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Plant biomes demonstrate that landscape resilience today is the lowest it has been since end-Pleistocene megafaunal extinctions

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Abstract

Resilient landscapes have helped maintain terrestrial biodiversity during periods of climatic and environmental change. Identifying the tempo and mode of landscape transitions and the drivers of landscape resilience is critical to maintaining natural systems and preserving biodiversity given today's rapid climate and land use changes. However, resilient landscapes are difficult to recognize on short time scales, as perturbations are challenging to quantify and ecosystem transitions are rare. Here we analyze two components of North American landscape resilience over 20,000 years: residence time and recovery time. To evaluate landscape dynamics, we use plant biomes, preserved in the fossil pollen record, to examine how long a biome type persists at a given site (residence time) and how long it takes for the biome at that site to reestablish following a transition (recovery time). Biomes have a median residence time of only 230–460 years. Only 64% of biomes recover their original biome type, but recovery time is 140–290 years. Temperatures changing faster than 0.5°C per 500 years result in much reduced residence times. Following a transition, biodiverse biomes reestablish more quickly. Landscape resilience varies through time. Notably, short residence times and long recovery times directly preceded the end-Pleistocene megafauna extinction, resulting in regional destabilization, and combining with more proximal human impacts to deliver a one-two punch to megafauna species. Our work indicates that landscapes today are once again exhibiting low resilience, foreboding potential extinctions to come. Conservation strategies focused on improving both landscape and ecosystem resilience by increasing local connectivity and targeting regions with high richness and diverse landforms can mitigate these extinction risks.

KEYWORDS

biome, extinction, landscape resilience, last interglaciation, North America, pollen

1 | INTRODUCTION

A resilient landscape is a region that sustains ecological functions, biodiversity, and landscape processes over time, under changing conditions and despite multiple stressors (Beller, Robinson, Grossinger, & Grenier, 2015; Beller et al., 2019). Resilient landscapes have helped maintain biological diversity for millennia and have the potential to protect biodiversity into the future (Gavin et al., 2014; Moritz & Agudo, 2013). For example, Beringia provided a refugium for megafauna species and woody plants during the last glaciation, allowing biodiversity to persist and ecosystems to flourish (Graham et al., 2016; Wang et al., 2017, 2018). However, climate-resilient landscapes are persistently being threatened by accelerated human modification, leading to fragmentation and loss (Folke et al., 2004). Conservation biologists are actively working to identify and conserve landscapes that will promote resilience to climate change (Anderson et al., 2016; Beller et al., 2019). However, we do not yet understand the drivers of resilience or the tempo and mode of landscape change that occurs during periods of major environmental change. By identifying resilient landscapes, we will be able to better protect natural systems against perturbations from climate and land use change.

Resilience is defined as the capacity of the system to absorb change while maintaining the same identity (Folke et al., 2010; Holling, 1973). It encompasses two processes: persistence and recovery. Persistence measures the ability of the system to maintain the same state, while recovery measures the time it takes for the system to return to its original state following a landscape change (Côté & Darling, 2010; Lake, 2013). We quantify these two components of landscape resilience by calculating the residence time (persistence) and recovery time (recovery) of the plant biomes of North American landscapes at the site level. Landscape resilience (sometimes called spatial resilience; Allen et al., 2016; Chambers, Allen, & Cushman, 2019) differs from ecosystem resilience in that it is a property of specific geographic locations as measured by biome dynamics relative to geography (Allen et al., 2016; Beller et al., 2015, 2019; Chambers et al., 2019). Because landscape resilience is spatially explicit, the local disruption of regional ecosystem function can translate across trophic levels (Beller et al., 2015, 2019). However, the subject of ecosystem resilience is the ecosystem itself, which may shift across the landscape while remaining intact.

To understand the mechanisms behind resilience we must first identify and study landscapes that have exhibited resilience. Some research has examined resilience either by performing experiments at specific sites (e.g., Hoffmann et al., 2012; Hoover, Knapp, & Smith, 2014; Norden, Chazdon, Chao, Jiang, & Vílchez-Alvarado, 2009) or by examining changes at the regional to global scale over the last several decades (e.g., Oliver et al., 2015; Ponce-Campos et al., 2013; Stevens-Rumann et al., 2018). However, resilient landscapes are difficult to recognize on short time scales, given that perturbations are challenging to quantify and ecosystem state changes are very rare (Barnosky et al., 2012; Oldfather et al., 2016). By examining long timescales, we can observe the trending resilience in landscapes as they rebound toward equilibria following disturbances or resist disturbances entirely (Angeler et al., 2016). Here, we examine landscape resilience in North America over the past 20,000 years. Over this time period, North America experienced substantial environmental change: the retreat of Laurentide ice sheets (Dyke & Prest, 1987), human settlement and population increase (Davis et al., 2019), abrupt climate change, novel climates, no-analog plant communities (Williams & Jackson, 2007), and megafaunal extinctions (Faith & Surovell, 2009). By revealing landscape resilience patterns through space and time in North America over the past 20,000 years, we can identify risks and opportunities for maintaining biodiversity today and going forward.

Here, we explore landscape resilience by calculating the residence and recovery times for plant biomes, as recorded in the fossil pollen record, at sites across North America. We use these metrics to define landscape resilience over the last 20,000 years. Throughout this manuscript we use the term ‘biome’ as the unit of study for evaluating landscape resilience. We analyzed landscape resilience patterns both across biome types and through time. We also analyzed the potential drivers of landscape resilience, including biodiversity, rates of climate change, and landform characteristics.

2 | MATERIALS AND METHODS

2.1 | Pollen records from Neotoma

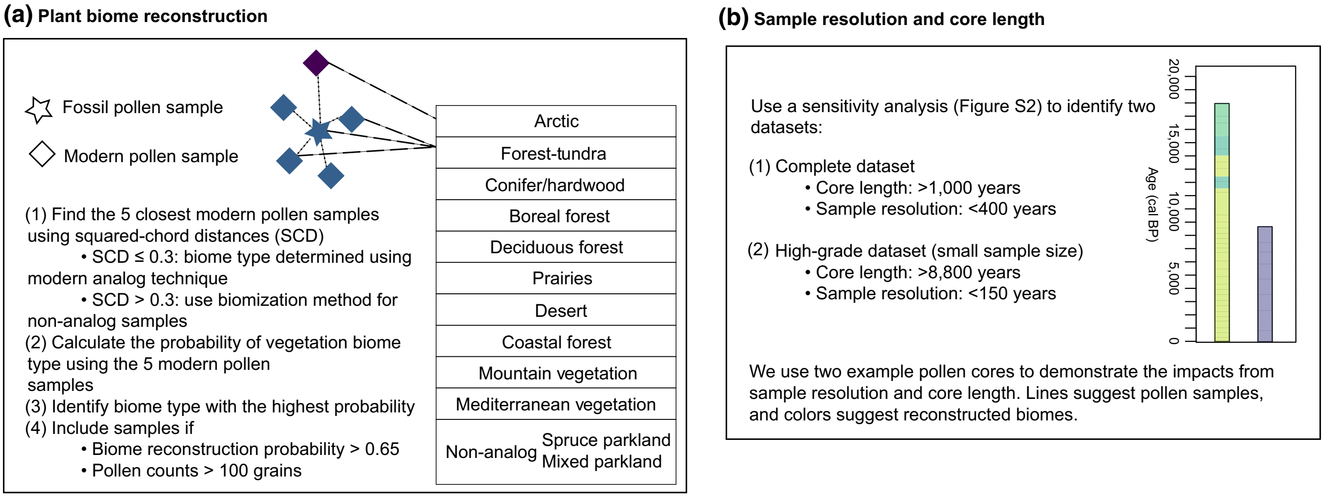
We used the pollen record to reconstruct biome dynamics across the landscape (Figure 1). We analyzed 14,189 pollen samples after the last glaciation (20 to 0 ka) from 358 sites across North America using the Neotoma Paleoecology Database (Neotoma; Goring et al., 2015; Williams et al., 2018; Table S1). Neotoma provides an open and sustainable repository for multiple types of paleoecological data, including over 32,000 datasets across more than 16,000 globally distributed sites. All pollen cores used had high-quality chronologies and high-quality biome reconstructions, discussed below. At some sites, there are multiple pollen cores in Neotoma. If the cores overlap in time, we selected the longest and most recently collected core. If the cores present plant biomes from different periods, we constructed a composite core.

2.2 | Chronology of sediment cores

We only used pollen records that have high-quality chronologies (Wang, Goring, & McGuire, 2019). Records with high-quality chronologies have dense geochronological age controls for the age–depth model. There are at least three continuous geochronological age controls, and the maximum interval between two neighboring age controls is fewer than 3,000 years. Either the complete core or a subset of the core has sufficiently dense geochronological age controls. We built the age–depth relationship using Bacon, a widely used Bayesian age–depth model (Blaauw & Christen, 2011; Wang et al., 2019). In addition to these data, we also included six varve cores that have at least three pollen samples each (Table S1). All sites have associated age error estimations. The samples have age errors ranging from 40 to 1,000 years (interquartile range [IQR]: 170–540 years; median: 340 years).

2.3 | Biome reconstruction

We used the modern analog technique (Simpson & Oksanen, 2018; Williams & Shuman, 2008; Williams, Shuman, & Webb, 2001) and biomization method (Williams et al., 2001) to reconstruct 12 biome



(a) Plant biome reconstruction

(1) Find the 5 closest modern pollen samples using squared-chord distances (SCD)
- SCD ≤ 0.3: biome type determined using modern analog technique
- SCD > 0.3: use biomization method for non-analog samples

(2) Calculate the probability of vegetation biome type using the 5 modern pollen samples

(3) Identify biome type with the highest probability

(4) Include samples if
- Biome reconstruction probability > 0.65
- Pollen counts > 100 grains

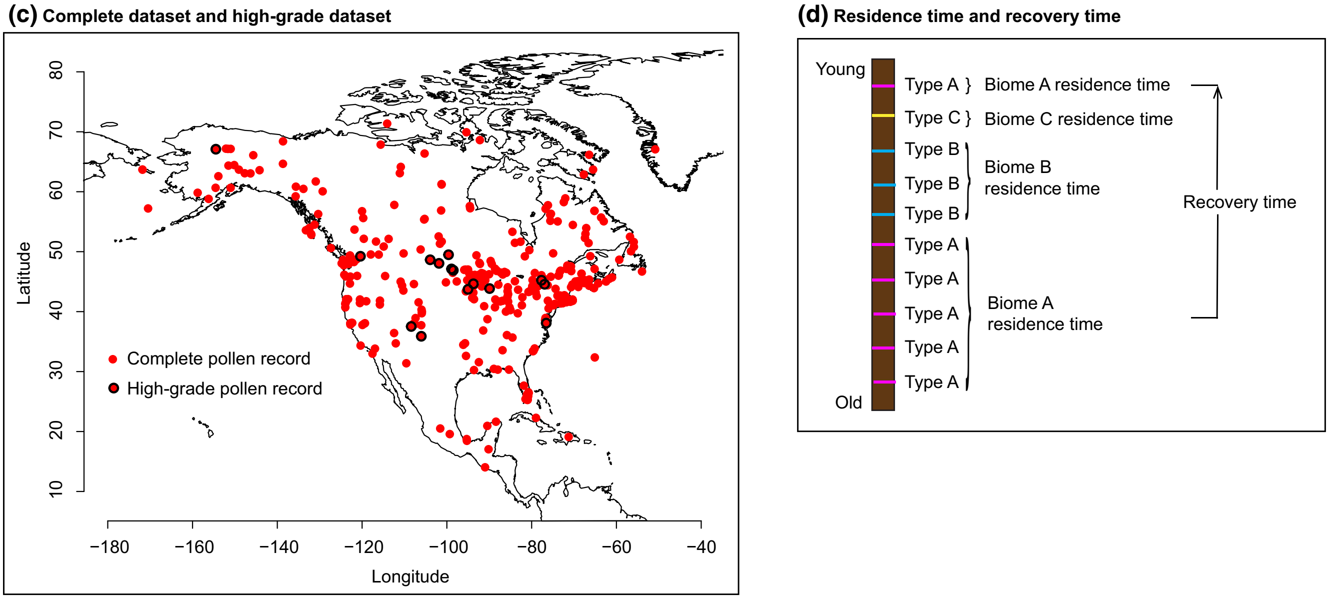
(b) Sample resolution and core length

Use a sensitivity analysis (Figure S2) to identify two datasets:

(1) Complete dataset
- Core length: >1,000 years
- Sample resolution: <400 years

(2) High-grade dataset (small sample size)
- Core length: >8,800 years
- Sample resolution: <150 years

We use two example pollen cores to demonstrate the impacts from sample resolution and core length. Lines suggest pollen samples, and colors suggest reconstructed biomes.



(c) Complete dataset and high-grade dataset

(d) Residence time and recovery time

FIGURE 1 Study design. We used three filters to select appropriate pollen samples and sediment cores over 20–0 ka in North America from Neotoma (Williams et al., 2018): high-quality chronology (Wang et al., 2019), high confidence of plant biome reconstruction (a), and pollen sample resolution and sediment core length (b) assessed using a sensitivity test (Figure S3). We calculated the landscape resilience using two datasets: the complete dataset containing 14,189 pollen samples at 358 sites, indicated by the red dots on the map (c), to calculate the longest estimation of residence time and recovery time, and a high-grade dataset containing 2,016 samples across 15 sites, indicated by the red dots with black outlines (c), to represent the shortest estimation of residence time and recovery time. We calculated residence time and recovery time to analyze landscape resilience (d)

types from pollen samples (Figure 1a). The modern analog technique is a well-established pollen-vegetation method to reconstruct plant biomes by finding the modern analog of fossil pollen samples. For the modern dataset, we used the North American surface pollen dataset (Whitmore et al., 2005). This dataset provides more than 4,500 surface pollen samples covering 134 pollen taxa across North America and contains related vegetation and climate information on each surface sample. We categorized pollen taxonomy according to an established 64-taxon list (Williams & Shuman, 2008). We calculated square chord distance (SCD) to find modern analogs of fossil pollen samples.

Here, we established a method to estimate the uncertainty of the modern analog technique, and we selected only pollen samples that have confident biome reconstructions (Figure 1a). To reconstruct the fossil biome type, the original modern analog technique identifies one modern analog nearest to each fossil pollen sample (Williams & Shuman, 2008). However, this does not estimate uncertainty in the pollen biome reconstructions. Inaccurate biome reconstructions can falsely accelerate transitions in landscape dynamics analyses. Instead, we found the closest five modern analogs of each fossil sample. We then calculated the distance-weighted probability of biome types based on the five modern analogs. We used the biome type with the highest probability as the biome type for the fossil pollen sample. We excluded pollen samples that have a probability of biome reconstruction lower than 0.65. This is the 90% confidence level when using the modern analog technique to reconstruct modern plant biomes using surface pollen samples.

We reconstructed no-analog biomes using the biomization method based on the association of plant functional types (Williams et al., 2001; Figure 1a). No-analog fossil samples contain high percentages of boreal conifers (*Picea* and *Larix*), herbs, and temperate deciduous broad-leaf trees (*Fraxinus* and *Carpinus*; Williams et al., 2001). No-analog biomes are uncommon today but were widespread in the past, especially between 17 and 12 ka, centering in the Great Lakes region (Overpeck, Webb, & Webb III, 1992; Williams et al., 2001). We designated a sample as no-analog when the SCD of the modern analogs is greater than 0.3 (Goring et al., 2015; Williams & Shuman, 2008).

Finally, we compiled pollen records with high-quality pollen biome reconstructions from only high-quality chronology records that also have more than 100 pollen grains (Figure 1a). We used 12 established biome types, including five forest types—forest-tundra, conifer/hardwood, boreal forest, deciduous forest, and coastal forest, five shrub/herb biome types—Arctic vegetation, desert, mountain vegetation, prairies, and Mediterranean vegetation, and two no-analog biome types—spruce parkland and mixed parkland (Figure 1a). There are only 11 plant biome types reconstructed in the fossil pollen dataset out of the 12 biome types; no Mediterranean vegetation samples were confidently reconstructed (Figure 2).

2.4 | Landscape resilience: Residence and recovery time

We analyzed landscape resilience using residence and recovery times. Residence time is the time that the biome persists in the same state at a particular site. Recovery time is the time that the biome

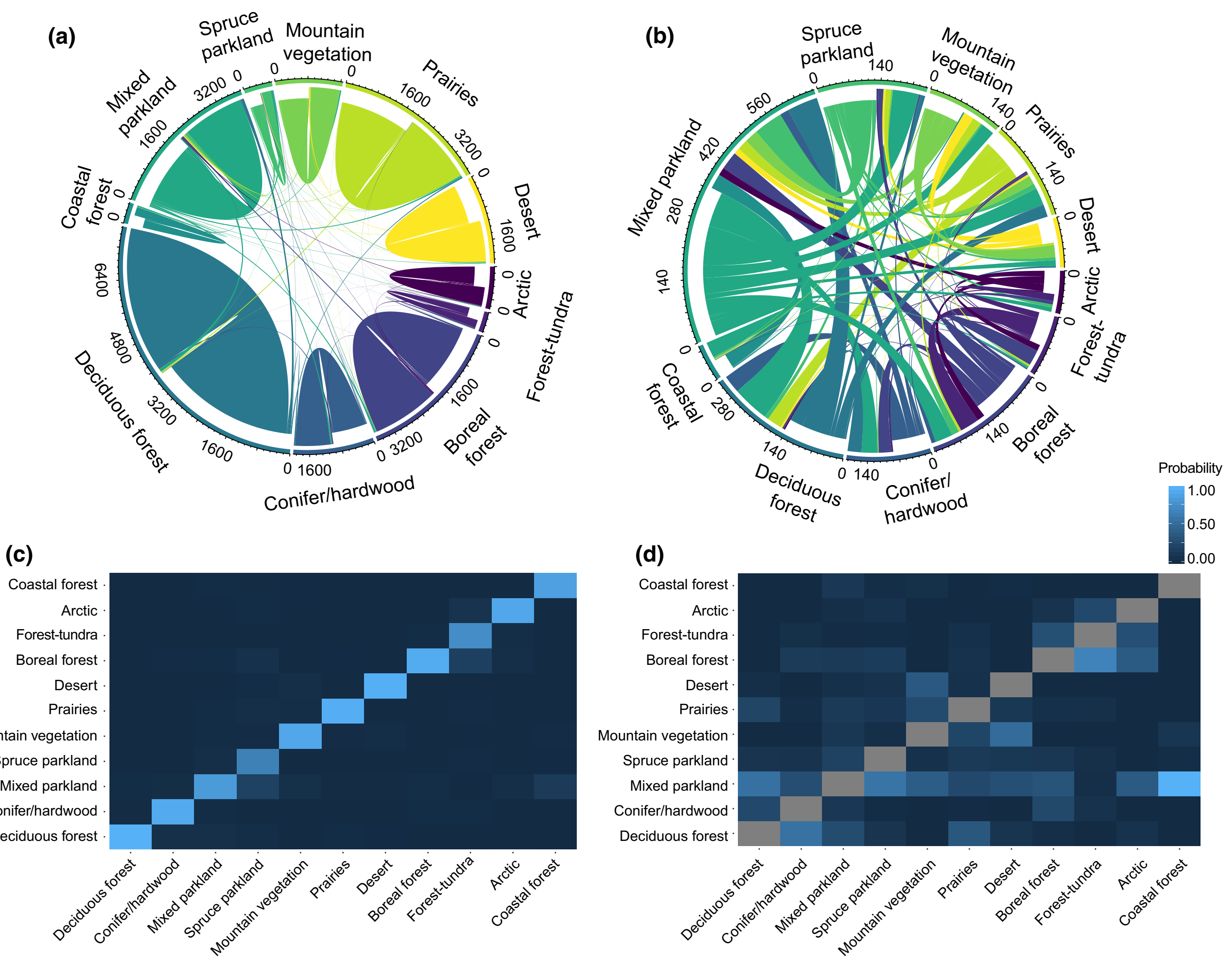


FIGURE 2 Transitions of biome based on fossil pollen samples. (a) and (b) are transition matrix circular plots. Each color represents one type of biome. Ribbon suggests the transition from one type of biome to another, and the white gap between the ribbon and the scale bar indicates the older biome from which the transition originates. Ribbon width represents the number of pollen samples in transition. Numbers outside the scale bar indicate the number of pollen samples within a certain type of biome. (c) and (d) are transition matrix heatmap. Light blue indicates a higher probability from one type of biome transitioning to another one from columns to rows, while dark blue indicates a lower transition probability. Circular plot (a) and heatmap (c) include all transitions between fossil pollen samples, including maintaining the same biome, and is indicative of total biome sample sizes. Circular plot (b) and heatmap (d) only include transitions from one biome type to a different biome type

takes to return to its original state at that site. One challenge is in designating the precise timing of biome transitions. A biome transition can occur at any time in the interval between the two adjacent fossil pollen samples of different biome types. The midpoint of the interval gives the average estimation of the transition time. We calculated the residence time of biomes within each core using the midpoint between the two adjacent fossil samples where biomes transition (Figure 1d). We calculated the recovery time as the interval between the last occurrence of the biome type to the first reoccurrence (Figure 1d). If the same type of biome does not reoccur, we designated the biome type as not recovering back. We then calculated recovery probability based on the reoccurrence frequency in each core.

In addition, we calculated landscape resilience in two ways: (a) landscape resilience for each biome type and (b) landscape resilience patterns through time. Residence and recovery times are calculated as median values for each instance of a biome type from throughout all sediment cores. Residence and recovery patterns through time are calculated as the median residence or recovery time of any biome from within a specific time window. This method identifies patterns in resilience, but necessarily double-counts biomes that persist for a long time. The distribution of persistence is highly right skewed, with few long-persistent biomes and many intermittent ones (Figure S1). This doubling-counting results in longer residence and recovery times than when considering biomes separately.

2.5 | Sensitivity test: Sample resolution, core length, and edge effects

Other challenges in calculating residence time and recovery time include uneven sampling resolution, short core lengths, and edge effects (Figure S2). Short core lengths may artificially truncate edge biomes. Coarse sampling resolution may underestimate the frequency of biome shifts due to temporal gaps between fossil samples (Figure 1b). An edge effect may influence resilience calculations at both the beginning and end of the cores, where biomes and biome transitions are truncated. To understand these systematic errors in residence and recovery times calculations, we conducted a sensitivity analysis of residence and recovery times to core length, sampling resolution, and edge effects (Figures S3 and S4). Results suggest that for the cores that are longer than 1,000 years, core resolution has little effect on median residence and recovery times of all biomes when sampling resolution is coarser than 400 years (Figure S3a,b). Results also suggest that core resolution does not influence median residence and recovery times of all biomes when core length is longer than 8,800 years (Figure S3c,d) and when sampling resolution is finer than 150 years (Figure S3e,f). Based on the results of core length and sampling resolution analyses, we used two datasets to calculate residence and recovery times that bound our estimations (Figure 1b,c). Our high-grade dataset contains 2,016 samples across 15 sites whose core length is longer than 8,800 years and sampling resolution is finer than 150 years. Our complete dataset contains 14,189 pollen samples at 358 sites where core length is longer than 1,000 years and sampling resolution is finer than 400 years. The two datasets set the lower/higher boundaries of median residence and recovery times. To avoid mid-domain effects resulting from edge effects, we analyzed residence time over the past 20,000 years but analyzed recovery time and recovery probability only before 3 ka (Figure S4; Appendix S1). We also did not include recovery time and recovery probability before 16 ka due to the small sample sizes (<10) for recovery calculations (Figure S5; Appendix S1).

2.6 | Drivers: Biodiversity, rate of climate change, and landform characteristics

We used pollen richness to estimate plant biodiversity. However, pollen–plant richness relationships are biased by sample size, taxonomic precision, and taphonomic processes (Birks et al., 2016; Goring, Lacourse, Pellatt, & Mathewes, 2013). Pollen richness depends on the pollen-count size (Rull, 1987), thus the comparisons of pollen richness should be based on the estimation from the same size of pollen grains. Pollen grains are identified to the genus or family level, and this low taxonomic resolution leads to non-linear relationships between pollen richness and plant richness (Birks et al., 2016; Goring et al., 2013). Pollen taxa from wind-pollinated plant taxa with high pollen production are over-presented in pollen samples, whereas pollen taxa with low pollen production and low dispersal ability are underestimated.

We accounted for these biases by using a rarefaction analysis. Rarefaction analyses estimate the pollen richness by subsampling *n* pollen grains selected at random without replacement from the sample (Birks & Line, 1992; Hurlbert, 1971). This method standardizes the count size and allows comparisons between the samples. We calculated the pollen richness of each biome type by using all the fossil pollen samples of the specific type. We used the subsample size of 100,000 in the rarefaction, in which 100,000 is the lowest number of pollen grain counts of the 11 biome types. This large subsample size reduces the underestimation of rare pollen taxa in the pollen richness calculation. Modern ecology and biogeography studies suggest that plant richness can be predicted from the richness of a few common genera and families (Mazaris, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2010), which indicates the ability to use a pollen record with low taxonomic resolution to predict plant richness. Previous studies indicate robust relationships between plant richness and pollen richness after rarefaction (Birks et al., 2016; Felde, 2015; Odgaard, 2013). Though there are still challenges in pollen–plant richness estimations, pollen richness after rarefaction can reflect the plant richness trends at the continental scale for the purpose of these analyses.

Another potential driver of landscape resilience considered was rate of climate change. The climate data used consist of biased downscaled CCSM3 data (He et al., 2013; Lorenz, Nieto-Lugilde, Blois, Fitzpatrick, & Williams, 2016). The climate variables include mean/minimum/maximum annual temperatures/precipitations, and annual climate water deficit (potential evapotranspiration − actual evapotranspiration). All climate variables are calculated as the rates of mean value change across a 500 year window. Climate variables are highly correlated (Table S2). Thus, we used the rate of mean annual temperature change as the primary climate variable.

Finally, landform diversity is considered a likely driver of landscape resilience (Whittaker, 1956, 1967). We used digital elevation models from the US Geological Survey to identify relevant landform characteristics (Danielson & Gesch, 2011). We calculated the average/range/standard deviation of elevation and slope. We considered two spatial buffers around fossil pollen sites: 30 and 1 km.

We used a generalized additive model (GAM; Wood, 2011) to analyze the relationships between landscape resilience (residence and recovery times) and pollen richness, rate of climate change, and landform characteristics. We calculated adjusted R^2 values and *p*-values to analyze the strengths of the relationships.

3 | RESULTS

3.1 | The tempo of landscape resilience

Using our complete dataset, we find that the median biome persists on a landscape for 460 years (IQR: 150–1,630 years; Table 1; Figure 3; Video S1). After transitioning (Figure 2; Table S3), recovery

TABLE 1 Residence time, recovery time, and recovery probability of all 11 biome types. IQR is the interquartile range by Q1 (lower quartile of residence/recovery times)–Q3 (upper quartile of residence/recovery times)

	Residence time (years)		Recovery time (years)		
Biome type	Median	IQR	Median	IQR	Recovery probability
Deciduous forest	1,020	326–2,524	276	118–544	0.76
Boreal forest	855	205–3,469	322	130–827	0.53
Conifer/hardwood	743	274–1,997	560	234–1,470	0.67
Coastal forest	527	250–1,048	535	324–1,420	0.76
Forest-tundra	376	151–785	450	163–981	0.48
Arctic	1,023	281–2,469	374	61–951	0.42
Desert	788	199–2,755	263	119–858	0.70
Prairie	570	148–1,603	129	65–497	0.64
Mountain vegetation	319	132–1,462	299	171–611	0.83
Mixed parkland	313	120–873	317	138–741	0.66
Spruce parkland	181	77–427	147	64–434	0.57
Forest biomes	702	229–2,339	362	158–918	0.64
Shrub/herb biomes	340	120–1,193	261	99–642	0.65
Total	458	154–1,628	293	118–752	0.64

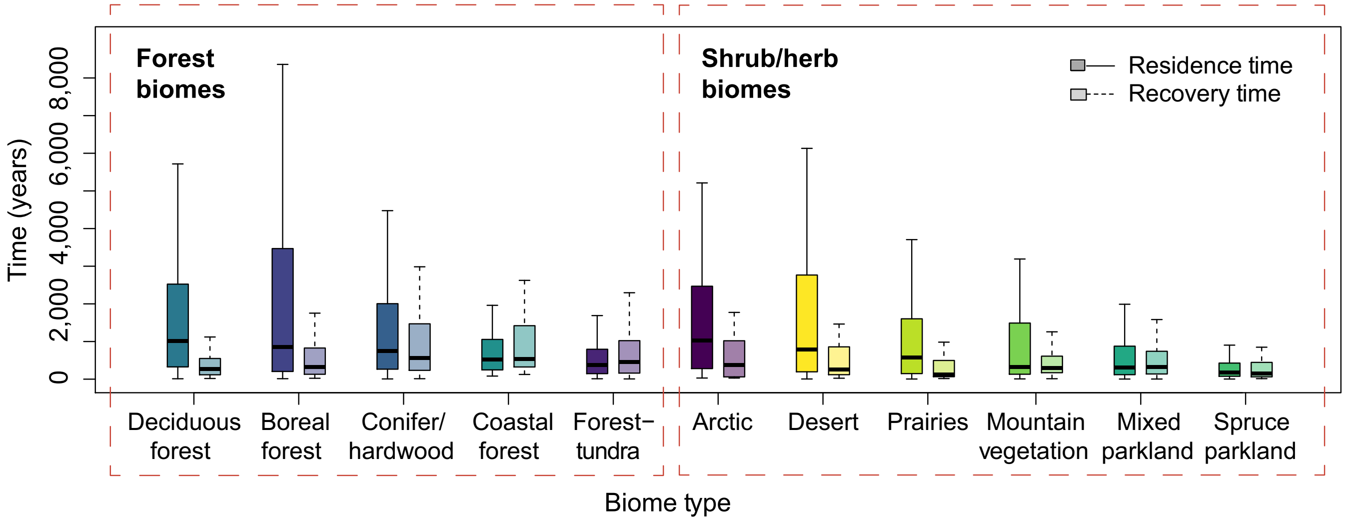


FIGURE 3 The landscape resilience, residence and recovery times, conferred by the 11 established biome types

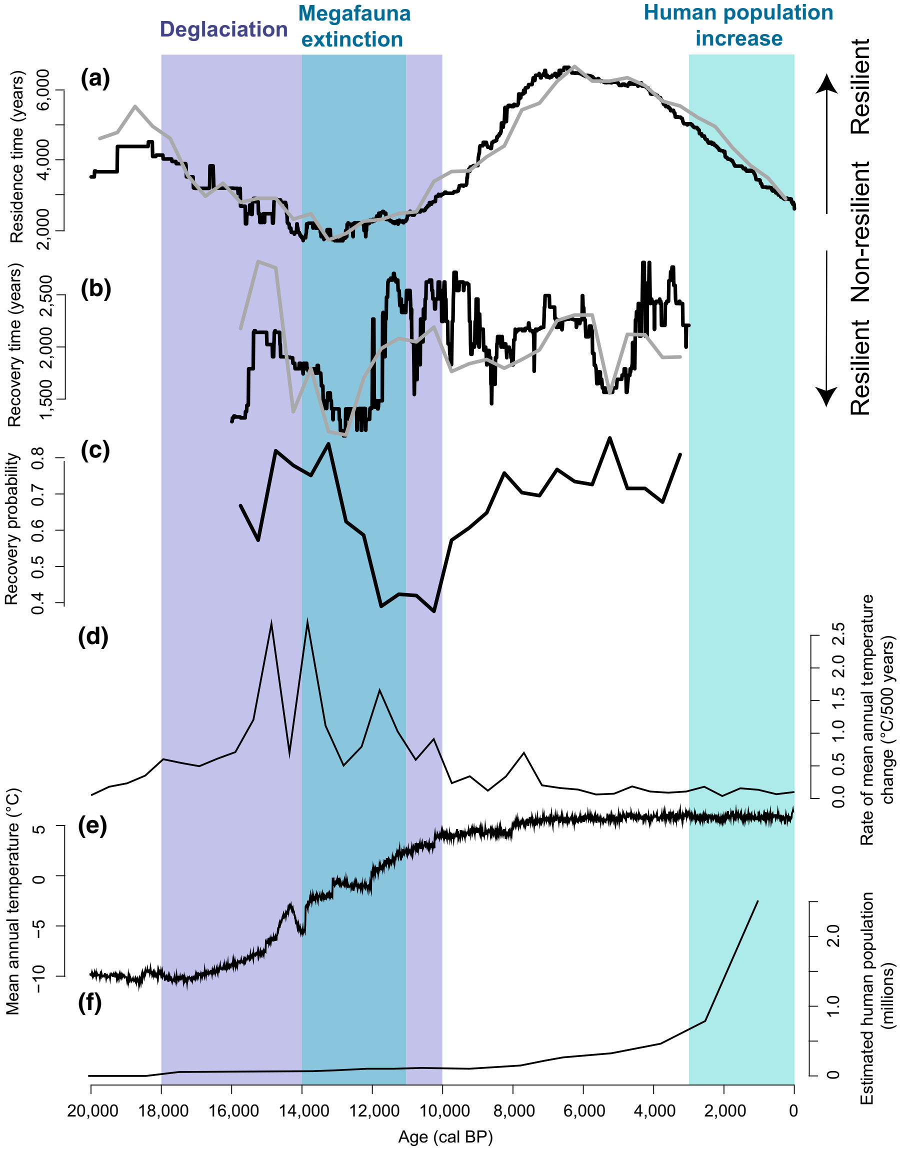


FIGURE 4 Landscape resilience patterns through time, including median values of residence time (a) and recovery time (b) across all plant biomes, calculated using moving windows of 10 years (black) and 500 years (gray), and recovery probability across all plant biomes every 500 years (c). Environmental data include the rate of temperature change per 500 years across all sites (Lorenz et al., 2016) (d), decadal mean annual temperature across all sites (Lorenz et al., 2016) (e), and human population sizes in North America (Peros et al., 2010) (f). Ages are presented as calendar years before the present (cal BP, where the present is 1950 AD)

occurs in 64% of biomes with a median recovery time of 290 years (IQR: 120–750 years), while the other 36% never reestablish (Table 1; Figure 3; Video S2). The high-grade dataset estimates the median residence time as 230 years (IQR: 70–990 years) and median recovery time as 140 years (IQR: 60–410 years). Taken together, these provide a range of confidence for residence and recovery times. We used the complete dataset in all further analyses, and we used the high-grade dataset only to estimate a lower boundary of median residence and recovery times due to the relatively small sample size in the high-grade dataset.

Biome identity has a strong effect on landscape resilience. Forests persist longer (t_{res} = 700 years [230–2,340 years] (median [IQR])) and reestablish more slowly (t_{rec} = 360 years [160–920 years]), while shrub/herb biomes persist for less time (t_{res} = 340 years [120–1,190 years]) and reestablish more quickly (t_{rec} = 260 years [100–640 years]; Table 1; Figure 3). Arctic vegetation is the most stable biome type, with a median residence time of 1,020 years (IQR: 280–2,470 years; Table 1; Figure 3). Prairies are the quickest to recover (t_{rec} = 130 years [70–500 years]), perhaps due to the dynamics of prairie–forest ecotones; conifer forests (t_{rec} = 560 years [230–1,470 years]) and coastal forests (t_{rec} = 540 years [320–1,420 years]) are the slowest to recover (Table 1; Figure 3). More than 50% of Arctic vegetation and forest-tundra biomes do not recover (Table 1), likely due to the warming trend during the examined period. Deciduous forests are the most common plant biome in North America following the last glaciation (Figure 2), and it is the forest biome that confers the highest landscape resilience, with the longest residence time (t_{res} = 1,020 years [330–2,520 years]) and shortest recovery time (t_{rec} = 280 years [120–540 years]; Table 1; Figure 3). No-analog biomes, including spruce parkland (t_{res} = 180 years [80–430 years]) and mixed parkland (t_{res} = 310 years [120–870 years]), exhibit short residence times (Table 1; Figure 3) and confer a high probability of transition (28% of pollen samples transition biome types; Figure 2; Table S3). This makes sense, as these no-analog biomes are defined as temporary communities found in areas that exhibit higher-than-present temperature seasonality and megaherbivore release, common between 17 and 9 ka (Gill, Williams, Jackson, Lininger, & Robinson, 2009; Williams & Jackson, 2007). The short residence time and high sample transition probability imply quick, dynamic changes and low resilience in these no-analog biomes resulting from novel climates and megafauna extinction.

3.2 | The mode of landscape resilience: Patterns through time

Looking at landscape resilience patterns through time, we find that resilience decreased and remained low during deglaciation (18–10 ka), well before Native Americans arrived in North America (nearly 16 ka; Davis et al., 2019) and before the end-Pleistocene megafaunal extinctions began (14–11 ka; Figure 4). This low resilience was represented by decreasing residence time, increasing recovery time, and decreasing recovery probability (Figure 4a–c). Landscapes persist for a short time and frequently shifted between different biome types under rapid environmental disturbances during deglaciation. After 10 ka, when the climate was stable, landscapes persist in the same state for a long time without frequent shifts between different biome types, represented by long residence times (Figure 4a). After 3 ka in the Woodland period, when the human population in North America began to increase rapidly (Peros, Munoz, Gajewski, & Viau, 2010; Figure 4f), landscape resilience decreased despite the relatively stable climate (Figure 4d,e), as demonstrated by decreasing residence time (Figure 4a).

3.3 | Drivers of landscape resilience

We find that pollen richness increases landscape resilience by decreasing recovery times. Recovery times demonstrate a strong, negative linear relationship with species richness (adjusted R^2 = .426, p = 0.0175; Figure 5a), implying that landscapes containing more species reestablish more quickly. Unexpectedly, pollen richness does not correlate with residence times (adjusted R^2 = −.0502, p = 0.488; Figure 5b).

Rapid climate change decreases landscape resilience by accelerating transitions. Examining residence times through time, we found that short residence times are correlated with rapid temperature change, as demonstrated by GAM analysis of residence time and the rate of mean annual temperature change (adjusted R^2 = .468, $p = 2.30 \times 10^{-5}$; Figure 6a; Table S4). Over the past 20,000 years, a 1°C increase in temperature per century resulted in a 260 year decrease in residence time across all biome types. Notably, residence times are not affected by a rate of temperature change smaller than 0.5°C/500 years but decreases significantly when the rate of temperature change is higher than 0.5°C/500 years (t test: $p = 8.82 \times 10^{-7}$, $df = 35$; Figure 6b).

We find weak relationships between landform characteristics and landscape resilience, implying no effects of landform characteristics on landscape resilience. All adjusted R^2 values in the GAM analysis examining landscape resilience (mean values of residence and recovery times at each site) and landform characteristics (mean, range, and standard deviation values of elevation and slope around the site with buffers of 30 and 1 km) are smaller than 0.05 (Table S5).

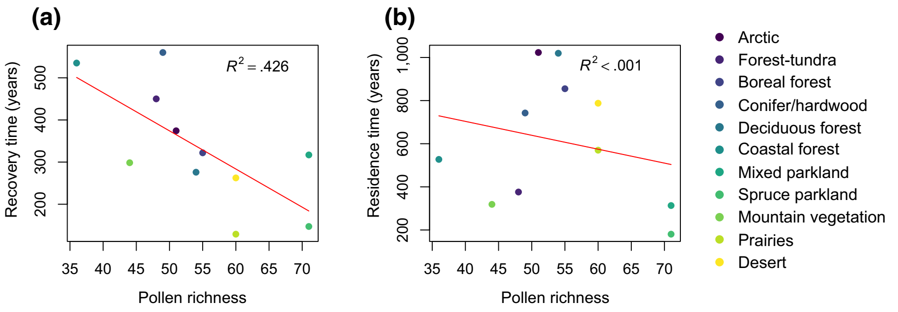


FIGURE 5 Pollen richness impacts on landscape resilience, including residence time (a) and recovery time (b). Residence and recovery times are presented as median values

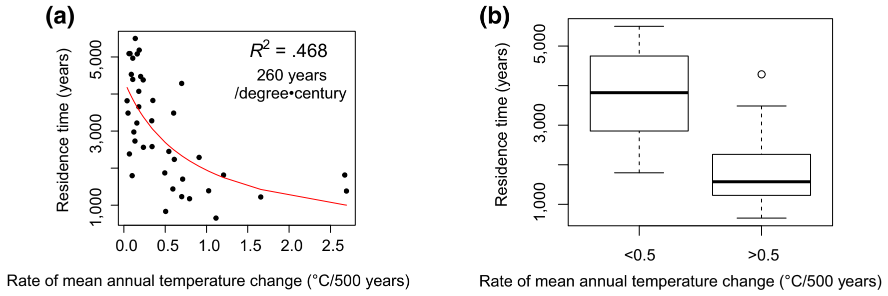


FIGURE 6 Rate of mean annual temperature change on landscape resilience, including generalized additive model analysis (a) and residence times when the rate of temperature change is lower than 0.5°C/500 years and when the rate of temperature change is higher than 0.5°C/500 years (b). Residence time is the median value every 500 years

4 | DISCUSSION

4.1 | The tempo of landscape resilience

Our results quantify the tempo of landscape dynamics, demonstrating that biomes transition rapidly, on the order of hundreds of years. This is the first work to quantify residence and recovery time over long time periods. Other studies have calculated the residence times of temperature using climate velocity within each type of biome, resulting in climate biome residence times on the order of decades (Loarie et al., 2009). Our work differs from these calculations in that we estimate the residence time of the biomes from the biomes themselves, which exhibit ecosystem resilience despite changing climates. Our findings are in agreement with a study examining fossil pollen records in tropical forests, which suggests a recovery time of 210 years following disturbances (Cole, Bhagwat, & Willis, 2014).

The responses of landscapes to climate change are the culmination of individual species responses and species interactions. Species respond individualistically to climate change, and at the continent-scale plant species track climate change (Davis & Shaw, 2001). However, the responses of plant communities to climate change vary due to species disaggregation and recombination (Jackson & Overpeck, 2000). Previous work suggests that biome-level assemblages begin to disaggregate when examined across long timescales, on the order of 10,000–15,000 years (Jackson, 2006; Jackson & Blois, 2015). Our work explores how the landscapes themselves maintain or lose resilience under climate change and species recombination (no-analog plant biomes). Although individual species, ecosystems, or biomes may exhibit their own level of individual resilience, these metrics can be challenging to implement in a conservation context (Allen et al., 2016; Beller et al., 2015, 2019; Chambers et al., 2019). The strength of landscape resilience is that it can identify spatial elements to conserve that will be important for conserving broader scales of biodiversity despite the dramatic environmental changes washing over the continent (Allen et al., 2016; Beller et al., 2015, 2019; Chambers et al., 2019).

Here, we assume that the perturbations resulting in biome transitions are comparable. However, in general, biome types are transitioning all the time in response to many different types of drivers (Figure 4). Some types of biomes may shift in response to smaller, more gradual changes (e.g., changing temperatures); whereas others may require more intense forcing events (e.g., a forest fire). Different types of environmental perturbations (i.e., small, gradual changes vs. large, abrupt events) may lead to different tempos of landscape dynamics. When evaluating landscape resilience on a local scale, the different types and scopes of these drivers can obscure the relationships between individual events and either richness or climate change (Figure S6). However, by analyzing median values (Figure 5), we can distill the general trend of changes and avoid the stochastic influences from transition events that act at smaller spatial scales. Further work considering the specific forcing events that result in biome transitions are needed to understand landscape dynamics and landscape resilience in the perspective of external environmental changes.

4.2 | Landscape resilience drivers

4.2.1 | Biodiversity increases recovery but not persistence

Our work suggests that pollen richness increases landscape resilience by reducing recovery time. This is consistent with previous experimental work, which indicates that species diversity enhances local community biomass recovery by promoting the reestablishment of productivity by the dominant plant species (Reusch, Ehlers, Hämmerli, & Worm, 2005; Van Ruijven & Berendse, 2010). Other work also implies that asynchrony in species recovery times following a disturbance may promote the coexistence of species and enhance recovery rates (Jump & Penuelas, 2005; Lavergne, Mouquet, Thuiller, & Ronce, 2010; Tilman, Isbell, & Cowles, 2014).

Counter to the prevailing ecological theory, our work also suggests that pollen richness does not correlate with residence time. Ecological theory posits that biodiversity increases ecosystem resilience by improving "functional redundancy", allowing a system to maintain stability even if a single or several species are lost (Elmqvist et al., 2003; Folke et al., 2004). But species richness does not necessarily reflect functional redundancy, and as a result may not be correlated with ecosystem stability. We would have anticipated that the relationship between richness and ecosystem resilience would have translated to landscape resilience as well, allowing biomes to persist locally for longer periods of time. However, previous experimental work also suggests that richness stabilizes grassland biomass production but not the relative abundances of species, likely due to strong competitive effects (Tilman, 1996). This translates to the larger spatio-temporal scales of our work where recovery, but not persistence, is affected by richness. Our results also likely result from residence time being influenced by other factors, such as regional differences in climate change during deglaciation. For example, the temperate climates of deciduous forests were relatively stable during deglaciation, resulting in longer residence times.

4.2.2 | Rapid climate change decreases landscape persistence

Rapid temperature changes lower landscape resilience by decreasing residence times. This implies that landscapes do not remain static when climate changes rapidly. These results agree with the short-term evaluation of landscape resilience using satellite data, which indicates that boreal forests and tundra are not resilient to changing climates by shifting to the unstable states of open woodlands (Scheffer, Hirota, Holmgren, Van Nes, & Chapin, 2012). Dynamic vegetation model simulations also suggest widespread vulnerability of ecosystems to current rapid climate change (Gonzalez, Neilson, Lenihan, & Drapek, 2010).

4.2.3 | Landform characteristics do not affect landscape resilience

Our work suggests little effect from landform characteristics on landscape resilience. Several papers demonstrate that gradients of environmental variables—especially slope, aspect, and soil moisture—drive plant community composition and are predictive of how they would shift given environmental change (Whittaker, 1956, 1967). These ideas form the foundation of the one of the core precepts of landscape resilience, that heterogeneous landscapes form the core of climatically resilient regions (Allen et al., 2016; Beller et al., 2015, 2019; Chambers et al., 2019). In recent years, researchers have hypothesized that certain physiographic features can be used to diagnose regions as climatically resilient (Anderson, Clark, & Sheldon, 2014; Theobald, Harrison-Atlas, Monahan, & Albano, 2015). However, our work implies that physiographic features are not related to landscape resilience. Though environmental variables can structure community-level characteristics, climate variables may play a more critical role than physiographic features.

It is possible that the apparently small effect that landform characteristics have on landscape resilience may result from the spatial averaging and the relatively large spatial scale inherent to using pollen data (Prentice, 1985; Sugita, 1993). The source area of fossil pollen assemblages for lake sediments is related to lake basin size and proportions of pollen taxa (Sugita, 1993). For pollen from a lake in a large basin, the source area can be greater than 200 km (Prentice, 1985). This large spatial scale averages the landscape dynamics around the site and decreases the signal of landform characteristics on landscape resilience. Further analyses involving basin sizes and fossil pollen source areas are needed to explore the influences of landform characteristics on landscape dynamics and resilience.

4.3 | The mode of landscape resilience

4.3.1 | Decreased landscape resilience sets the stage for megafaunal extinction

Although it has been hypothesized that climate had destabilized North American ecosystems prior to human arrival (Blois, McGuire, & Hadly, 2010; Delcourt, Haccou, Delcourt, & Delcourt, 2004), our study is able to conclusively demonstrate short residence times and long recovery times in the lead up to these megafaunal extinctions. This rapid turnover would have resulted in locally unstable foraging and habitat conditions for large herbivores. It has been demonstrated that during the deglaciation, ecosystems were able to track changing climates (Jackson & Overpeck, 2000). This indicates that this low landscape resilience belies the high climate resilience of the individual biomes as they shift across the landscape. Nonetheless, the local disruption and decreased landscape resilience as these biomes transitioned, even over relatively short time periods, would have been sufficient to devastate the population sizes and fecundity of many vertebrate species (Chambers et al., 2019; Mann, Groves, Gaglioti, & Shapiro, 2019; Ovaskainen, 2002). Large herbivores are particularly influenced by the unstable foraging habitats, as these taxa require abundant food sources and large habitat areas to support viable populations (Crooks et al., 2017; Ripple et al., 2017). Loss of habitat, indicated by this work and previous works (e.g. Mann et al., 2019), together with other environmental disturbances, including abrupt climate change (Barnosky, Koch, Feranec, Wing, & Shabel, 2004) and human settlement (Smith, Smith, Lyons, Payne, & Villaseñor, 2019), contributed to the megafaunal extinction at 14–11 ka.

Decreases in landscape resilience and herbivore extinctions combine to promote landscape destabilization and trophic collapse. Our work suggests that landscape resilience contributes to megafaunal extinctions, implying “bottom-up” regulation. However, we also see evidence of simultaneous "top-down" regulatory effects. Megafaunal extinction is related to the inability of landscapes to recover to their original states. During and after the extinction event, recovery times were longer, and the recovery probability was low (Figure 4b,c). This could in part result from top-down interactions between herbivores and the plants that rely on them for seed dispersal and forest regeneration, leading to a landscape with low resilience (Chapman, 1995). The temporary no-analog communities resulting from megaherbivore niche release resulted in quick biome transitions and short residence times (Gill et al., 2009; Williams et al., 2001). This indicates that megafaunal extinctions led to rapid changes where plant communities transitioned through multiple alternative states rapidly and took longer to return to their original states. The combination of top-down and bottom-up regulations forms a positive feedback loop and makes landscapes increasingly less resilient: decreases in landscape resilience lead to herbivore extinctions, and then the loss of herbivores reinforce low landscape resilience.

4.3.2 | Recent decreased landscape resilience heralds a sixth mass extinction

Decreases in landscape resilience over the past 3,000 years, resulting from expanding human activities, indicate that today's landscapes may be primed to herald a major extinction event. Although climate remained stable from 10 ka until recently, residence time decreased after 3 ka (Figure 4a). This timing corresponds with the Woodland period when human populations in North America rapidly increased (Peros et al., 2010; Figure 4f), agricultural productivity increased, and societies advanced their cultural development by forming a hierarchical structure (Griffin, 1967). Intensifying human pressure likely facilitated biome shifts and decreased landscape resilience by increasing disturbances. The low residence times and rapid biome shifts, reminiscent of the low resilience at 18–10 ka before megafaunal extinction, may lead to local ecosystem destabilization and species extinctions today. This may be exacerbated by high levels of habitat fragmentation that may prevent plant biomes from exhibiting their inherent resilience by tracking climate across the landscape (McGuire, Lawler, McRae, Nuñez, & Theobald, 2016). Research that has examined recent extinction rates suggest that we are rapidly approaching a sixth mass extinction (Barnosky et al., 2011). Today's accelerated extinction rates may continue to increase if landscape resilience continues to decrease, which is likely as observed decreases in residence times will be further exacerbated as rapid climate change continues. High extinction rates combined with low residence times may again reestablish the positive feedback loop of "top-down" and "bottom-up" regulations, resulting in low landscape resilience and high species extinction risk going forward.

4.4 | Implications of promoting landscape resilience for extinction risk mitigation

Strategies to increase both biome and landscape resilience will help mitigate current extinction risks resulting from local instability. We have demonstrated that the two components of landscape resilience, persistence and recovery, have different sets of drivers. Rapid, significant climate change drives landscapes to transition and decreases the landscape's stability. High biodiversity improves landscape recoverability. Today's increased human pressure may supersede these drivers, making landscapes more vulnerable to environmental disturbances and causing more ecosystem destabilization. Conservation policies focused on these drivers should be prioritized to promote landscape resilience. For example, microrefugia and microclimates that buffer climate change should be identified and preserved as a strategy to increase climate resilience (Maclean, Hopkins, Bennie, Lawson, & Wilson, 2015; Scherrer & Körner, 2011). Strategies of promoting effective urban-nature integration are essential in landscape resilience conservation, given the intensified human pressure today. One effective practice, particularly given the dynamic responses necessary to maintain ecosystem resilience to changing climates, is to increase connectivity across fragmented landscapes. Constructing landscape corridors and expanding reserve sizes to decrease habitat fragment enhances ecosystem resilience by improving recovery capacity (Mumby & Hastings, 2008) and promoting climate connectivity (McGuire et al., 2016). Finally, when disturbances resulting from environmental change today become too strong, the prioritization of regions containing rich ecosystems and high biodiversity will promote ecosystem recovery. To that end, large protected areas have been demonstrated to maintain biodiversity and landscape resilience (Naughton-Treves, Holland, & Brandon, 2005). As we demonstrate here, decreases in landscape resilience contributed to ecosystem destabilization leading up to the megafaunal extinction event. We can learn from this event, and enact strategies that will increase landscape resilience as a way to mitigate the current extinction crisis (Barnosky et al., 2011).

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AUTHOR CONTRIBUTION

Y.W. and J.L.M. conceived the study and designed the experiment. Y.W. collected and analyzed the data. B.R.S. collected the data. D.A.L. and R.P. analyzed the data. J.L.M. supervised the project. Y.W. and J.L.M. led the writing, but all the authors were involved.

DATA AVAILABILITY STATEMENT

The fossil pollen data and the related plant biome information are openly available in figshare at http://doi.org/10.6084/m9.figshare.12673580.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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