

LETTER

Emergence patterns of locally novel plant communities driven by past climate change and modern anthropogenic impacts

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Abstract

Anthropogenic disturbance and climate change can result in dramatic increases in the emergence of new, ecologically novel, communities of organisms. We used a standardised framework to detect local novel communities in 2135 pollen time series over the last 25,000 years. Eight thousand years of post-glacial warming coincided with a threefold increase in local novel community emergence relative to glacial estimates. Novel communities emerged predominantly at high latitudes and were linked to global and local temperature change across multi-millennial time intervals. In contrast, emergence of locally novel communities in the last 200 years, although already on par with glacial retreat estimates, occurred at midlatitudes and near high human population densities. Anthropogenic warming does not appear to be strongly associated with modern local novel communities, but may drive widespread emergence in the future, with legacy effects for millennia after warming abates.

KEYWORDS

anthropogenic warming, dispersal, fossil pollen assemblage, glacial retreat, human impacts, novel ecosystems, post-glacial warming, quaternary, temperature change

INTRODUCTION

Profound anthropogenic environmental change is driving the emergence of previously unseen ecological states across the Earth's biomes (Hobbs et al., 2006). Climate change will increase global temperatures, as well as alter rainfall patterns and seasonality and the prevalence of extreme weather (IPCC, 2021), all of which are expected to increase the rate that new, 'novel', ecological communities appear into the future (Hobbs et al., 2009). Past periods of geological warming also caused ecological change (Nolan et al., 2018): in particular, the warming that drove glacial retreat and the end of the last Ice Age from 19,000 to 11,000 years before present (ybp) (Clark et al., 2012). During this period, average global

temperatures rose by 4°C over the course of 8000 years (Jasechko et al., 2015). This warming led to substantial changes in vegetation (Burke et al., 2019; Finsinger et al., 2017; Mottl et al., 2021; Stivrin et al., 2016), including a peak in communities not present in modern ecosystems (called 'no-analogue' communities) (Overpeck et al., 1992; Williams et al., 2001).

Research into ecological novelty has focused on the management of modern human-degraded systems (Heger et al., 2019; Hobbs et al., 2006) as well as the broad measurement of continuous novelty across space (Burke et al., 2019; Finsinger et al., 2017; Radeloff et al., 2015), identifying mixtures of species unlike any in the past, making comparisons across large, even continental, regions (i.e. 'novel' as 'not observed anywhere else'). This

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aligns with the need to identify past and present communities with no natural precedent in order to understand how to manage modern novel ecosystems (Hobbs et al., 2013). Spreading invasive species, widespread climate change and other human drivers can, however, drive communities into novel states relative to their past, but which already occur in other places (Figure 1). This ‘local novelty’, where a community differs in state is compared to its own past, without comparison to communities in other places, aligns with the reference site-based comparisons made in restoration ecology (Hobbs et al., 2014). Even where locally novel states may have been observed at other locations, profound site-specific compositional shifts can alter the provision of ecosystem services and affect the planning and success of conservation networks and restoration action (Bridgewater & Yung, 2013; Hobbs et al., 2009). In addition, local novelty occurs much more often than community states that are only novel when also compared across space, potentially acting as a more sensitive signal of ecological change (Figure 1). Local novelty has been relatively unexplored from a broader ecological perspective, and there is an opportunity to leverage palaeoecological records to quantify patterns through time and correlate those patterns with environmental drivers (Fordham et al., 2020).

It remains unclear to what extent post-glacial warming increased the frequency that locally novel community states emerged, and how these past patterns compare to recent human-induced instances of novelty. Increases in cross-space novelty have been observed in the actively warming period prior to 10,000 ybp (Finsinger et al., 2017), and in short-term novelty, with divergent temporal patterns between Europe and North America (Burke

et al., 2019). Vegetation change during this period was greater at higher latitudes, reflecting poleward migration of taxa expected in global warming scenarios (Chen et al., 2011; Davis, 1989; Pecl et al., 2017), but also that polar regions warmed substantially more than lower latitudes (‘polar amplification’: Jasechko et al., 2015). In contrast, human landscape modification has dramatically intensified over the last few centuries (Ellis et al., 2010), but, especially in the Northern Hemisphere, predominantly at mid rather than high latitudes (Sanderson et al., 2002).

Disentangling the impact of climate warming and other human impacts on local novelty remains a challenge, in part because lags between drivers and resulting ecological change are extremely common (Jackson & Sax, 2010; Tilman, 1994). Multi-century lags have been observed in climate-driven changes to forestation (Chapin & Starfield, 1997), as well as from contemporary habitat fragmentation (Vellend et al., 2006). These lags can be caused by taxa generation times, dispersal limitation and interspecific interactions (Jackson & Sax, 2010). Abiotic change such as climate warming shifts species ranges, principally via migration (Webb & Bartlein, 1992), altering the pool of potential taxa that can disperse into a community, adding and removing species from the regional pool (Blonder et al., 2015; Lenoir et al., 2020). Warming also directly impacts local environmental and biotic filters, changing not only temperature but also precipitation patterns, disturbance regimes and food webs (COHMAP members, 1988; Gill et al., 2009; IPCC, 2021). Biotic responses to past periods of warming lagged behind observed temperature change, particularly because climate change

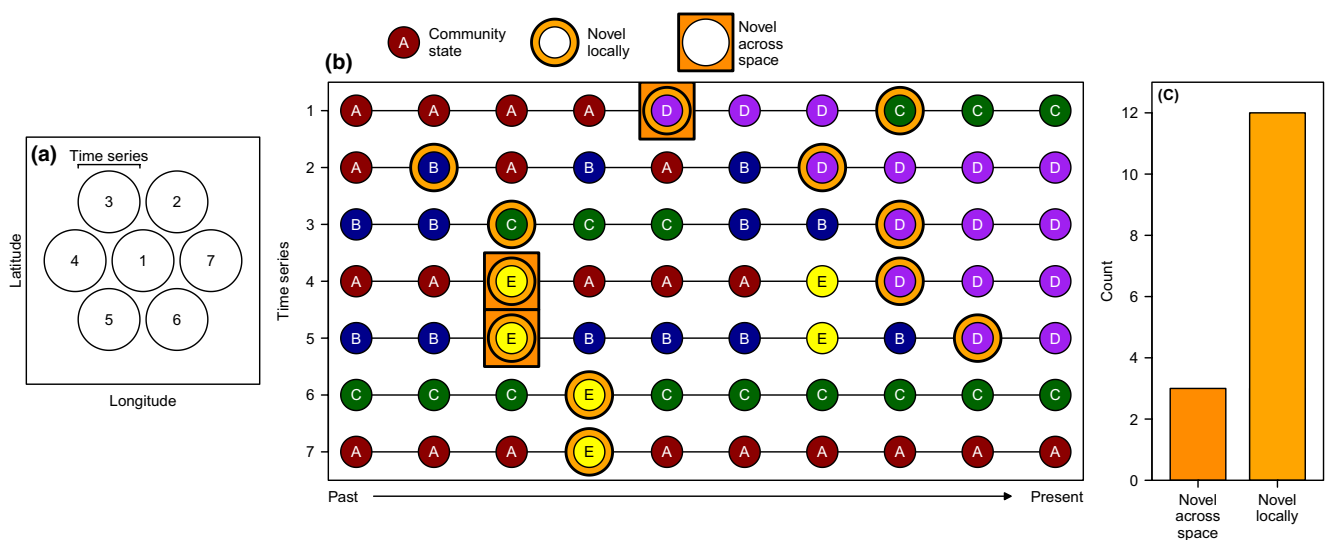


FIGURE 1 Examples of differences between the emergence of ‘local’ and ‘cross-space’ novel communities. (a) Example data are time series from spatially clustered communities. (b) Community time-series samples from past to present, with five different potential community states. Communities are locally novel if they are a state that has not been observed prior in the time series; novel across space classifications are reserved for states that have not been observed prior in any time series. While all communities that are novel across space are also locally novel (c), there are additional locally novel communities that reflect the spread of an invasive species (state ‘D’) or transient community states that occasionally occur in different time series (state ‘E’)

velocity exceeded dispersal rates (Blonder et al., 2015; Normand et al., 2011). In some cases, the lag between climate warming and plant community response extended to multiple millennia, especially in taxa with limited dispersal (Butterfield, Holmgren, et al., 2019; Davis, 1989).

Community responses to environmental change likely differ based on composition and life histories. Grasslands and forests, for instance, will have different rates of ecological change, and therefore, different expectations for what is sufficient change to be ‘novel’. We have developed a framework that standardises the measurement of local novelty onto probability scales, using site-specific expectations of ecological change that can change flexibly over time (Pandolfi et al., 2020). In this

manner, we can extend the two continuous measures of novelty used in past palaeoecological work, which quantified both short- and long-term novelty (‘transient’ or ‘instantaneous’ and ‘accumulated’ or ‘cumulative’ novelty, respectively) within each time series (Burke et al., 2019; Pandolfi et al., 2020). Our method detects the emergence of a local novel community as a time point along a time series in which rapid, punctuated and divergent ecological change occurs (Figure 2). This approach differs from novelty considered across space and from methods that cluster points along time series based on similarity of community composition (as in pollen zonation) or present to past methods that detect the last occurrence of a state with no modern comparison (Overpeck et al., 1992) (Figure 2).

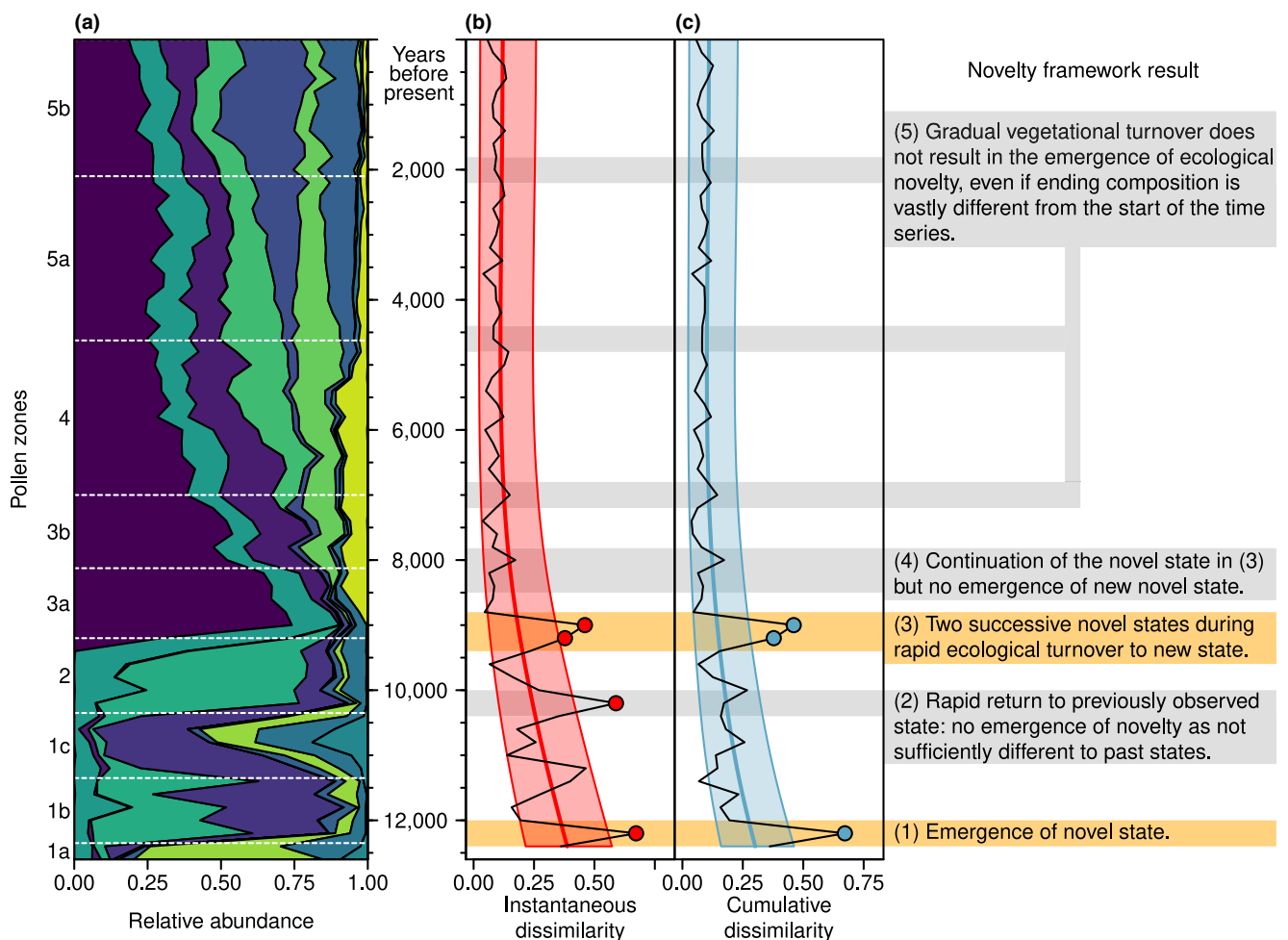


FIGURE 2 Comparison of local novel community detection framework, genus relative abundance and pollen zonation for a single time series. (a) Genus-level pollen relative abundance for site in Lough Mallaghlan, Republic of Ireland, at a 200-year resolution over the past c. 12,500 years. Pollen zonation (labels and dashed white lines) were determined by Fossitt (1994). (b–c) Two sets of Bray–Curtis compositional dissimilarities for the time series. (B) Rate-of-change along the time series, using the compositional dissimilarity between each community and the one immediately prior. (c) Dissimilarities between each time point and the most similar past composition in the time series (larger values reflect greater dissimilarity to past states). Coloured lines and polygons are mean and 95% quantiles of expected dissimilarities, respectively, which can increase or decrease along the time series to track changes in community dissimilarities. Observed dissimilarities exceeding the upper 95% quantile of both sets of expectations are classified as ‘novel communities’ (labels (1) and (3) in orange). Time points where only one dissimilarity exceeds expectations do not qualify as ‘novel communities’, even though they exhibit one of the two novelty signals (as in label (2) in grey). Labels (2), (4) and (5) indicate points where pollen zonation boundaries do not reflect the emergence of novel communities. This process was conducted separately for all time series in the processed Neotoma data set

We applied our framework to detect the emergence of locally novel plant communities over the last 25,000 years across Europe and North America, using 2135 pollen assemblage time series housed in the Neotoma Paleoecology Database (Williams et al., 2018) (Figure S1). With 1259 local novel communities detected by this framework, we asked the following questions:

1. Did the emergence probability of locally novel communities rise during the Pleistocene–Holocene post-glacial warming, and how did past patterns compare to the modern day (1850 AD onwards)?
2. Do latitudinal emergence patterns of past and modern local novel communities reflect warming-driven expectations?
3. (a) Did emergence of local novel communities correlate with change in local and global temperatures, (b) which temperature change time interval best describes local novelty patterns and (c) were these intervals consistent across Europe and North America?

MATERIALS AND METHODS

All data processing and analyses were conducted in R version 4.1.2 (R Core Team, 2021). Model summaries, diagnostic tests, supplementary analyses and extensive sensitivity analyses used to assess potential biases are available in the [Supporting Information](#).

We accessed the Neotoma Paleoecology Database on 24 July 2020 using the *neotoma* R package (Goring et al., 2015; Williams et al., 2018), and after cleaning and processing (see Supplementary Methods), retained pollen count data from 2135 sites. These sites comprise single or multiple sediment cores, most often from lake sediments, at a single geographic location (herein referred to as ‘time series’). For each time series, we summed pollen observations at the plant family level within 200-year sampling bins and converted them to relative abundances (square root transformed). For each time series, we converted family abundance matrices into time series-specific dissimilarity matrices, calculated using Bray–Curtis (Bray & Curtis, 1957) (*vegdist* function, *vegan* package: Oksanen et al. (2022)). We refer to the pollen data contained within a time series as a ‘community’, with changes in composition over time as alterations to the ‘community state’. We chose this term to align with the concept of ‘novel communities’, although we acknowledge that the compositional data used are likely reflective of assemblages rather than full communities (Stroud et al., 2015).

We applied our novel community detection framework to each time series dissimilarity matrix in the processed Neotoma data set (Pandolfi et al., 2020). Our framework quantified two components of ecological change.

The first component was the dissimilarity between pairs of bins along the time series, akin to rate-of-change in composition along the time series and complementary to ‘transient novelty’ in Burke et al. (2019), except restricted to within each time series. The second component estimated the ‘novelness’ of the community, measuring the dissimilarity between each bin and all previous bins in the time series (high values = greater novelness). These are similar to ‘accumulated novelty’ used in Burke et al. (2019) and novelty as used in Radeloff et al. (2015), except our measurements were made through time for a given space, rather than across space for a given window of time (Pandolfi et al., 2020). In this manner, each sampling bin in a time series had a single accumulated novelty value.

Our framework uses a parametric spline-based model for each set of dissimilarities in each time series, standardising raw measurements of novelty into probability-based expectations (generalised additive models fit using the *mgcv* package in R (Wood, 2017)) (Figure 2b–c). These expectations were relative to each time series, and also through time, as the flexible spline terms allowed expected dissimilarities to rise and fall along the time series. These models were used to generate one-tailed 95% predictive intervals for each sampling bin in each time series. Sampling bins in which both dissimilarity scores exceeded those thresholds were classified as ‘local novel communities’ (Figure 2b–c). This resulted in local novel communities detected as probabilistic outliers of standardised expectations that were local in both space (per time series) and time (changes in splines across the time series).

Statistical analyses

Emergence probability of novel communities through time

We estimated the probability of local novel community emergence using a binomial generalised additive model (GAM: logit link, *gam* function, *mgcv* package (Wood, 2017)), fit with all data from 25,000 to 1000 ybp. The response variable in this model was binary, treating local novel community emergence as successes. This model contained one main fixed effect, the centre of each 200-year sampling bin, fit as a continuous thin plate spline. We also included five covariates to account for potential bias on novel community detection (herein ‘novelty covariates’): (1) time lag between adjacent sampling bins in each time series (ln-transformed ybp), (2) sampling bin position along the time series (ln-transformed, increasing from the earliest bin of the time series), (3) time series length (ln-transformed, count of sampling bins in each time series), (4) time series gamma diversity (ln-transformed, total number of families observed along

the time series) and (5) site elevation (ln-transformed, metres above sea level). The rationale and effect of novelty covariates are outlined in detail in the [Supporting Information](#). To examine recent local novel community emergence in more detail, we modelled the emergence probability of local novel communities separately for the six most recent sampling bins: those centred at 0, 200, 400, 600, 800 and 1000 ybp. These bins were fit as a six-level categorical fixed effect, setting the modern bin (centred at 0 ybp) as the reference level. We used a binomial generalised linear model (GLM: logit link) and included novelty covariates. We also conducted variants of both models, fitting separate main effects to Europe and North American continental regions.

Palaeotemperature correlation

We tested for a correlation between the emergence of local novel communities and both global temperature and local temperature change. We used two global temperature reconstructions which covered our study period: Kaufman et al. (2020), which covers 12,000 ybp to 1950 AD, and Shakun et al. (2012), covering 22,000–6500 ybp. The Shakun et al. (2012) temperatures were temperature anomalies relative to the 6500–1500 ybp mean, while Kaufman et al. (2020) temperatures were temperature anomalies relative to 1961–1990 AD. We corrected the Shakun et al. (2012) temperatures to the same scale by adding the 11,500–6500 ybp mean from Kaufman et al. (2020) to all observations, including only Shakun et al. (2012) observations from 22,000–12,000 ybp (beyond the overlap with Kaufman et al. (2020)). We used a local scale palaeoclimate model, CHELSA-TraCE21k v1.0 (Karger et al., 2021), to obtain estimates of local temperature. This product modelled temperature at a 30'' scale in 100-year time steps across the last 21,000 years. We extracted local temperature conditions for each time series using longitude and latitude coordinates (extract function, raster package (Hijmans, 2022)).

We interpolated both temperature data sets to obtain estimates that matched our 200-year sampling bins. For global temperatures, we interpolated between the two reconstructions using a single GAM. For local temperatures, we fit separate GAMs to the 100-year temperature estimates at each time-series location. In all models, we predicted temperatures every 50 years along splines, starting at –50 ybp (2000 AD). Each 200-year sampling bin was represented by the mean of four temperature predictions spaced 50 years apart, except for the modern bin centred at 0 ybp, which was represented by three (i.e. at 1900, 1950 and 2000 AD).

Local novel communities likely emerged in response to changing climate conditions, rather than the magnitude of temperature (as in species range shifts Davis,

1989; Pecl et al., 2017). Despite this, it is unclear what temporal scale of temperature change best correlated with novelty, as dispersal and local-scale processes operate with substantial time lags. We tested multiple measures of temperature change, calculated with different time intervals, to identify the best correlate of local novel community emergence. We fit 625 candidate models, one model for each combination of global and local temperature change at intervals from 200 to 5000 years, in units of 200 years. Temperature change was calculated as the mean temperature for each 200-year sampling bin minus the mean temperature for a past bin, matching each time interval (e.g. a 400-year time interval used average temperature in the n-2 bin to estimate temperature change). These global and local temperature changes measures were fit as fixed effects in a binomial GLM along with their interactions and novelty covariates (logit link). All models were fit with the same subset of observations; we excluded sampling bins prior to 17,000 ybp in all models, as these did not have temperature change estimates at a 5000-year time interval. We also excluded the most recent three sampling bins (centred at 0, 200 and 400 ybp) from models to reduce the influence of their strong human signature on temperature change correlations. Best-fitting global and local temperature intervals were evaluated via AIC (Akaike, 1974). We also examined residuals from the best-fitting model. Given our binary response variable, residuals were bimodal. We subtracted the mean residual value for successes and failures from all residuals, which centred them while preserving any temporal signal.

We repeated this model selection process, allowing the time intervals for global and local temperature change to differ between Europe and North America. Given this exponentially increased the number of model combinations, we fit time intervals in units of 1000 years (to a maximum of 5000 years) to maintain the number of candidate models at 625.

Latitudinal differences in novel community emergence

We modelled novel community emergence probabilities across both time (ybp) and latitude, fitting these variables as a two-dimensional tensor product smoother in a binomial GAM (t2 function, mgcv package (Wood et al., 2013; Wood, 2017)). We also modelled probabilities across the six most recent sampling bins and latitude. We used a binomial GAM fit with a two-dimensional tensor product smooth, as per the previous latitude model, treating time and latitude as continuous variables. Both models included all novelty covariates, and we ran a variant of models with separate intercepts and smoothers for Europe and North America.

RESULTS

Local novel community trends over time

Prior to the start of the glacial retreat, the emergence probability of local novel communities was low and stable, but rose to three times higher during subsequent warming (Figure 3a). The peak of post-glacial emergence probability occurred at 10,000 ybp, preceded by *c.* 8000 years of accelerating novel community emergence (Figure 3a). After this peak, emergence probability decreased over the subsequent 3000 years during the early Holocene Thermal Maximum (Figure 3a). Emergence probabilities over the most recent millennia were similar up until the bin centred at 400 years ybp (from 1450 AD onwards) (Figure 3b). The probability of modern and pre-modern novel community emergence exceeded prior estimates back to the peak of the post-glacial period (Figure 3a–b). Disaggregating pollen into genera to detect novel communities amplified the magnitude of

the post-glacial peak relative to family-level results presented here, especially in North America, and slightly depressed the probability of modern novel communities emerging (Figure S9).

Local novel community emergence trends over time were similar between European and North American continental regions (Figure 3c, d). Both regions showed increases during the glacial retreat, with Europe trends peaking twice, with the second *c.* 1000 years after the North American peak. Post-peak decreases during the Holocene Thermal Maximum were also similar in both regions until *c.* 3500 ybp (non-overlapping 95% confidence intervals in Figure 3c). After this time, the North American emergence probability continued to decline over 2000 years to *c.* 0.5%, while European probabilities stabilised at *c.* 2–3% (Figure 3c). In the most recent millennium, the observed global increase in emergence probability was driven entirely by North America, with modern-day European emergence probabilities no different from earlier sampling bins (Figure 3d).

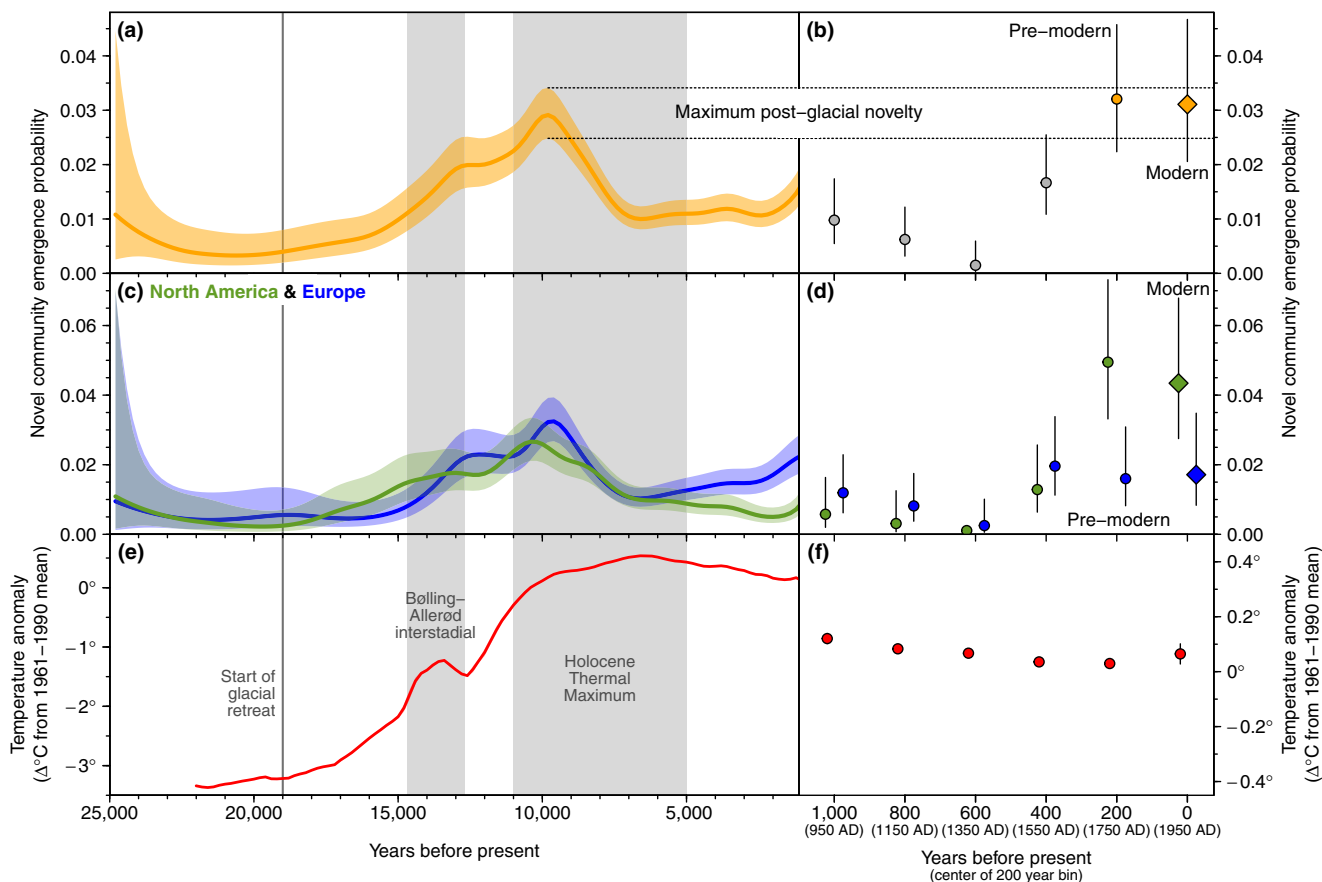


FIGURE 3 Trends in emergence probability of novel plant communities and global temperature over the last 25,000 years. Spline in (a) is mean predicted probability of a local novel community emerging in a given 200-year sampling bin, with 95% confidence intervals (Figure S2; Table S1). Estimates in (b) are separate mean probabilities for the last six sampling bins, with 95% confidence intervals (Table S2). (c) and (d) are equivalent to (a) and (b), fitting separate splines to North America and Europe (green and blue respectively). (e) Surface temperature estimates derived from global reconstructions (Kaufman et al., 2020; Shakun et al., 2012). Points in (f) are mean surface temperature estimates for each sampling bin from Kaufman et al. (2020). Timing of the start of the glacial retreat (Clark et al., 2012), Bølling-Allerød interstadial (Thiagarajan et al., 2014) and Holocene Thermal Maximum (Renssen et al., 2012) are indicated in grey

Latitudinal and human density patterns of local novelty community emergence

Post-glacial warming resulted in elevated novel community emergence at all latitudes (Figure 4a; Figure S7), with highest probabilities concentrated at high latitudes (Figure 4a). In modern bins, we only observed elevated probability of novel community emergence at mid latitudes (Figure 4b). Both of these patterns were conserved in the continent-specific trends, although European emergence probabilities in the post-glacial warming were concentrated at latitudes $>45^\circ$, while elevated probabilities were observed at all North American latitudes (Figure S7). European emergence probabilities in the modern bin were elevated at midlatitudes, but were only a fraction of the North American latitudinal peak (Figure S7). Modern novel community emergence was significantly correlated with nearby human population density, with a tenfold increase in probability from 0 to 1000 people km^{-2} (Figure S5).

Correlation with temperature change

Local and global temperature change variables were positively correlated but did not lead to multicollinearity:

Correlation coefficients were ≤ 0.58 and variance inflation factors were < 1.51 across all interval combinations. Both local and global temperature change were strong predictors of local novel community emergence (Figure 5a–b). The likelihood of a local novel community emerging was best predicted by the global temperature change over 2800 years, and local temperature change over 5000 years (Figure 5a). Global and local temperature change had a significant positive interaction effect (Figure 5b). Sampling bins during periods of global temperature change that were not experiencing local change, and those with local change during periods of global stability, were not associated with high probabilities of local novel community emergence (Figure 5b).

Prior to 8000 ybp, residuals from this model were negative, indicating that local novel communities were generally rarer than predicted by temperature change (Figure 5c). Residuals shifted directions at 8000 ybp, and subsequent residuals were positive, indicating greater observed novel community emergence than predicted by temperature change alone. Consistently from 5000 ybp onwards, 95% of residuals were positive, indicating a poor fit of observed novelty patterns to temperature change expectations.

Fitting separate temperate change intervals and separate model intercepts and slopes to North American

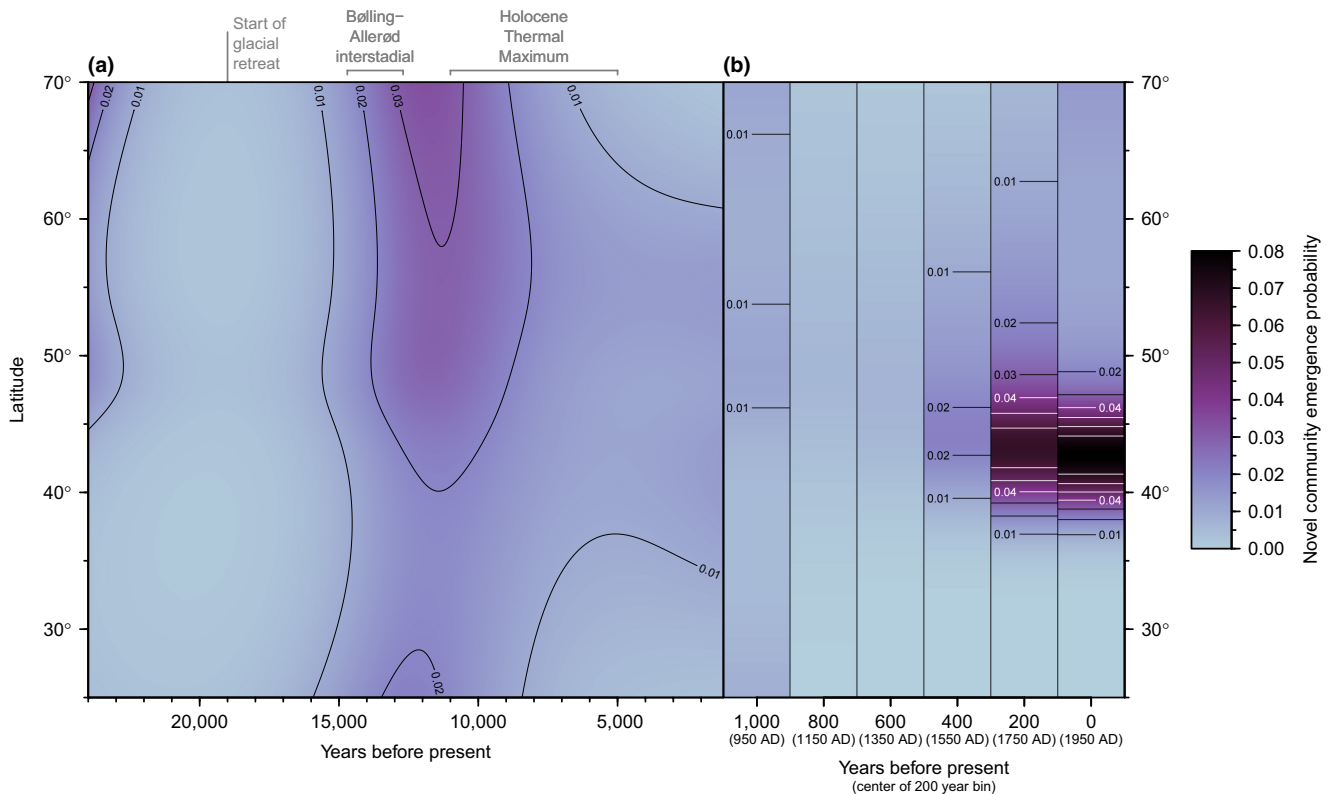


FIGURE 4 The probability of local novel community emergence over latitude and time. Separate models were fit to (a) sampling bins between 1000 and 25,000 years before present (Table S8), and (b) the six most recent 200-year sampling bins (Table S8). White contours were only used to increase contrast against dark gradient colours. Sampling and 95% confidence intervals are shown in Figure S6

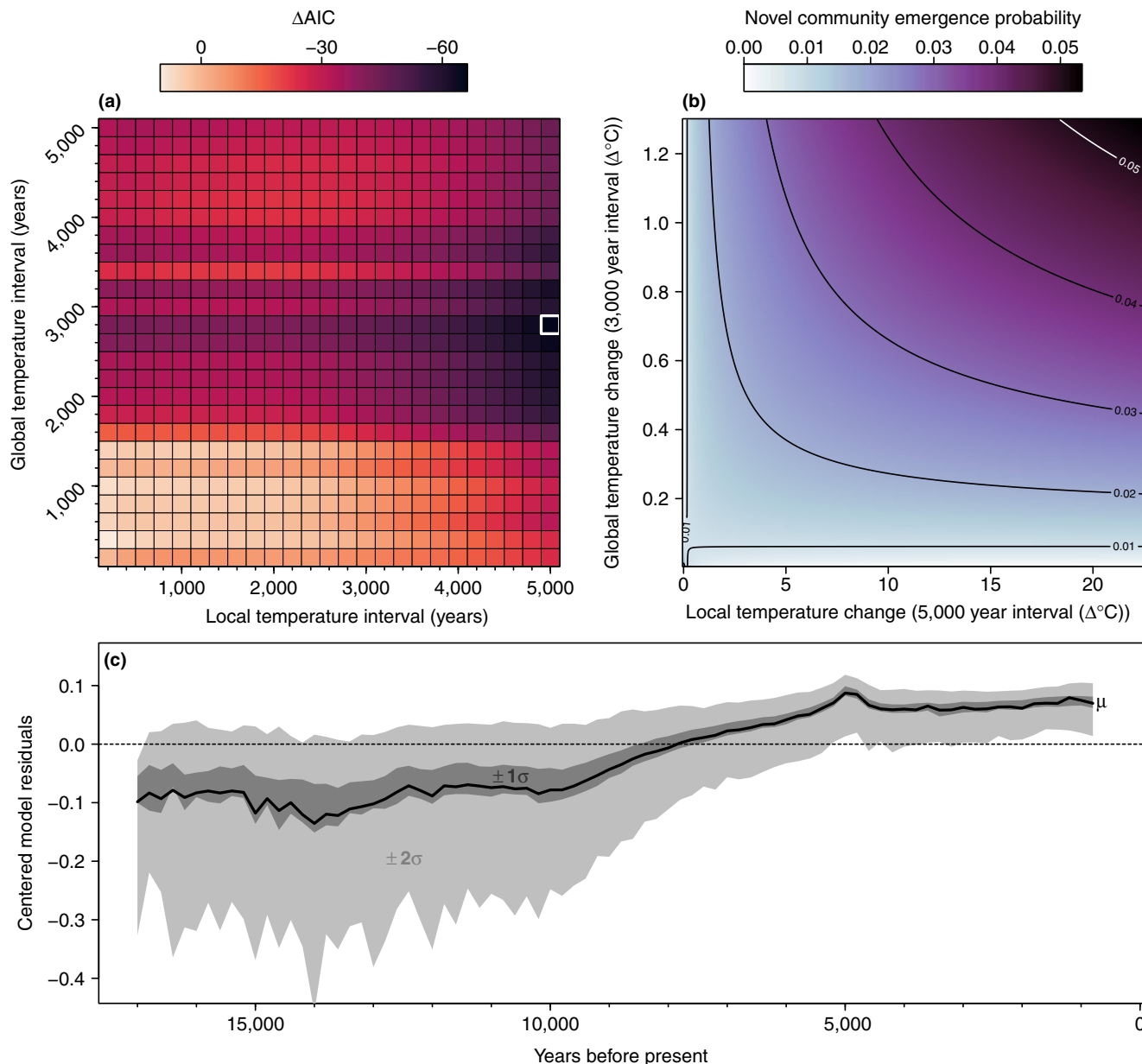


FIGURE 5 Model selection of temperature change time intervals that best correlated with the emergence of local novel communities, interaction surface and temporal patterns of model residuals (Table S5). (a) Change in AIC for models fit with differing time intervals for global and local temperature change variables, relative to the model fit with 200-year intervals. Each square reflects a separate logistic generalised linear model fit with different temperature change intervals to the same local novelty data. Best-fitting model is outlined in white. (b) Interaction between global and local temperature change was positive, indicating a multiplicative effect of both main effects on the probability of a local novel community emerging. (c) Residuals from best-fitting temperature change model over the study period, thresholds at one and two standard deviations above and below mean displayed

and European time series improved in AIC relative to the global model ($\Delta AIC = -36.5$). This regional model provided global and local temperature interaction surfaces that accorded with the global model (Figure S4), but the best-fitting global time intervals differed across continents. Local novelty in Europe was best explained by global temperature change over 3000 years, compared to 2000 years in North America, while the best-fitting local temperature interval was consistently 5000 years for both continents (Figure S4).

DISCUSSION

Climate warming from the recent geologic past was linked to a marked increase in the rate that local novel ecological communities emerged, with temporal patterns that aligned consistently across Northern Hemisphere continents. These patterns do not reflect the already well-documented gradual community change associated with this warming (Overpeck et al., 1992), trends in turnover rate (Mottl et al., 2021)

or novelty as assessed via continental comparisons (Burke et al., 2019). Instead, we uncovered increases in the occurrence of rapid, punctuated compositional change to novel states relative to each community's past. Emergence of these local novel communities correlated with both global and local change in temperatures over substantial, multi-millennial time intervals, reflective of the slow pace of post-glacial temperature change, delayed migration and subsequent changes to local abiotic and biotic regimes. These palaeoecological patterns predict large increases in local novel communities into the future as anthropogenic climate change manifests, potentially for thousands of years after warming abates. We also identified evidence that human impacts over the last 400 years coincided with rates of local novel community emergence that are already elevated and similar to observations during the global warming that ended the last Ice Age. Patterns in the last 400 years do not accord with either temperature change or latitudinal expectations, supporting the conclusion that current human-driven ecological novelty is primarily a product of non-climatic impacts.

Novel community emergence is driven by both global warming and human landscape modification

We identified a threefold increase in the rate that local novel communities emerged relative to pre-warming icehouse conditions, globally and separately across Europe and North America. This similarity between Northern Hemisphere continents was largely undetectable in cross-space measurements of novelty that tracked raw compositional dissimilarities from different sites (Burke et al., 2019) (Supporting Information). In this past work, stark differences in European and North American trends in novelty over time were explained in terms of differing geography and climate (Burke et al., 2019). The primary difference between the Burke et al.'s (2019) methodology and ours is our correction of novelty for site-based expectations ('standardisation'). Post-standardisation, we uncovered cross-Atlantic trends that hint at a single underlying ecological response in the rate and timing of local novel community development in the wake of global warming. Separate work examining peaks in rate of vegetation turnover during the same time period were consistently earlier in time than those in our study (Mottl et al., 2021). This contrast suggests that rate of vegetation change and emergence of locally novel community states, while likely somewhat correlated, have different temporal patterns during the glacial retreat. In all these cases, knowledge of past community states only extends as far as the pollen core, mostly to a point during the glacial maximum or the glacial retreat. Some of the novel communities we detected may have been present beyond the

start of the time series further into the past (i.e. the last interglacial), and may not have been novel if the time series encapsulated these earlier states.

The breakdown of synchronised patterns in novel community emergence between Europe and North America between 13,000 and 9000 ybp, and from *c.* 3000 ybp onwards highlights the valuable insights that can be gleaned from the study of palaeoecological resources (Fordham et al., 2020). The 4000 years following the Bølling–Allerød interstadial includes the Younger Dryas, a sudden return to cooler temperatures that was especially strong in Europe (Clark et al., 2012). This climatic instability may have induced the higher probabilities of local novel community emergence in Europe relative to North America (Figure 3c). After 3000 ybp, North American novelty declined while European novelty stabilised at *c.* 2–3%, culminating in a rapid increase in present-day North America that was absent in Europe. The higher rate of European novelty across recent millennia likely reflects its long history of human landscape modification. Extensive European deforestation has been documented from 3000 year ago (Kaplan et al., 2009; Roberts et al., 2018), almost exactly when North American and European emergence probabilities diverged in our results. Widespread human landscape modification has been cited as causing high rates of cross-space novelty in Europe over the last few millennia (Finsinger et al., 2017). Our results accord with this explanation. Our combined North America and European trends highlight this explicitly, with synchronised post-glacial trends that only deviated when human impacts intensified in Europe. Our results support the conclusion that human landscape transformation is detectable in palaeoecological records (Nogué et al., 2021).

Links between local novel community emergence and global and local temperature change

The latitudinal differences between present day and past warming suggest a non-climatic origin for many modern novel communities. Past novel community emergence aligned with warming-driven expectations, with elevated probabilities of local novel communities in higher latitudes across both continents. Over the last 400 years, we observed increased novel community emergence probability only at midlatitudes, a sharp contrast with these post-glacial, 'climate-only', patterns. Many species, particularly long-lived taxa like trees, are not currently exhibiting expected climate range shifts (Bertrand et al., 2011; Zhu et al., 2012) and the numerous species undergoing range shifts (Lenoir et al., 2020; Lenoir & Svenning, 2015; Pecl et al., 2017) may still be rare at their leading edge. While potential maladaptive responses of dominant species to climate change may accelerate their

decline (e.g. Snell-Rood et al., 2018), it may still take generations for community composition to alter to the point where novelty, as outliers of expectations of community-level turnover, is detectable.

Past climate warming has been well documented as driving the loss of past plant community types (Overpeck et al., 1992; Williams et al., 2001) and vegetation change (Chapin & Starfield, 1997; Iglesias et al., 2018; Mottl et al., 2021). More recent studies of vegetation novelty found climate links to within-site rates of turnover (Finsinger et al., 2017) and short-term cross-space measurements of ecological novelty (Burke et al., 2019). Our results build on this past work, finding that global warming appears to create a legacy effect of ecological inertia that continues to drive rapid, locally novel community change for thousands of years after temperatures stabilise (Figure 3a). When broken down into the time intervals of global and local temperature change, the emergence of local novelty best correlated with multi-millennial time intervals. This is likely a combination of both the slow pace of past global warming, as climate disequilibrium gradually accumulated to drive range shifts and altered local scale filters, and ecological lags between these drivers and resulting ecological change. Long colonisation lags in the order of millennia have been observed as taxa ranges shifted in response to climate disequilibrium (Butterfield, Holmgren, et al., 2019), particularly via rare long distance dispersal events (Cain et al., 1998, 2000; Clark, 1998). The best-fitting global temperature change intervals in our model may reflect that, on average, multiple millennia were required for taxa to disperse via these rare events, and then alter site relative abundances sufficiently and fast enough to be detected as a local novel community.

All temperature change models predicted elevated probabilities of local novel community emergence where sites exhibited both a local temperature change across a long time interval, during a period of global temperature change. As with the global time interval, instances of local novelty were best explained by local temperature change across a millennial scale (5000 years). This suggests that in the absence of extreme human land modification, local and larger scale environmental forcing were requirements for most instances of local novelty to occur. In terms of community assembly, this result suggests it is generally insufficient for re-assortment of the regional species pool to drive novelty in the absence of local environmental change, or for abiotic change to drive novelty in the absence of larger scale ecological re-assortment. This reflects the joint consideration of environmental conditions and species composition made in early frameworks of novel ecosystems (Hobbs et al., 2009).

Despite similarly shaped interaction effects, global temperature change compared to 3000 years prior provided the best fit for the emergence of local novel communities in Europe, compared to only 2000 years in North America. This longer European time interval

was likely driven by stronger dispersal barriers during the post-glacial period. The east–west oriented Alps, the Pyrenees and Balkan alps and even the Mediterranean Sea, all acted as strong dispersal barriers for poleward migration during the post-glacial (Petit et al., 2002; Taberlet et al., 1998). These barriers may have delayed both dispersal-based migration and reduced the probability of long-distance dispersal (Alsos et al., 2007), particularly when the Alps were still ice-covered (Hewitt, 1999). By contrast, the north–south orientation of mountain ranges in North America may have aided post-glacial dispersal, or at least not acted as an impediment (Comes & Kadereit, 1998). This difference in dispersal barriers may have been reflected in the 1000-year difference in global temperature change time interval that best explained North American novel community emergence relative to Europe.

Our models assumed temperate change was a direct correlate of novel community emergence, or at least acting as a proxy for other abiotic drivers. After temperatures stabilised, flow-on changes to other climatic conditions, such as rainfall patterns (IPCC, 2021), disturbance regimes or higher trophic interactions (Gill et al., 2009), may have been the ultimate drivers of local novelty, resulting in an overestimate of the actual lag between the true abiotic driver and resulting local novelty. In spite of these potential limitations, past work has identified links between temperature change and ecological change, including a shift from positive to negative temperature change correlations like that observed in the residuals from our temperature change model (Finsinger et al., 2017).

The future of local novel community emergence

Our results highlighted warming as a major driver of local novel community emergence prior to the industrial period. Predictions of global temperature increases by 2100 AD are within the bounds of the post-glacial warming (Clark et al., 2012; Sherwood et al., 2020), suggesting that anthropogenic warming may be accruing a similar potential for elevated levels of warming-driven local novelty. In spite of this, observed dispersal during the Pleistocene–Holocene boundary exceeded the maximum expected (Clark, 1998; Huntley, 1991), and the temperature change time intervals that best described local novelty in our results were 2000 years at their shortest. This suggests that novelty inertia generated by anthropogenic warming may not be fully realised until long after 2100 AD, even in the unlikely event that modern plant taxa can track warming without impediment (Robillard et al., 2015).

Our past-to-present patterns, alongside the broad response of ecosystems to anthropogenic climate change (Scheffers et al., 2016), suggest that anthropogenic warming will increasingly contribute to the emergence of

locally novel community states. The rate of emergence in the future will likely exceed any point in the recent geological past, as the impact of climate change compounds with increasingly intense and pervasive human activities that open more regions of the Earth to intensive management (Schramski et al., 2015). The ultimate legacy of the post-glacial warming was multiple millennia of elevated local novelty, long after temperatures stabilised. Even if warming is arrested at best-case 2100 AD predictions, or non-climate human impacts were to immediately cease, these past trends suggest that our actions will drive widespread ecological novelty for millennia into the future. While we define local novel communities in terms of ecological change, and make no judgement about a novel community's value, either in humans or ecological terms, high rates of local novelty will alter the conservation, economic and social value that are provided by the natural systems we rely on.

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CONFLICT OF INTEREST

Authors declare no competing interests.

AUTHOR CONTRIBUTIONS

The ideas for the paper were conceived by all authors; TLS undertook all analyses and developed analytical approaches with input from JMP and WK; TLS and JMP wrote the paper with contributions from WK.

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DATA AVAILABILITY STATEMENT

R code to download and process Neotoma Paleoecology Database data, conduct all analyses and produce all tables and figures are available at Zenodo (<https://doi.org/10.5281/zenodo.6456616>).

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SUPPORTING INFORMATION

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