the region based on their high temporal sampling density and complete reports of the plant macrofossils found in the middens (Table 1). Only macrofossils identified to species were used in our analysis. The focal study sites vary substantially in elevation and are distributed from the winter-precipitation dominated Mojave Desert in the west to the summer-precipitation dominated Chihuahuan Desert further east (Figure 1). Our objective was to look for general trends that were consistent among midden series despite substantial spatial differences in climate.

Changes in community composition were estimated separately within each of three time periods: 30–20, 20–10 and 10–0 kybp. Only midden series with at least three samples during a given time period were used ($n = 5$ for 30–20 kybp, $n = 11$ for 20–10 kybp, $n = 15$ for 10–0 kybp). The dates used represent the mid-point between the upper and lower estimates of the calibrated radiocarbon dates. In cases where multiple samples were dated to within 100 years of each other, all but the youngest sample in that set was discarded in order to reduce influence on estimates of change. This resulted in a total of 72 samples during 30–20 kybp, 309 during 20–10 kybp and 1,420 during 10–0 kybp. The mean (± 2 SE, minimum–maximum) species richness of each assemblage (sample) was 17.4 (± 0.88 , 4–34) during the 30–20 kybp period, 16.9 (± 1.2 , 6–29) during the 20–10 kybp period and 8.4 (± 1.3 , 4–16) during the 10–0 kybp period.

2.2 | Climate tolerances

Species-specific tolerances of temperature and precipitation variables were estimated based on contemporary distributions (Butterfield, 2015; Butterfield & Munson, 2016). While imperfect estimates of species climatic tolerances, species distribution limits tend to correspond well with their niche limits (Lee-Yaw et al., 2016). Only taxa resolved to species were analysed, avoiding some of the issues associated with other palaeorecords such as pollen cores that are often only resolved to genus or family. Species occurrence records were acquired from the Global Biodiversity Information Facility via the `rgbif` function in the `dismo` R package (Hijmans, Phillips, Leathwick, & Elith, 2015). Geographic and climatic outliers were removed, as were duplicates within the same c. 1-km climate grid cell. Species with fewer than 20 records were excluded from further analysis (Thuiller, Lavorel, Araujo, Sykes, & Prentice, 2005), resulting in a total of 269 species with climate estimates out of 291 taxa identified to species (92%). The 5th and 95th percentiles of climate values were used as species tolerance estimates for mean annual temperature, temperature seasonality, mean annual precipitation and precipitation seasonality, extracted from WorldClim 30

TABLE 1 Primary references, locations and number of samples for each midden series

Site	Name	Location		# Samples ^a			Reference
		Longitude	Latitude	30–20	20–10	10–0	
1	Alabama Hills	-118.093	36.626	6	3	10	Koehler, Anderson, and Spaulding (2005)
2	Joshua Tree	-116.139	34.083	0	10	231	Holmgren, Betancourt, and Rylander (2014)
3	Sierra Juarez	-115.780	32.165	45	105	136	Holmgren et al. (2006)
4	Sierra San Pedro Martir	-115.425	31.143	15	28	153	Holmgren, Betancourt, and Rylander (2010)
5	Cataviña	-114.771	29.803	3	0	171	Betancourt (unpublished data)
6	Picacho Peak	-114.664	32.973	0	28	91	Cole (1985)
7	Puerto Blanco	-112.797	31.981	0	0	91	Van Devender (1980)
8	Sierra Bacha	-112.547	29.751	0	0	36	Van Devender, Burgess, Piper, and Turner (1987)
9	Waterman Mtns	-111.466	32.325	0	6	21	Anderson and Van Devender (1991)
10	Peloncillos	-109.082	31.315	3	78	153	Holmgren, Betancourt, and Rylander (2011)
11	Playas Valley	-108.453	31.441	0	3	6	Holmgren, Peñalba, Rylander, and Betancourt (2003)
12	Navar Ranch	-106.150	31.897	0	21	78	Van Devender, Bradley, and Harris (1984)
13	Sacramento Mtns	-105.914	33.050	0	6	45	Van Devender, Betancourt, and Wimberly (1987)
14	Rough Canyon	-105.881	32.376	0	21	153	Betancourt, Aasen Rylander, Peñalba, and McVickar (2001)
15	Last Chance Canyon	-104.650	32.267	0	0	45	Van Devender (1994)

^aNumber of middens/assemblages in the given time period, in units of thousand years before present.

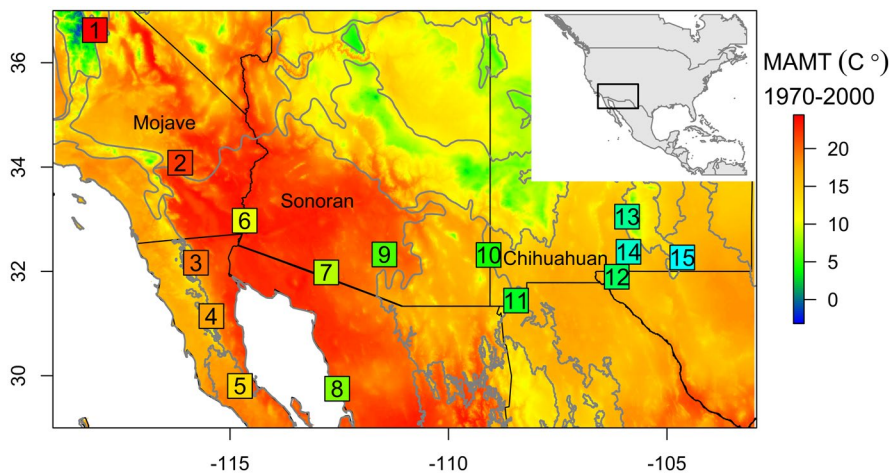


FIGURE 1 Map of study sites overlain on modern mean annual monthly temperature (MAMT). Study site numbers and colours provide cross-reference to assemblage-mean cold tolerance in Figure 2a and study information in Table 1. Grey polygons are Level III Ecoregions of North America. Climate values are 1970–2000 norms from WorldClim [Colour figure can be viewed at wileyonlinelibrary.com]

arc-second raster layers (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). AM climatic tolerances were then calculated for each midden sample (all or portion of a midden dated to the same time period) as the unweighted mean of climatic tolerances of all species present within that sample.

Changes in species distributions during the period from 10 to 0 kypbp, when average annual temperatures did not follow any strong directional trends, have been attributed in some cases to changes in the amount and timing of precipitation, and of temperature seasonality (Prentice et al., 1991; Williams, Shuman, Webb, Bartlein, &

Leduc, 2004). Strong correlations between AM climate tolerances and sample age during the 10–0 kybp period would suggest directional responses to climate change. Thus, we conducted a supplementary analysis to assess the strength of the relationship between AM tolerances of low and high mean annual temperature, mean annual precipitation, temperature seasonality and precipitation seasonality with sample age during each of the three time periods. The results (see Table 2) supported moving forward with a focus on AM cold tolerance [5th percentile of mean annual temperature (MAT) values], although we briefly touch on variation in the tolerances of other climate variables in the Discussion.

2.3 | Plant assemblage dynamics

The Euclidean distance of AM cold tolerance was calculated between each sample within a period, resulting in $(s^2 - s)/2$ estimates of change during each time period for each midden series with at least three samples, where s is the number of samples. The change in AM cold tolerance was then divided by the Euclidean distance of the number of years between samples in order to provide an estimate of the rate of change, specifically $(AMcold_1 - AMcold_0)/(year_1 - year_0)$, where subscripts indicate different samples. This approach was taken rather than calculating sequential changes (i.e., a regression of AM cold tolerance versus time) in order to reduce the influence of (a) samples that were close together in time, and (b) large changes in composition between sequential samples that may include contamination or identification errors.

Effects of colonization and extinction on the rate of change in AM cold tolerances were calculated on the same set of samples as above. The effect of colonization on the rate of change in AM cold tolerances was calculated as the difference between the AM cold tolerance calculated with and without newly colonizing species, specifically $(\sum_{i=1}^n R_i + \sum_{j=1}^m C_j)/(n+m) - \bar{R}$, where R_i is the cold

tolerance of resident species i at time t , C_j is the cold tolerance of colonizer species j at time $t + 1$, n and m are the number of resident and colonizer species, respectively, and \bar{R} is the mean cold tolerance of the resident species. The effect of extinction was calculated as $\bar{R} - (\sum_{i=1}^n R_i - \sum_{j=1}^m E_j)/(n+m)$, where E_j is the cold tolerance of species j that is going locally extinct at time $t + 1$. For a purely taxonomic assessment of colonization and extinction rates, the number of colonization and extinction events between each sample was also determined. All estimates were converted to rates by dividing by the time between samples.

2.4 | Analysis

To test the hypothesis that rates of change did not differ from zero, confidence intervals were calculated based on the weighted means and standard errors for rates of change in AM cold tolerance, colonization and extinction in order to account for variation in sampling intensity among midden series. Data were first \log_{10} transformed in order to achieve normality. The weighted mean was calculated as $\bar{x} = \sum_{i=1}^n w_i x_i$, where x_i is the mean change in for example AM cold tolerance for midden series i , and w_i is the standardized weight for midden series i , calculated as the number of comparisons within a time period for that midden series relative to all comparisons across all midden series during that time period, such that all weights sum to 1. A 95% confidence interval of the weighted mean was calculated as $\bar{x} \pm SE_{\bar{x}}$, where $SE_{\bar{x}} = \sigma_{\bar{x}}/\sqrt{n}$, in which n is again the number of midden series, and $\sigma_{\bar{x}}^2 = \sum_{i=1}^n w_i^2 \sigma_i^2$, where $\sigma_{\bar{x}}$ is the standard deviation of the weighted mean. The estimates of x_i and σ_i were themselves weighted by the number of years between sample points used to calculate the rate of change in for example AM cold tolerances in order to further reduce the influence of sample points in close temporal proximity to one another. Thus, $x_j = \sum_{i=1}^m w_j x_j$, for rates of change j through m , and $\sigma_j^2 = (\sum_{i=1}^m w_j (x_j - x_i)^2) / \sum_{i=1}^m w_j$, which is the weighted sum of squares divided by the sum of weights. The confidence intervals were used to test the hypothesis that the weighted mean rates differed from a null expectation of zero. All data were back-transformed for visualization.

Differences in rates among time periods were assessed with one-way analysis of variance of the weighted means calculated above, followed by Tukey's honestly significant difference (HSD) post-hoc comparisons. Comparisons among time periods were only made for rates of the same type, that is, among colonization rates or among extinction rates, but not between colonization and extinction rates. Differences between colonization and extinction rates were only assessed within a time period, using Student's t test.

As an independent check on our analysis, we estimated the difference between AM cold tolerances and local temperatures at c. 21 and c. 6 kybp, two time points for which downscaled climate reconstructions are readily available from WorldClim (Hijmans et al., 2005). Mean temperature values from three general circulation models (GCMs)—CCSM4, MIROC-ESM and MPI-ESM-P—were used to provide more robust climate estimates than any one

TABLE 2 Correlation coefficients and standard errors between assemblage-mean climatic tolerances and sample age during each of the three focal time periods

Climate tolerance	Time period (kybp)		
	30–20	20–10	10–0
MAT05	–0.05 (0.37)	–0.54 (0.16)	–0.56 (0.14)
TS05	0.23 (0.32)	0.50 (0.17)	0.12 (0.17)
MAP05	–0.29 (0.28)	0.53 (0.16)	0.36 (0.12)
PS05	–0.06 (0.37)	–0.09 (0.23)	–0.33 (0.18)
MAT95	–0.67 (0.15)	–0.63 (0.14)	–0.58 (0.15)
TS95	–0.64 (0.26)	–0.01 (0.23)	0.20 (0.16)
MAP95	0.35 (0.35)	0.30 (0.19)	0.31 (0.13)
PS95	–0.34 (0.32)	–0.43 (0.20)	–0.08 (0.17)

Note: MAT05 indicates the mean of the 5th percentiles of species mean annual temperature distributions, MAT95 the 95th percentiles, etc. Abbreviations: MAT, mean annual temperature; TS, temperature seasonality; MAP, mean annual precipitation; PS, precipitation seasonality.

model. AM cold tolerances were calculated from samples within 1,000-, 2,000- and 3,000-year windows of the downscaled climate estimates. The 3,000-year window analyses are presented due to the relatively low temporal density of samples surrounding the Last Glacial Maximum, although results did not differ among time windows for the mid-Holocene. The differences between AM cold tolerances and local temperatures were analysed with *t* tests. All analyses were conducted in R version 3.2.2, with $\alpha = 0.05$ as the critical threshold (R Core Team, 2018).

3 | RESULTS

3.1 | Changes in AM climate tolerances

AM temperature tolerances recorded in the packrat middens were strongly correlated with sample age (average $r = -0.56$ to -0.58) from 10 to 0 kybp, whereas AM tolerances of annual precipitation (average $r = 0.31$ – 0.36), temperature seasonality (average $r = 0.12$ – 0.20) and precipitation seasonality (average $r = -0.08$ – 0.33) were more weakly correlated with sample age (Table 2). This suggests that from 10 to 0 kybp assemblages maintained lagged responses to past temperature increases, although this does not exclude the possibility of responses to other driving variables as well. Nonetheless, subsequent analyses focus solely on change in AM cold tolerances through time.

AM cold tolerances generally became more positive through time (i.e., communities were comprised of less cold tolerant species) from 20 to 0 kybp (Figure 2a). However, continued changes in AM cold tolerances during the past 10,000 years can only be attributed to lagged responses to past temperature increases if assemblages did not keep pace with warming during the preceding period of deglaciation. Indeed, while the average rate of change in AM cold tolerance during deglaciation (20–10 kybp) was significantly positive ($1.0^{\circ}\text{C} \times 10^{-4}/\text{yr}$, Figure 2b), even the upper 95% confidence boundary of the estimated rate of change ($1.7^{\circ}\text{C} \times 10^{-4}/\text{yr}$) lagged considerably behind the average rate of global temperature increase during that time (6 – $7^{\circ}\text{C} \times 10^{-4}/\text{yr}$). The average rate of change in AM cold tolerance from 10 to 0 kybp ($1.2^{\circ}\text{C} \times 10^{-4}/\text{yr}$) was not significantly different from that observed during 20 to 10 kybp, and the rate of change during both of those time periods was nearly an order of magnitude greater than the rate of change from 30 to 20 kybp ($0.14^{\circ}\text{C} \times 10^{-4}/\text{yr}$), which was only marginally different from the expected rate of zero given the lack of directional warming during the Late Pleistocene. Taken together, these results indicate that the climate warming trajectories established for most plant assemblages during deglaciation were maintained for the duration of the Holocene.

Analyses of community–climate differences at c. 21 and c. 6 kybp reinforced the conclusions presented above. AM cold tolerances were not significantly different from local temperatures at c. 21 kybp (mean difference = 2.0°C ; $t_6 = 1.1$, $p = 0.33$), and were significantly lower (i.e., tolerant of colder temperatures) than local temperatures at c. 6 kybp (mean difference = -3.8°C ; $t_{14} = -4.6$, $p < 0.001$).

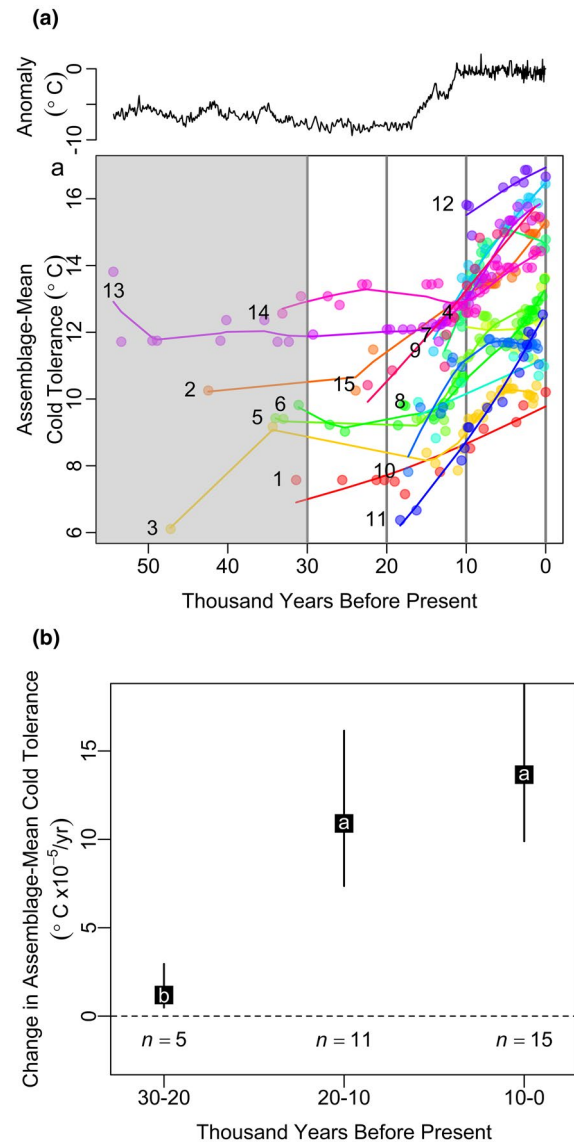


FIGURE 2 Change in assemblage-mean cold tolerance through time. Estimated values for each sample in the 15 midden series (colour-coded separately) are presented in (a), along with temperature anomaly relative to present day reconstructed from the Vostok ice core (Petit et al., 1999). Lines are spline fits to the data within each midden series. Grey bars separate discrete sample periods in which rates of change were analysed. Samples dated to > 30 kybp were not used in analyses due to insufficient sample size, but are provided here for reference. In (b), the weighted mean and back-transformed standard error of the rate of change are presented during the three focal time periods. The same lower-case letter indicates a similar rate among periods. Sample sizes refer to the number of midden series that met the criterion for inclusion (at least three samples) during each time period. Note that the expected rate of change from 0–10 kybp is approximately zero, and is 60 – $70^{\circ}\text{C} \times 10^{-5}/\text{yr}$ during the 10–20 kybp period, which is above the vertical range of the plot [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Colonization and extinction rates

Colonization and local extinction made comparable contributions to changes in AM cold tolerances throughout deglaciation and the

Holocene, although the numbers of species driving those changes varied significantly (Figure 3). The effects of colonization and local extinction were not different from zero during the 30–20 kybp period (as expected), but were significantly positive and similar during both the 20–10 and 10–0 kybp periods (Figure 3, left axis). However, looking at species turnover rather than the effects of that turnover on AM cold tolerances, rates of species colonization significantly exceeded rates of species local extinction during the 20–10 kybp period (Figure 2, right axis), and were higher than colonization rates during the 30–20 kybp period. Extinction rates were highest during 10–0 kybp, lower during 20–10 kybp and lower still during 30–20 kybp (Figure 2, right axis). In summary, because the effects of colonization and local extinction on AM cold tolerance were comparable, the large number of species colonizing during deglaciation must have had cold tolerances similar to the assemblage mean, whereas the small number of species going local extinct must have had cold tolerances that were far more negative than the assemblage mean.

4 | DISCUSSION

The assemblages studied here demonstrated fairly consistent increases in occupied temperature niche space throughout deglaciation and the Holocene, resulting in community–climate lags that varied in magnitude and type through time. While the observation of a lagged response to warming is not new, the high rate of community response during the Holocene and its multi-millennial duration are dramatic. These findings stem in part from the assemblage-level focus of this study, rather than on species' individualistic responses to environmental change. For example, it has been argued that temperate tree taxa in eastern North America kept pace with climate

change during roughly the same time period as our study, based on pollen records and seed dispersal models (Clark, 1998; Prentice et al., 1991). Differences in life-history strategies between dryland and temperate taxa could explain this discrepancy, as could differences in the rate and nature of climate change between western and eastern North America, or the generally lower taxonomic and spatial resolution of pollen records relative to midden records. However, it is also likely that the assemblage-level analysis presented here and individual species-level analyses conducted in other studies are inherently different. The leading edge of some species' distributions may roughly keep pace with climate change, but their ability to fill all newly suitable habitat depends on numerous dispersal and population dynamics processes. The northward expansion of Utah juniper (*Juniperus osteosperma*) from Utah into Wyoming and Montana during the Holocene provides an excellent example, in which rare long-distance dispersal events and subsequent infill of suitable habitat took thousands of years (Lyford et al., 2003). While both species- and assemblage-level perspectives are valuable, only the latter can identify dynamics of local diversity, which has clear implications for management and feedbacks to ecosystem processes.

The equivalent contributions of colonization and local extinction to community–climate disequilibrium also highlight a discrepancy in how we think about community responses to environmental change. A great deal of emphasis has been placed on understanding colonization dynamics in the palaeorecord (Clark, 1998; Clark et al., 1998), while the focus on the trailing edge of species distributions has largely revolved around evolutionary processes (Hampe & Petit, 2005), and less so on community dynamics. On the other hand, modern extinction debts are being studied intensively (Dullinger et al., 2012; Kuussaari et al., 2009). Our results demonstrate that both colonization and local extinction processes make important contributions to community reassembly, although the nature of those processes varies significantly through time.

The colonization and local extinction patterns found here can be viewed through the lens of a generalized model of community reassembly in response to shifting environmental filters interacting with dispersal processes (Figure 4). Effects of local extinction on the rate of change in AM cold tolerances were equivalent during the period of warming from 20 to 10 kybp and the period of no directional trends in mean annual temperature from 10 to 0 kybp, although fewer species went extinct from 20 to 10 kybp. This indicates outsized effects of those few species that went extinct from 20 to 10 kybp on rates of change in AM cold tolerance. This reflects the loss of particularly cold-adapted species (e.g., conifers) for which temperature thresholds were rapidly and substantially exceeded, resulting in the loss of the lower tail of assemblage cold tolerance distributions (Figure 4i). Many cool-adapted species persisted in otherwise unsuitable habitat, as demonstrated by the large number extinctions from 10 to 0 kybp. This pattern is consistent with a population dynamics model of persistence in degrading habitats, where the demographic rates that can buffer population declines depend on how far species occur from their environmental optima (Dullinger et al., 2012). Both abiotic

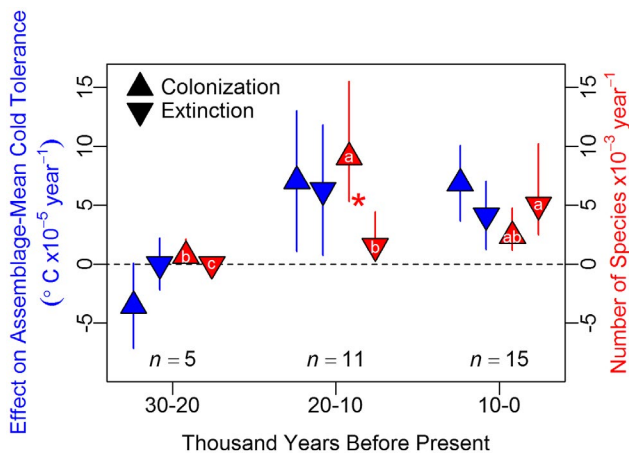


FIGURE 3 Colonization and local extinction rates through time. The effects of colonization and local extinction on assemblage-mean cold tolerance are presented in blue (left axis), and the rate of species colonization and extinction in red (right axis). The same lower-case letter indicates a similar rate among periods with respect to colonization or local extinction; asterisks indicate differences between colonization and local extinction within a single time period [Colour figure can be viewed at wileyonlinelibrary.com]

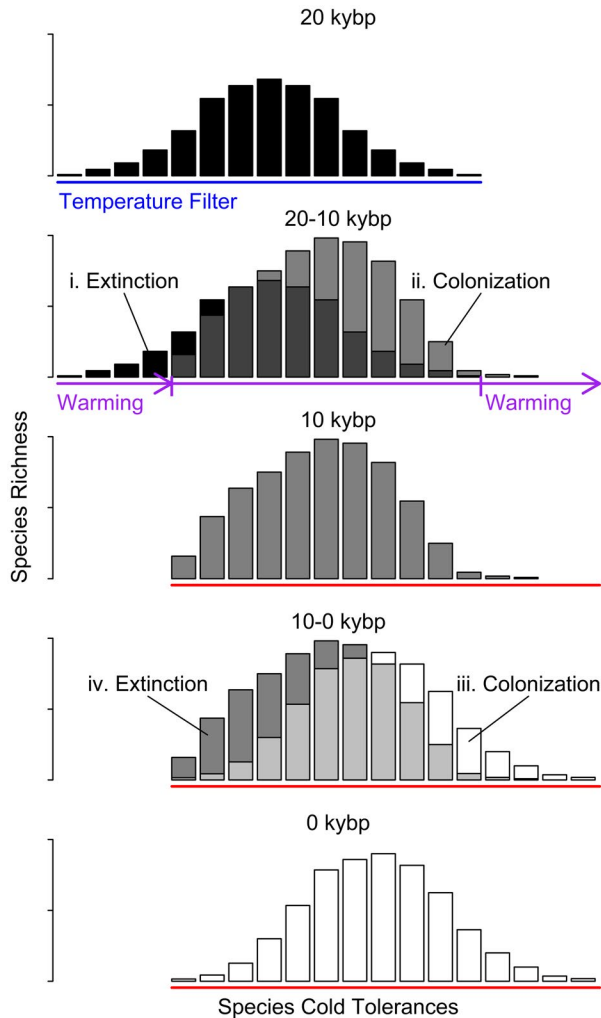


FIGURE 4 Conceptual model of colonization and local extinction through time. A small number of cold-adapted species are excluded, and a large number of warm-adapted species colonize, during deglaciation. A large number of cool-adapted species go locally extinct, and a comparable number of hot-adapted species colonize, during the Holocene [Colour figure can be viewed at wileyonlinelibrary.com]

microrefugia (Anderson, 1996; Hannah et al., 2014) and facilitation (Valiente-Banuet, Rumebe, Verdú, & Callaway, 2006) could also substantially influence long-term persistence of populations in warming environments, effectively buffering hyper-local change in temperature and other factors.

Much like extinction, effects of colonization on the rate of change in AM cold tolerances were similar between the 20–10 and 10–0 kybp periods, although the rate of species colonization was much higher during 20–10 than 10–0 kybp. This difference between taxonomic and climatic descriptions of colonizing species indicates that many of the colonizing species during the 20–10 kybp period had only marginally more positive cold tolerances than the average resident species (Figure 4ii). This pattern is consistent with colonization by species from adjacent warmer (micro-) habitats that rapidly colonized newly suitable habitat as minimum temperature thresholds were exceeded. Similar rapid upslope range expansion has

occurred in contemporary montane ecosystems (Steinbauer et al., 2018), where temperature clines are quite steep and spatially narrow. While differences in the range of cold tolerances between time periods could also influence variation in the contributions of species turnover to changes in AM cold tolerances, such differences were not found ($F_{2,28} = 1.1, p = 0.34$).

Dispersal limitation likely continued to play a role in assemblage responses to warming during the 10–0 kybp period, even after temperature increases had ceased. Competitive exclusion by resident species could also have played a role in delayed colonization (Cole, 1985). However, the prevalence of available microsites for establishment and the importance of positive, rather than negative, plant–plant interactions for establishment make competitive exclusion less likely in many desert ecosystems (Butterfield, Betancourt, Turner, & Briggs, 2010). The rate of colonizing species was somewhat, although not significantly, lower during the 10–0 than the 20–10 kybp period. Again, because the contribution of colonization to the rate of change in AM cold tolerance was equivalent between these two time periods, the later colonizers must have been substantially more heat-adapted on average than the resident species (Figure 4iii). Velocities of climate change were high across many of the expansive, broad climate gradients of the study region, which could have exacerbated dispersal limitation and led to the substantial lag in colonization (Loarie et al., 2009).

The relatively high rate of local extinctions during this same time period represented a surprisingly slow repayment of the extinction debt as populations of cool-adapted species disappeared during the Holocene (Figure 4iv). The long duration of these local extinctions may reflect the ability of populations to persist in microrefugia, or of metapopulations to persist within a landscape in which periodic local extinctions and recolonizations occurred in response to fluctuating climatic conditions (Cheddadi et al., 2016). Source–sink dynamics have been incorporated into models predicting the duration of future extinction debts (Dullinger et al., 2012), but their interaction with fluctuating climatic conditions has not. When climate variability is considered, the role of refugia and source populations may be even more important in allowing populations to persist in slowly degrading habitat.

5 | CONCLUSIONS

By focusing on changes in occupied niche space through time, rather than on the dynamics of individual species, we can begin to identify the broader assembly processes that structure patterns of biodiversity, if not the exact species present. Further research into understanding how responses to environmental change are linked to functional traits that drive ecosystem processes is critical for our ability to predict feedbacks between biotic and abiotic components of ecosystems (Suding et al., 2008). The results of this study further reinforce the importance of better integrating dispersal dynamics and environmental heterogeneity into community assembly models over a variety of spatial and temporal scales (Leibold et al., 2004).

Indeed, the fairly long colonization and extinction lags found in this and other studies suggest that community–climate disequilibrium may be the norm, and should be embraced by models, and managers, of biodiversity.

The results presented here are contingent upon the quality of the niche estimates used. Intraspecific variation in environmental tolerances could result in different sensitivities of leading- and trailing-edge populations. Non-current-analogue climate conditions could also blur our ability to track responses to specific aspects of climate, as could interactions among climatic factors. The fairly strong trend of increasing AM drought tolerance (5th percentile of mean annual precipitation niche [MAP05]) during deglaciation, for example, could indicate combined responses to temperature and precipitation limitation (or simply that these variables were correlated). Finally, our results suggest that some of these species may still not be in equilibrium with their climate niche, although most are likely to occupy the lower limits of their fundamental temperature niches. Development of tools and databases for estimating and disseminating information on thermal and other environmental limits, and continued application to growing databases for rodent middens in the Americas and other palaeobotanical records, would greatly improve our ability to model and predict responses of biodiversity to past, present and future environmental change.

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DATA ACCESSIBILITY

Species arrival and departure dates for each midden series are provided in Supporting Information Table S1. Species climate tolerance estimates are provided in Supporting Information Table S2. Raw data were extracted from the primary literature (references provided in Table 1), much of which is available from the Neotoma Paleoecology Database (www.neotomadb.org).

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REFERENCES

Anderson, R. S. (1996). Postglacial biogeography of Sierra lodgepole pine (*Pinus contorta* var. *murrayana*) in California. *Écoscience*, 3, 343–351. <https://doi.org/10.1080/11956860.1996.11682352>

- Anderson, R. S., & Van Devender, T. (1991). Comparison of pollen and macrofossils in packrat (*Neotoma*) middens—A chronological sequence from the Waterman Mountains of southern Arizona, USA. *Review of Palaeobotany and Palynology*, 68, 1–28. [https://doi.org/10.1016/0034-6667\(91\)90054-7](https://doi.org/10.1016/0034-6667(91)90054-7)
- Betancourt, J. L., Aasen Rylander, K., Peñalba, C., & McVickar, J. L. (2001). Late Quaternary vegetation history of Rough Canyon, south-central New Mexico, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 165, 71–95. [https://doi.org/10.1016/S0031-0182\(00\)00154-1](https://doi.org/10.1016/S0031-0182(00)00154-1)
- Blonder, B., Enquist, B. J., Graae, B. J., Kattge, J., Maitner, B. S., Morueta-Holme, N., ... Violle, C. (2018). Late Quaternary climate legacies in contemporary plant functional composition. *Global Change Biology*, 24(10), 4827–4840. <https://doi.org/10.1111/gcb.14375>
- Blonder, B., Nogués-Bravo, D., Borregaard, M. K., Donoghue, J. C., Jørgensen, P. M., Kraft, N. J. B., ... Enquist, B. J. (2015). Linking environmental filtering and disequilibrium to biogeography with a community climate framework. *Ecology*, 96, 972–985. <https://doi.org/10.1890/14-0589.1>
- Butterfield, B. J. (2015). Environmental filtering increases in intensity at both ends of climatic gradients, though driven by different factors, across woody vegetation types of the southwest USA. *Oikos*, 124, 1374–1382. <https://doi.org/10.1111/oik.02311>
- Butterfield, B. J., Betancourt, J. L., Turner, R. M., & Briggs, J. M. (2010). Facilitation drives 65 years of vegetation change in the Sonoran Desert. *Ecology*, 91, 1132–1139. <https://doi.org/10.1890/09-0145.1>
- Butterfield, B. J., & Munson, S. M. (2016). Temperature is better than precipitation as a predictor of plant community assembly across a dryland region. *Journal of Vegetation Science*, 27, 938–947. <https://doi.org/10.1111/jvs.12440>
- Cheddadi, R., Araújo, M. B., Maiorano, L., Edwards, M., Guisan, A., Carré, M., ... Pearnan, P. B. (2016). Temperature range shifts for three European tree species over the last 10,000 years. *Frontiers in Plant Science*, 7, 1581. <https://doi.org/10.3389/fpls.2016.01581>
- Clark, J. S. (1998). Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *The American Naturalist*, 152, 204–224. <https://doi.org/10.1086/286162>
- Clark, J. S., Fastie, C., Hurtt, G., Jackson, S. T., Johnson, C., King, G. A., ... Wyckoff, P. (1998). Reid's paradox of rapid plant migration. *BioScience*, 48, 13–24. <https://doi.org/10.2307/1313224>
- Cole, K. (1985). Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. *The American Naturalist*, 125, 289–303. <https://doi.org/10.1086/284341>
- Dial, K. P., & Czaplewski, N. J. (1990). Do woodrat middens accurately represent the animals' environments and diets? The woodhouse mesa study. In J. L. Betancourt, T. R. Van Devender, & P. S. Martin (Eds.), *Packrat middens: The last 40,000 years of biotic change* (pp. 43–58). Tucson, AZ: The University of Arizona Press.
- Dullinger, S., Gatzinger, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., ... Hülber, K. (2012). Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, 2, 619–622. <https://doi.org/10.1038/nclimate1514>
- Finley, R. B. Jr. (1990). Woodrat ecology and behavior and the interpretation of paleomiddens. In J. L. Betancourt, T. R. Van Devender, & P. S. Martin (Eds.), *Packrat middens: The last 40,000 years of biotic change* (pp. 28–42). Tucson, AZ: The University of Arizona Press.
- Fukami, T. (2015). Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, 46, 1–23. <https://doi.org/10.1146/annurev-ecolsys-110411-160340>
- Giesecke, T., Bennett, K. D., Birks, H. J. B., Bjune, A. E., Bozilova, E., Feurdean, A., ... Wolters, S. (2011). The pace of Holocene vegetation change—Testing for synchronous developments. *Quaternary Science Reviews*, 30, 2805–2814. <https://doi.org/10.1016/j.quascirev.2011.06.014>

- Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, 8, 461–467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>
- Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology and Evolution*, 29, 390–397. <https://doi.org/10.1016/j.tree.2014.04.006>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978. <https://doi.org/10.1002/joc.1276>
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2015). Dismo: Species distribution modeling. R package version 1.0-12. Retrieved from <http://CRAN.R-project.org/package=dismo>
- Holmgren, C. A., Betancourt, J. L., Peñalba, M. C., Delgado, J., Zuravansky, K., Hunter, K. L., ... Weiss, J. L. (2014). Evidence against a Pleistocene desert refugium in the Lower Colorado River Basin. *Journal of Biogeography*, 41, 1769–1780. <https://doi.org/10.1111/jbi.12337>
- Holmgren, C. A., Betancourt, J. L., & Rylander, K. A. (2006). A 36,000-yr vegetation history from the Peloncillo Mountains, southeastern Arizona, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 240, 405–422. <https://doi.org/10.1016/j.palaeo.2006.02.017>
- Holmgren, C. A., Betancourt, J. L., & Rylander, K. A. (2010). A long-term vegetation history of the Mojave-Colorado desert ecotone at Joshua Tree National Park. *Journal of Quaternary Science*, 25, 222–236. <https://doi.org/10.1002/jqs.1313>
- Holmgren, C. A., Betancourt, J. L., & Rylander, K. A. (2011). Vegetation history along the eastern, desert escarpment of the Sierra San Pedro Mártir, Baja California, Mexico. *Quaternary Research*, 75, 647–657. <https://doi.org/10.1016/j.yqres.2011.01.008>
- Holmgren, C. A., Peñalba, M. C., Rylander, K. A., & Betancourt, J. L. (2003). A 16,000 14C yr B.P. packrat midden series from the USA-Mexico Borderlands. *Quaternary Research*, 60, 319–329. <https://doi.org/10.1016/j.yqres.2003.08.001>
- Koehler, P. A., Anderson, R. S., & Spaulding, W. G. (2005). Development of vegetation in the Central Mojave Desert of California during the late Quaternary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 215, 297–311. <https://doi.org/10.1016/j.palaeo.2004.09.010>
- Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., ... Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends in Ecology and Evolution*, 24, 564–571. <https://doi.org/10.1016/j.tree.2009.04.011>
- La Sorte, F. A., & Jetz, W. (2012). Tracking of climatic niche boundaries under recent climate change. *Journal of Animal Ecology*, 81, 914–925. <https://doi.org/10.1111/j.1365-2656.2012.01958.x>
- Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergő, A. M., Noreen, A. M. E., ... Angert, A. L. (2016). A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters*, 19, 710–722. <https://doi.org/10.1111/ele.12604>
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., ... Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7, 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, 462, 1052–1055. <https://doi.org/10.1038/nature08649>
- Lyford, M. E., Jackson, S. T., Betancourt, J. L., & Gray, S. T. (2003). Influence of landscape structure and climate variability on a late Holocene plant migration. *Ecological Monographs*, 73, 567–583. <https://doi.org/10.1890/03-4011>
- Mateo, R. G., Mokany, K., & Guisan, A. (2017). Biodiversity models: What if unsaturation is the rule? *Trends in Ecology and Evolution*, 32, 556–566.
- McGill, B., Enquist, B., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21, 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Menéndez, R., Megías, A. G., Hill, J. K., Braschler, B., Willis, S. G., Collingham, Y., ... Thomas, C. D. (2006). Species richness changes lag behind climate change. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1465–1470. <https://doi.org/10.1098/rspb.2006.3484>
- Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., ... Jackson, S. T. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, 361, 920–923. <https://doi.org/10.1126/science.aan5360>
- Noy-Meir, I. (1973). Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics*, 4, 25–51. <https://doi.org/10.1146/annurev.es.04.110173.000325>
- Petit, J. R., Jouzel, J., Raynaud, D., Barkov, N. I., Barnola, J.-M., Basile, I., ... Stievenard, M. (1999). Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, 399, 429–436.
- Prentice, I. C., Bartlein, P. J., & Webb, T. (1991). Vegetation and climate change in eastern North America since the Last Glacial Maximum. *Ecology*, 72, 2038–2056. <https://doi.org/10.2307/1941558>
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Spaulding, W. G., Betancourt, J. L., Croft, L. K., & Cole, K. L. (1990). Packrat middens: Their composition and methods of analysis. In J. L. Betancourt, T. R. Van Devender, & P. S. Martin (Eds.), *Packrat middens: The last 40,000 years of biotic change* (pp. 59–84). Tucson, AZ: The University of Arizona Press.
- Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., ... Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556, 231–234. <https://doi.org/10.1038/s41586-018-0005-6>
- Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., ... Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, 14, 1125–1140. <https://doi.org/10.1111/j.1365-2486.2008.01557.x>
- Thuiller, W., Lavorel, S., Araujo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, 102, 8245–8250. <https://doi.org/10.1073/pnas.0409902102>
- Valiente-Banuet, A., Rumebe, A. V., Verdú, M., & Callaway, R. M. (2006). Modern Quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages. *Proceedings of the National Academy of Sciences USA*, 103, 16812–16817. <https://doi.org/10.1073/pnas.0604933103>
- Van Devender, T. R. (1980). Holocene plant remains from Rocky Arroyo and Last Chance Canyon, Eddy County, New Mexico. *The Southwestern Naturalist*, 25, 361–372. <https://doi.org/10.2307/3670692>
- Van Devender, T. R. (1987). Holocene vegetation and climate in the Puerto Blanco Mountains, southwestern Arizona. *Quaternary Research*, 27, 51–72. [https://doi.org/10.1016/0033-5894\(87\)90049-4](https://doi.org/10.1016/0033-5894(87)90049-4)
- Van Devender, T. R., Betancourt, J. L., & Wimberly, M. (1984). Biogeographic implications of a packrat midden sequence from the Sacramento Mountains, South-Central New Mexico. *Quaternary Research*, 22, 344–360. [https://doi.org/10.1016/0033-5894\(84\)90028-0](https://doi.org/10.1016/0033-5894(84)90028-0)
- Van Devender, T. R., Bradley, G. L., & Harris, A. H. (1987). Late Quaternary mammals from the Hueco Mountains, El Paso and Hudspeth counties, Texas. *The Southwestern Naturalist*, 32, 179–195. <https://doi.org/10.2307/3671561>
- Van Devender, T. R., Burgess, T. L., Piper, J. C., & Turner, R. M. (1994). Paleoclimatic implications of Holocene plant remains from the Sierra Bacha, Sonora, Mexico. *Quaternary Research*, 41, 99–108. <https://doi.org/10.1006/qres.1994.1011>
- Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences USA*, 104, 5738–5742. <https://doi.org/10.1073/pnas.0606292104>

Williams, J. W., Shuman, B. N., Webb, T., Bartlein, P. J., & Leduc, P. L. (2004). Late-quaternary vegetation dynamics in North America: Scaling from taxa to biomes. *Ecological Monographs*, 74, 309–334. <https://doi.org/10.1890/02-4045>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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