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Differing climatic mechanisms control transient and accumulated vegetation novelty in Europe and eastern North America

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Understanding the mechanisms of climate that produce novel ecosystems is of joint interest to conservation biologists and palaeoecologists. Here, we define and differentiate transient from accumulated novelty and evaluate four climatic mechanisms proposed to cause species to reshuffle into novel assemblages: high climatic novelty, high spatial rates of change (displacement), high variance among displacement rates for individual climate variables, and divergence among displacement vector bearings. We use climate simulations to quantify climate novelty, displacement and divergence across Europe and eastern North America from the last glacial maximum to the present, and fossil pollen records to quantify vegetation novelty. Transient climate novelty is consistently the strongest predictor of transient vegetation novelty, while displacement rates (mean and variance) are equally important in Europe. However, transient vegetation novelty is lower in Europe and its relationship to climatic predictors is the opposite of expectation. For both continents, accumulated novelty is greater than transient novelty, and climate novelty is the strongest predictor of accumulated ecological novelty. These results suggest that controls on novel ecosystems vary with timescale and among continents, and that the twenty-first century emergence of novelty will be driven by both rapid rates of climate change and the emergence of novel climate states.

This article is part of a discussion meeting issue ‘The past is a foreign country: how much can the fossil record actually inform conservation?’

1. Introduction

Conservation biologists, tasked with stewarding biodiversity during the Anthropocene, face the challenge of managing systems during a time of rapid environmental change and the shifting of the climate system to a state unlike any in societal experience. Atmospheric CO₂ is now comparable to Pliocene levels [1] and, if rises continue, may lead to a hothouse future [2] the likes of which our planet has not experienced for tens of millions of years [3]. This raises questions about the adaptive capability of socioecological systems [4], the stabilizing or destabilizing effects of Earth system feedbacks [5,6], and how best to help species and ecosystems adapt

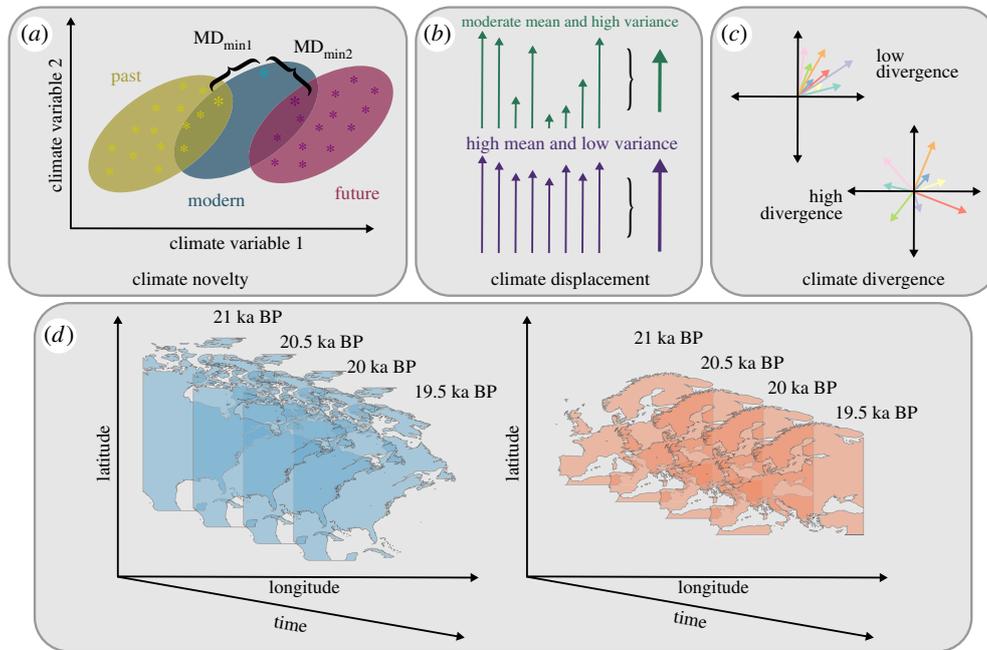


Figure 1. Schematic of climatic mechanisms that can generate novel mixtures of species (*a–c*, adapted from [27]), and spatio-temporal domain of this study (*d*). (*a*) Novel climates can enable novel mixtures of species by opening up new portions of climate space and new portions of overlap among fundamental niches of species. Climate novelty is measured by assessing the dissimilarity between the climate for a single location for one time period and its closest analogue among all locations in a reference baseline. Climate novelty can be assessed among present, past and future climates. (*b*) Climate displacement estimates the mean spatial rate of movement of individual climate variables based on the magnitude component of climate velocity vectors. Climate displacement can produce novel communities in two ways. First, if mean displacement is high and species distribution shifts differentially lag behind these rapid climate changes owing to interspecific differences in dispersal. Second, if displacement variance is high and species vary in their sensitivity to individual climate variables, causing them to be pulled to varying degrees. (*c*) Climate divergence represents the standard deviation in the direction of climate velocity vectors and, like displacement variance, can produce novel mixtures of species. All four mechanisms were mapped for Europe and eastern North America at 500-year intervals from 21 to 0 ka BP, at 50 km spatial resolution, using climate simulations derived from the CCSM3 SynTrace experiments [28–30].

to recent and projected climate changes via assisted migration, assisted evolution or other climate-targeted solutions in ecological renovation [7].

One expected outcome of current climate trends is the rapid reshuffling of species into novel mixtures. The mutability of species associations is well established by long-term ecological records [8–12], which show that species respond individually to environmental changes by shifting, expanding or contracting their distributions at rates and in directions that vary among species [13]. These species-level responses can be summarized at the assemblage level by dissimilarity indices that can capture compositional turnover over time [14] and identify ‘no-analogue’ species assemblages, i.e. emergent mixtures of species that lack a close analogue to any modern counterparts [8,9]. Ecosystem novelty is already rising, owing to a variety of anthropogenic factors and particularly the legacies of current and historical land use [15–17], and is expected to further increase as historically novel climates emerge and land use intensifies [18].

This emergence of novel environments and ecosystems in of itself is not inherently good or bad for biodiversity, but can lead to new adaptive challenges for species and ecosystem managers as new environmental states and unexpected ecological interactions emerge [10]. High levels of climate novelty create challenges for ecological forecasting owing to reduced predictive skill as future environmental states move outside the environmental domains used for model calibration and testing [19,20]. More broadly, the anticipated trajectory of ecosystems away from historic and well-understood baselines towards novel states is leading conservation biologists toward

a conceptual reframing that focuses on ecological renovation instead of restoration [7] and on enabling adaptive responses to directional changes, instead of facilitating ecosystem compositional resilience and recovery to stable baseline states [21–23]. Ecosystem and environmental novelty are central to this new framework: whether a contemporary ecosystem composition is novel relative to historic counterparts is a proposed first-order branch-point in environmental decision-making [24]. Novel ecosystems have raised ethical and sometimes heated debates about the proper value to place on novel ecosystems relative to those with historical counterparts [25,26].

As interest in novel ecosystems has grown, the number of proposed climatic mechanisms has increased (figure 1). Climatic dissimilarity, high rates of spatial climatic displacement (i.e. the magnitude of climate velocity vectors [31]), variation in rates of spatial displacement and divergence among bearings of velocity vectors are all hypothesized to produce novel species assemblages [9,10,27,32], each through different mechanisms. Climate novelty can produce ecological novelty by shifting the realized climate space into new areas of overlap among the fundamental niches of species, allowing new combinations of species to co-exist [10,11]. Conversely, disappearing climates can cause some species assemblages to disaggregate and may place some species at risk of extirpation (figure 1*b*) [33]. High climate displacement rates can produce transient novel communities as species vary in their rate of movement or dispersal, causing fast-dispersing species to mix in with slow-dispersing species [27]. High variance in the magnitude or bearing of climate velocities among climate variables can produce novel assemblages as species vary in their

sensitivity to climate variables and so each climate variable ‘pulls’ species in different directions and at different rates.

Because assessments of novelty depend strongly on choice of reference baseline [15,34], different choice of baselines can lead to different scales of inference (e.g. identifying climates that are continentally novel [35] or geologically novel [3]) and enable insights into the patterns and mechanisms governing the emergence of novel ecosystems over time. Here, we introduce the concepts of transient and accumulated novelty and separately analyse the effects of the above hypothesized climate mechanisms upon each. In transient novelty, each prior time step is the reference baseline for the current period of inference, so transient novelty better captures the short-term emergence of novel communities during periods of rapid environmental change rather than long-term tendencies [9]. In accumulated novelty, the temporal distance between inference time period and reference baseline can be large, so that a time period can be compared with increasingly distant time periods to study how ecological novelty changes over time. Most studies of past climate and vegetation novelty have focused on the novelty of distant past environments relative to the present [10] or among a variety of time periods [20] and are thus assessments of accumulated novelty; the recent assessment of novelty carried out by Finsinger *et al.* [9] conforms to our definition of transient novelty.

Here, we seek to assess the relative importance of these proposed climate mechanisms for generating novel species mixtures, based on a comparative analysis and spatial modeling of networks of fossil pollen records and transient climate simulations in Europe and eastern North America (ENA) from the last glacial maximum (21 ka BP; LGM) to the present. Europe and ENA offer excellent testing grounds for biogeographic theories owing to their spatio-temporal networks of fossil pollen sites which provide a well-understood and ever-improving framework of Late Quaternary climatic history [36–38] and vegetation dynamics [34,39–42]. Despite the extensive literature in both regions, most prior intercontinental comparisons have been qualitative, and each continental literature has tended to emphasize different aspects of vegetation dynamics, e.g. the ENA literature has emphasized fast vegetation responses to climate and novel climates as the primary driver of novel communities [8,43,44], while the European literature has emphasized dispersal limitation and delayed migration from refugia as a key control on postglacial dynamics and current patterns of biodiversity [45–49], although recent papers have explored these questions in both directions [9,50].

To explore the possible effects of the four proposed climatic mechanisms described above on ecological novelty, we first quantify their patterns in space and time for Europe and ENA back to the LGM (figure 1), using downscaled climate simulations from the Community Climate System Model, v. 3 (CCSM3) SynTrace experiment [28,29] and fossil pollen records from the European Pollen Database (EPD) and North American Pollen Database (NAPD) stored in the Neotoma Paleocology Database (hereafter Neotoma) [9,51]. Then, for transient novelty, we assess temporal trends and fit a series of mixed-effects models to the full spatio-temporal dataset, while for accumulated novelty we assess correlations. This work is the first to our knowledge to quantify and compare continental-scale vegetation novelty with climatic novelty, displacement and divergence simultaneously for Europe and ENA, and thereby offers one of the most comprehensive

assessments to date of the climatic mechanisms that cause species to reshuffle into new communities.

2. Material and methods

(a) Fossil pollen data and vegetation novelty

To quantify vegetation change and novelty across Europe, we use a selection of sites with standardized age models [52], previously assembled for mapping 43 of the most abundant terrestrial taxa in this region [53] (electronic supplementary material, table S1). We use the methods described in the associated publications [9,34,52,53], but also remove duplicate sequences from the same site (electronic supplementary material, appendix S1). The resulting 714 EPD pollen records (figure 2b) are collated into 43 consecutive 500-year-wide age bins, centred on 500-year intervals, from 21 to 0 ka BP (thousand years before present, present defined as 1950 Common Era). However, owing to the scarcity of samples prior to 15 ka BP, pollen samples from 21 to 15 ka BP are averaged into a single late-glacial age bin for each record. This allows us to make inference on critical early time periods throughout our analyses, but warrants some caution when comparing with other 500-year-wide time bins. When more than one sample from a pollen record fell within an age bin, pollen counts were averaged across all samples in that bin. The use of 500-year (or 1000-year) time intervals is common in Late Quaternary vegetation mapping, and is constrained by radiocarbon-dating uncertainties, which can range from 10^1 to 10^3 years and are often on the order of centuries. Other considerations include minimizing the number of bins with no data and maximizing temporal resolution [9]. To avoid sampling from ice-covered regions, we restrict analyses to locations with less than 50% ice cover, using a mask from the ICE-6G gridded data product [54]. Finally, to facilitate the use of time as a random effect in our mixed-effects model framework, we restrict each pollen record to include only its longest, uninterrupted sequence of 500-year binned samples ($n_{\text{samples_EPD}} = 8970$), so that there are no gaps within any given record. Thus, the final dataset consists of records that differ in temporal extent, beginning time and end time. The number of EPD records per age bin steadily increases from 14.5 ka BP until the Late Holocene, reaching 468 unique records by 2.5 ka BP (figure 2c). The aggregated full-glacial age bin (21 to 15 ka BP) comprises 76 unique records.

For ENA (figure 2a), we use fossil pollen data drawn from NAPD through Neotoma [51,55] (www.neotomadb.org, accessed on 26 November 2018). We include all datasets specified as ‘pollen,’ bounded within -105° to -52° longitude and 24° – 75° latitude, with calibrated radiocarbon or calendar-year age-depth models. Pollen counts are aggregated using a version of a standard 64-taxon list for North American pollen taxa [56], which we modify by aggregating all pollen types to the genus or family level and removing pollen types that are not well represented across ENA (though are common in western North America), resulting in 43 terrestrial taxa for ENA (electronic supplementary material, table S1). Duplicate sequences are removed, aggregated and masked from ice-covered environments as described for the EPD, resulting in 393 pollen sequences collated into 43 uninterrupted 500-year-wide age bins ($n_{\text{samples_NAPD}} = 3421$). The number of records per age bin steadily increases from 14.5 ka BP to 0 ka BP, reaching 305 unique records by 0 ka BP (figure 2c). Here, aggregation to a full-glacial bin results in with 94 unique records for 21–15 ka BP.

To quantify vegetation dissimilarity and novelty, we use the squared-chord distance (SCD) metric [8,42]. SCD is calculated for each pollen sample at a given time interval (the period of inference), relative to all pollen samples from a specified reference baseline. Hence, this analysis involves a series of one-to-many comparisons, where the minimum SCD indicates the

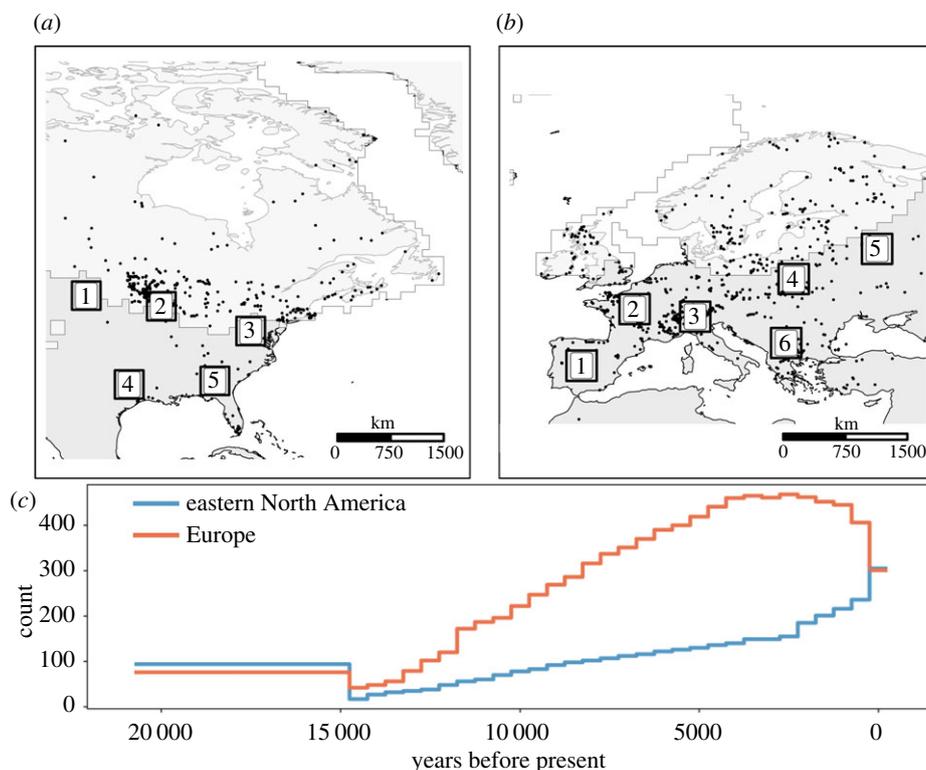


Figure 2. (a,b) Map of site locations for all fossil pollen records used to calculate vegetation novelty ($n = 393$ for ENA, and $n = 714$ for Europe) and ice extent at 21 ka BP from ICE-6G [54]. Numbered boxes indicate areas used to highlight regional climate trends in later analyses. (c) Time series showing the count of sites per time interval. Because of low site density in both ENA and Europe prior to 15 ka BP, pollen samples from 21 to 15 ka BP are grouped together into a single ‘full-glacial’ age bin.

dissimilarity between the target sample and its closest analogue in the reference baseline. SCD is calculated as follows:

$$SCD_{ij} = \sum_{k=1}^n (\sqrt{p_{jk}} - \sqrt{p_{ik}})^2,$$

where SCD_{ij} is the multivariate sum of $n = 43$ squared differences in pollen proportions between the inference period, p_{jk} , and the reference baseline, p_{ik} , where k is a given pollen taxon. We characterize vegetation novelty using $\min(SCD_{ij})$, thereby using a continuous rather than categorical definition of novelty that is conditioned on choice of baseline [15]. For transient vegetation novelty, the reference baseline consists of pollen samples from the immediately preceding age bin (e.g. for transient novelty at 6 ka BP, the baseline includes all samples from 6.5 ka BP). For accumulated novelty, we allow each time period to serve as the reference baseline for all other time periods. For example, accumulated vegetation novelty at 6 ka BP with respect to 12 ka BP is based on comparing pollen samples from 6 ka BP with those from 12 ka BP, thus assessing the accumulated effects of vegetation changes over a 6000-year period upon the emergence of vegetation novelty.

(b) Climate simulations and mechanisms of novelty

All palaeoclimate simulations are from the CCSM3 SynTrace experiments [28,29], bias-corrected and downscaled to $0.5^\circ \times 0.5^\circ$ following the methods described by Lorenz *et al.* [30]. Climate simulations are available as decadal averages of monthly values (T_{\min} , T_{\max} and P_{total}) from 22 to 0 ka BP (figure 3; present is defined as 1950 Common Era). We create a standard 200-year mean (20 simulated data points) climatology centred on each 500-year time interval from 21 to 0 ka BP (160 years for 0 ka BP). Monthly values of T_{mean} (mean of $T_{\max} + T_{\min}$) and P_{total} are summarized as three-month means ($n_{\text{variables}} = 8$) for: December, January, February (DJF); March, April, May (MAM); June, July, August (JJA); and September, October, November (SON). For visualization and to understand the behaviour of the simulations, we

also calculate annual means for temperature, precipitation and seasonal temperature range ($T_{\text{JJA}} - T_{\text{DJF}}$, figure 3). We apply an ice mask from ICE-6G [54] to restrict analyses to grid locations with less than 50% ice cover. Climate simulations are then projected to an Albers equal-area projection, with a spatial resolution of 50 km, to support calculations of displacement.

Calculation of climate dissimilarity and novelty follows a similar approach to that of vegetation novelty. However, instead of SCD, climate dissimilarity is quantified as the minimum Mahalanobis distance (MD), as it accounts for covariance among climate variables and thereby minimizes bias that may be introduced by strong correlations among seasonal variables [58]. MD is calculated as follows:

$$MD_{ij} = \sqrt{(\mathbf{b}_j - \mathbf{a}_i)^T \mathbf{S}^{-1} (\mathbf{b}_j - \mathbf{a}_i)},$$

where \mathbf{a}_i refers to a vector of climate variables ($n_{\text{variables}} = 8$) from focal cell i of the reference baseline dataset, \mathbf{b}_j refers to a vector of climate variables from focal cell j of the inference period for which dissimilarity is being assessed, and \mathbf{S}^{-1} is the covariance matrix of the data estimated from the inference and reference climatologies. Calculation of transient and accumulated climate novelty follows that for vegetation novelty.

Climate displacement vectors are calculated for each climate variable, at each grid location, using the local temporal rate of change (electronic supplementary material, appendix S2, figures S1 and S2) and spatial climate gradients, and are expressed in kilometres/decade [31]. The temporal rate of change is quantified for each 50 km grid cell using the slope coefficient from a linear model fitted using generalized least squares with an autoregressive term to account for temporal autocorrelation [27]. This slope is estimated using the 50 decades of climate simulations prior to a specified time interval. For example, the estimate of displacement for T_{DJF} at 1 ka BP for one location is based on the slope coefficient fitted to the 50 T_{DJF} values at that location between 1.5 and 1 ka BP. We use the prior time periods, rather than a time window centred on the interval, to minimize the use of future climate changes as

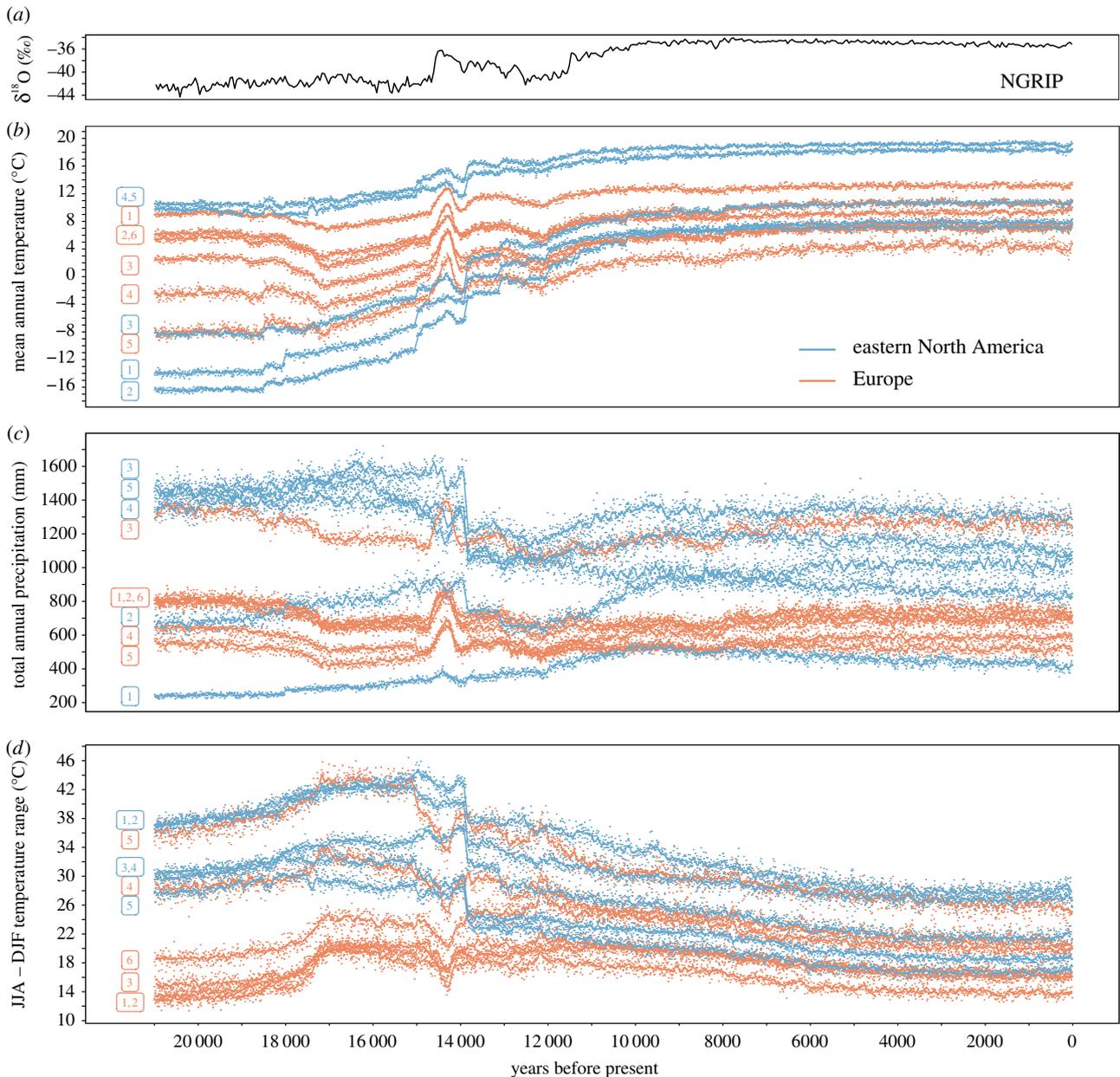


Figure 3. Observed and modelled climate trends from the LGM to the present. (a) Oxygen isotopes from NGRIP [57]. (b–d) Time series of simulated climates for mean annual temperature (b), total annual precipitation (c) and seasonal temperature range (d) for five regions across ENA, and six regions across Europe (locations shown in figure 2). The points in each time series show the decadal means from the downscaled climatologies.

predictors of vegetation novelty for a given time period. The local spatial gradient represents the change of a given variable per unit of distance [59], averaged across a 3×3 neighbourhood of grid cells.

The spatial orientation of each climate displacement vector is set by the local spatial gradient and the direction of the temporal change for each climate variable [60], so climate divergence represents the standard deviation among spatial bearing for each climate velocity vector. A low divergence suggests that all velocity vectors of all climate variables would tend to shift along the same axis of direction, whereas high divergences indicate that velocity vectors lack congruence in orientation and hence so might species distribution shifts.

(c) Statistical methods: climatic predictors of vegetation novelty

We tested the importance of hypothesized climate mechanisms of vegetation novelty using two tests, operating at different spatio-temporal grains. First, we modelled the predictors of vegetation novelty for the full spatio-temporal dataset, using a linear mixed-

effects model with the *nlme* and *MuMIn* packages in R [61–63]. We incorporate only the climatic mechanism data of grid locations containing a pollen record. Climatic dissimilarity, the mean and variance of displacement rates and divergence among bearings of displacement vectors are included as fixed effects, while we represent time as a random effect to test whether the mechanisms resulting in vegetation novelty change over time even after accounting for fixed effects. The model framework also considers the first-order interactions between fixed effects. The resulting 113 candidate models (based on all combinations of fixed effects) were fitted using the maximum-likelihood method and then compared using the Akaike information criterion. We use relative variable importance (RVI_v) as a metric to determine the strength of support for a given variable v , as a predictor of vegetation novelty. RVI_v is determined by summing the Akaike weights of each variable across all candidate models in which a given variable v occurs. RVI_v ranges from 0 to 1, where the larger an RVI_v value is the more important variable v is relative to other variables [64]. RVI_v values between first-order terms and interactions should be ranked independently, as the number of candidate models containing these variables differ. As a second test, we quantify

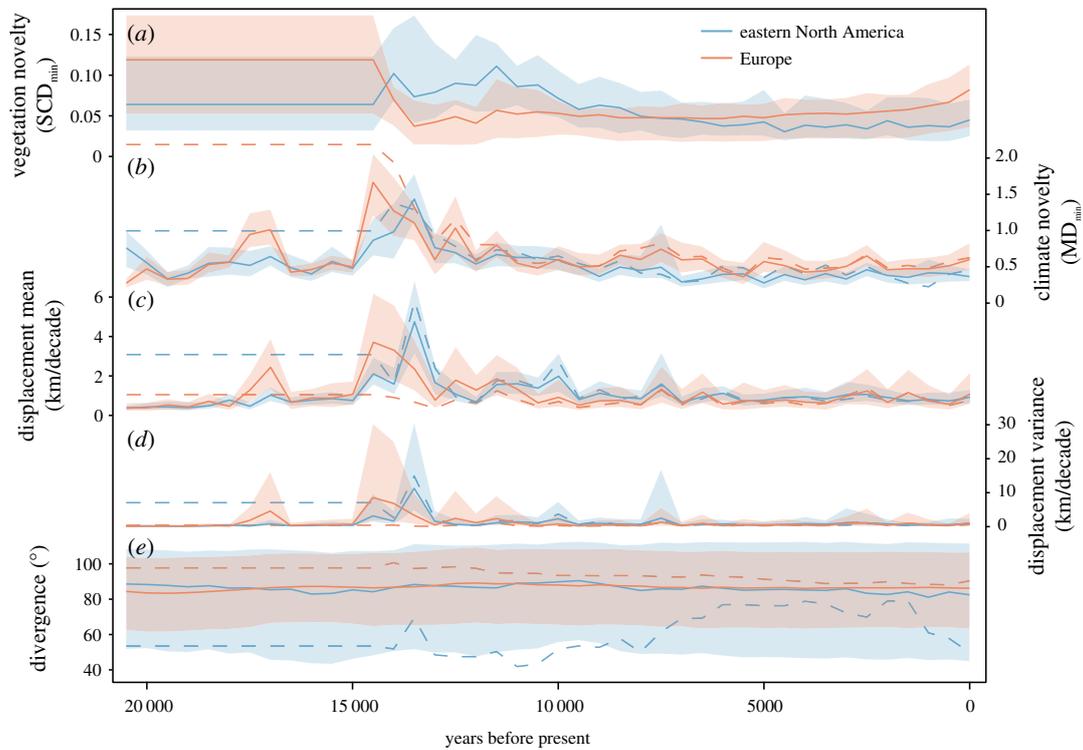


Figure 4. Temporal trends for transient vegetation novelty and hypothesized climatic mechanisms for ENA (blue) and Europe (orange) beginning 20 500 years before present. (a) Trends in transient vegetation novelty, based on fossil pollen data and SCD. Climatic mechanisms proposed to cause ecological novelty are derived from simulated climate data: (b) climate novelty; (c) mean of displacement; (d) variance of displacement; (e) divergence. Solid lines represent the continental median while shading represents the interquartile range for Europe and ENA. Dashed lines represent the subset of climate grid locations that contain a pollen record.

the correlation between regional median vegetation novelty values and each climatic mechanism. This comparison enables the inclusion of accumulated novelty and backwards displacement rates in addition to transient comparisons.

To assess whether analyses are affected by variations in spatial or temporal sample density, particularly with respect to time (figure 2), we run two series of sensitivity tests (electronic supplementary material, appendix S3, figures S3 and S4). In the first test, we test for the effects of data sparsity by proportionally reducing the dataset size by 20, 40, 60 and 80% across all time periods, with 50 replicate subsamples drawn per treatment level. In the second sensitivity test, we produce an even distribution of samples across time by randomly sampling 3000-year lengths from the pollen records until all time periods have 15, 25, 35 or 45 samples, with 100 replicate subsamples drawn per treatment level.

3. Results

(a) Climate trends: Europe and eastern North America

Mean annual temperatures in Europe and ENA rise throughout the deglaciation, culminating in the relatively stable temperatures of the Holocene. The simulated climate data align closely with temperature trends reconstructed from ice cores (figure 3*a,b*) [57]. However, several abrupt climatic episodes punctuated this warming trend, including Heinrich Event 1 (a cold interval, or stadial, with an onset *ca* 17 ka BP [65]), the Bølling/Allerød warm period (a warm interstadial beginning *ca* 14.67 ka BP [66]), and the Younger Dryas (stadial, *ca* 11.7 ka BP [67]). The climatic signals associated with these events vary within regions of Europe and ENA, as well as between Europe and ENA (figure 3*b*). The amplitude of simulated millennial-scale

temperature variations is higher in Europe, while the spatial gradient in temperature among locations is larger in ENA (figure 3*b*).

Annual precipitation levels in the climate simulations also show the strongest variation during the Bølling transition (figure 3*c*). Across Europe, precipitation decreases from the LGM until *ca* 15 ka BP. The Bølling transition is characterized by an abrupt increase, followed by an abrupt decrease *ca* 1000 years later. In ENA, precipitation shows a small increase from the LGM until the Bølling transition. Around 14 ka BP, it then declines rapidly before rising and remaining relatively constant throughout the Holocene. Regions near the continental interior of North America are modelled to be drier than present during the late-glacial period, while coastal regions are modelled to be comparably wet, or even wetter, than present.

As with mean annual temperature, seasonal temperature range increases during the last deglaciation, reaching a plateau beginning *ca* 17 ka BP (figure 3*d*). The duration of this plateau varies within and among regions. In Europe, the Bølling/Allerød marks a reduction in temperature seasonal range, and in Eastern Europe (regions 4, 5), seasonal temperature range continues to decline thereafter. In Western Europe (regions 1, 2, 3, 6), annual temperature range remains high until 12 ka BP, then gradually declines. In ENA, seasonal temperature range is high until 14 ka BP, then declines, first abruptly, then gradually. In all regions, seasonal temperature ranges are higher in the past than at the present. Seasonal temperature ranges are higher in all ENA regions than in Europe, except for the relatively continental regions in Eastern Europe.

(b) Transient novelty

Trends in transient vegetation novelty during the last deglaciation differ substantially between Europe and ENA (figure 4*a*).

Table 1. Summary of the mixed-effects modelling results, for the effects of climatic mechanisms on transient vegetation novelty. Climatic mechanisms are sorted by their Relative Variable Importance (RVI_v), which indicates the relative support of a variable as a predictor of transient vegetation novelty. Across all models, the average standardized β coefficients are shown for each variable. We include 8970 observations for Europe and 3421 observations for ENA, distributed across all 43 consecutive age bins.

term	RVI _v	average β	term	RVI _v	average β
Europe			ENA		
<i>first-order terms</i>			<i>first-order terms</i>		
Climate Novelty	1	−0.034	Climate Novelty	1	0.032
Displacement (Mean)	1	−0.015	Divergence	0.81	0.000
Displacement (Variance)	1	0.000	Disp. (Mean)	0.56	0.001
Divergence	0.68	0.000	Disp. (Variance)	0.54	0.000
<i>interactions</i>			<i>interactions</i>		
ClimNov : DispMean	1	0.013	DispMean : DispVar	0.62	0.000
ClimNov : DispVar	0.93	0.000	ClimNov : Divergence	0.26	0.000
DispMean : DispVar	0.62	0.000	ClimNov : DispMean	0.16	0.001
DispVar : Divergence	0.28	0.000	DispMean : Divergence	0.16	0.000
ClimNov : Divergence	0.23	0.000	ClimNov : DispVar	0.15	0.000
DispMean : Divergence	0.20	0.000	DispVar : Divergence	0.14	0.000

For Europe, the median regional novelty is highest at 14.5 ka BP (relative to a dataset comprising all pollen samples between 21 and 15 ka BP), then rapidly declines to a minimum by 13.5 ka BP. Transient novelty then rises to new plateau by 11.5 ka BP. Conversely, transient novelty in ENA is initially lower than in Europe, but then rises and remains high between 14 and 11.5 ka BP, gradually declining between 11.5 and 4.5 ka BP. Transient novelty in both continents remains relatively low during the Holocene. However, novelty increases beginning around 3 ka BP across Europe, perhaps owing to agricultural land use and land cover conversion [9,68].

These continental-scale trends in vegetation novelty are strongly driven by subcontinental-scale variations. For both continents, transient vegetation novelty is low at most locations (electronic supplementary material, figures S5 and S6), and regions of high novelty are locally confined. In Europe, transient novelty is highest during the Bølling transition, particularly across northern Europe, as is displacement (electronic supplementary material, figure S5). In ENA, transient novelty is high during the Bølling transition along the southern margin of the Laurentide Ice Sheet and along stretches of southeastern and coastal USA (electronic supplementary material, figure S6).

Climate novelty and the mean and variance of displacement rates show temporal trends broadly similar to vegetation novelty, while divergence shows few variations when aggregated across each continent (figure 4*b–e*). Climate novelty and displacement rates are highest at 14.5 ka BP for Europe, while peaking slightly later, at 13.5 ka BP, for ENA. In Europe, a secondary peak occurs at 12.5 ka BP, while in ENA climate novelty and displacement steadily decline through the Holocene. The continental-scale trends are similar between medians calculated for all locations versus those calculated just at locations with fossil pollen records (figure 4, dashed versus solid lines), particularly after 15 ka BP, indicating that the pollen site network in this study represents the regional climatic trends of the past 15 ka. Climate divergence is the exception, as values are nearly constant from 21 to 0 ka BP,

though some variation exists when considering only sites with pollen records.

The mixed-effects modelling results indicate that the controls on vegetation novelty differ by continent. In ENA, climate novelty is indicated as the most important predictor of vegetation novelty, followed by divergence (table 1). The primary importance of climate novelty as a driver of vegetation novelty in ENA is consistent with prior hypotheses for this region (RVI = 1). Among the interacting effects, we find moderate support (RVI = 0.62) for the interaction between the mean and variance of displacement rates as a predictor of vegetation novelty. Conversely, in Europe, climate novelty and the mean and variance of displacement rates are most important (RVI = 1), followed by divergence (RVI = 0.68) as a moderate predictor of vegetation novelty (table 1). Surprisingly, however, the fitted coefficients for climate novelty and mean displacement are negative (table 1), indicating that these predictors are negatively correlated to transient ecological novelty, contrary to expectation. Among the interacting effects, we find strong support for the interaction between the mean displacement rate and climate novelty as a predictor of vegetation novelty. The mixed-effects models also suggest that time acts as random effect, with different slopes and intercepts (electronic supplementary material, figure S7), indicating that the form of the fitted relationship between vegetation novelty and climatic predictors varies among time intervals.

The sensitivity tests indicate that the rank-ordering of RVI values for the most important predictors of vegetation novelty is largely insensitive to progressive reductions in dataset size (electronic supplementary material, figure S3), while there are minor changes in the ordering of the weakly predictive model variables. Similarly, subsampling tests with standardized numbers of samples for all time intervals mostly preserve the rank-ordering of RVI values (electronic supplementary material, figure S4). Model variables with the strongest support for being predictive of vegetation novelty have the highest RVI values, while there are some changes

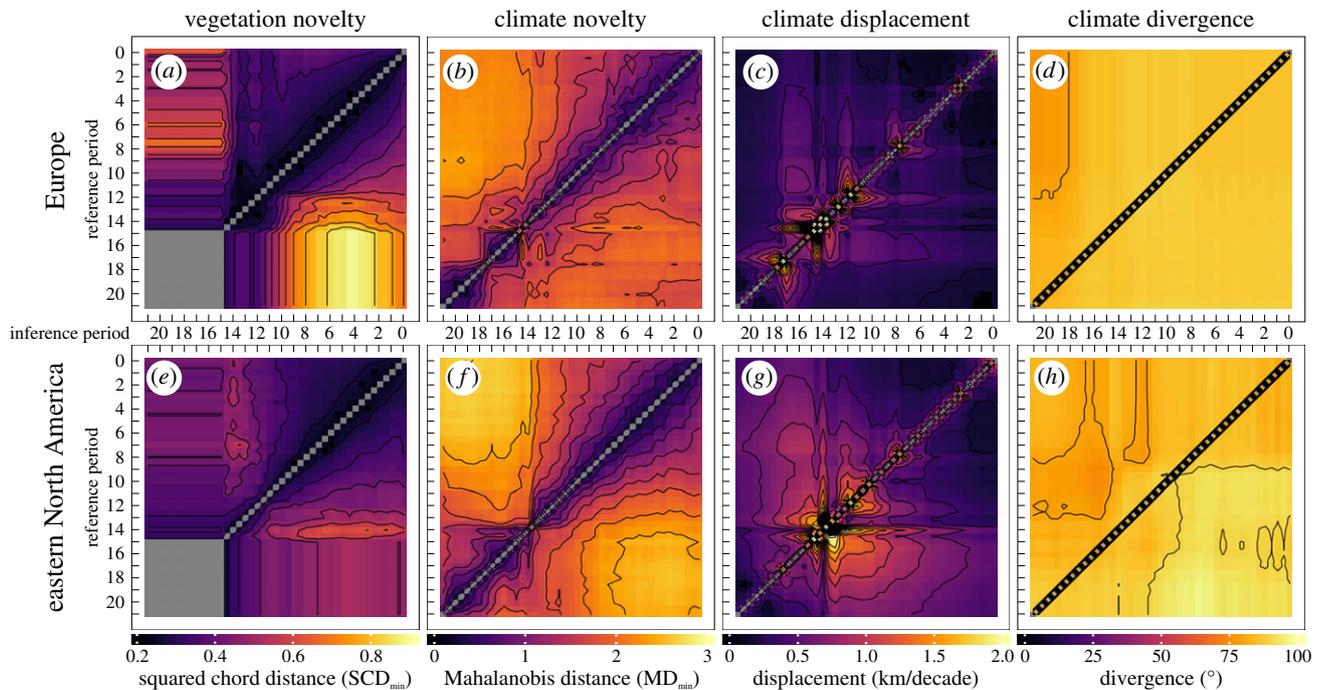


Figure 5. Median comparisons of accumulated (a) vegetation novelty, (b) climate novelty, (c) displacement and (d) divergence for Europe and ENA, for all pairs of time periods. Climatic mechanisms based on full domain of simulated climate data. Horizontal axes represent the time period for which a variable is being assessed, while vertical axes represent the reference baseline period. For example, the high novelty scores in the lower-right quadrant of panel (a) show that vegetation novelty in Europe is highest for the mid-Holocene relative to the late-glacial period.

for the weakly predictive variables. For ENA, the variance and mean of displacement rates increase with importance with temporally controlled subsampling, but remain secondary to transient climate novelty and divergence.

(c) Accumulated versus transient novelty

The mixed-effects modelling focused only on transient novelty (as in [9]), whereas most studies of novel climates and vegetation have focused on accumulated novelty (as in [8]). Figure 5 shows both: values adjacent to the diagonal are equivalent to transient novelty, whereas positions further from the main diagonal correspond to increasingly large temporal distances and accumulated novelty. Moving along the horizontal axis shows novelty of multiple time intervals relative to a single baseline, while moving along the vertical axis shows how dissimilar a single time period is relative to different reference baselines. Comparisons in the lower triangle of these panels follow time's arrow and so novelty here is interpreted as emerging novelty, while the upper panel is time-reversed and so novelty here indicates assemblages that have disappeared over time [33]. Because the spatio-temporal correlation structure in the multi-temporal accumulated data is complex, we present visual descriptions and correlations without attempting to assess significance. Across Europe, accumulated vegetation novelty is highest during Mid-to-Late Holocene relative to the late-glacial. SCD values have a maximum at 4.5 ka BP relative to the late-glacial age bin, but remain higher throughout the Holocene. For ENA, high SCD values are observed throughout the Holocene, with a maximum at 1.5 ka BP with respect to 14 ka BP. Accumulated vegetation novelty tends to be higher in Europe than in ENA, yet accumulated novelty values are more than sixfold the highest transient novelty values for Europe and ENA. Hence, ecological novelty can emerge within forest communities

over even short timescales (figure 4), yet novelty of these changes is small relative to the novelty that accumulates over time (figure 5).

Many assemblages of vegetation present during the late-glacial period disappeared by the Early Holocene (figure 5*a,e*, upper triangle). For example, in Europe, the pollen assemblages from the late-glacial are most dissimilar to pollen from a baseline of 7.5 ka BP (figure 5*a*). Similarly, for ENA, late-glacial assemblages differ the most from those of the Holocene (figure 5*e*).

Climatic novelty exhibits a temporal pattern that most closely resembles that of vegetation novelty (figure 5*b,f*). MD values are continuously high during the entirety of the Holocene with respect to the late-glacial (21–15 ka BP) for Europe, while showing the highest MD values during the Late Holocene (6–1 ka BP) relative to the late-glacial for ENA. MD values also suggest that climates were more novel across ENA than in Europe during these time periods.

Climate displacement rates indicate intervals of rapid climatic change (figure 5*c,g*). In this case, the lower triangle shows forward velocities, whereas the upper triangle shows backward velocities (cf. [69,70]). Displacement rates are high for both regions during the Bølling transition and the Younger Dryas, for example. Owing to time-averaging effects, estimated displacement rates decrease in magnitude as temporal distance increases. However, even several thousand years after these abrupt climate events, climate displacement rates remain high relative to the background mean, with e.g. elevated mean displacement rates persisting even 5 ka after onset of the Bølling transition. Climate divergence shows a similar and largely uniform pattern for both regions (figure 5*d,h*).

Accumulated vegetation novelty correlates most strongly with climate novelty for both Europe and ENA when comparing median values associated with the same reference and inference period (Pearson correlation of 0.61 for Europe, and

0.82 for ENA; electronic supplementary material, figure S8). Only weak correlation exists for displacement (Pearson correlation of -0.21 for Europe and 0.21 for ENA), and for divergence (Pearson correlation of 0.20 for Europe and 0.35 for ENA). For ENA, these results are consistent with the mixed-effects modelling for transient novelty in that climate novelty emerges as the most important predictor of vegetation novelty, followed by divergence. However, for Europe, the findings differ from the mixed-effects modelling for transient novelty, in that climate novelty is again the strongest predictor, but the sign of the coefficient is positive, consistent with prior expectation. Moreover, the correlation of accumulated novelty with climate displacement appears to be weaker than for the transient analyses. This suggests that the importance of climate novelty for ecological novelty may grow as time accumulates, while at shorter timescales additional processes may influence the emergence of novel communities.

4. Discussion

(a) Overview

Our results reinforce the hypothesis that past novel ecosystems form at least partially in response to past novel climates [10,71], while also lending support to fast spatial rates of climate change as important mechanisms for generating ecological novelty. Other work has shown that, for the twenty-first century, different climate predictors of ecological novelty (climate novelty, displacement rates, divergence among climate velocity vectors for individual climate variables) have very different predicted patterns for the twenty-first century [27,72]. Our findings and prior work thus lead to the expectation that, over the coming decades, novel ecosystems are likely to arise in different regions for different reasons: driven, for example, in tropical regions by the emergence of novel climates, owing to fast spatial rates of climate change in low-relief and high-latitude regions [27]. These analyses also indicate that the patterns and likely climatic drivers of ecosystem novelty differ between ENA and Europe and with timescale.

(b) Controls on transient and accumulated novelty in ENA and Europe

The differences reported here between transient and accumulated novelty and between ENA and Europe, two classic regions for studying past climate-driven vegetation dynamics, suggest that interregional differences in climate history can lead to different ecological outcomes and sensitivities. Much of these climatic and ecological differences can in turn be linked to geographical position and the known spatial variations in climate, both today and during the last deglaciation. Europe, given its position downwind of the North Atlantic, tends to show stronger signals of millennial-scale climate variations that are driven by meltwater inputs into the North Atlantic and corresponding changes in ocean circulation, heat content and sea ice extent (figure 3*b,c*; [73,74]). Similarly, because European climates have a strong maritime influence, seasonal temperature ranges, both past and present, tend to be reduced relative to temperature ranges in ENA, particularly in Western Europe (figure 3*d*). Hence, orbital-induced Late Quaternary variations in seasonal temperature range, which are hypothesized to be important drivers of past novel climates and an important control on the formation of late-glacial no-

analogue plant communities in ENA [10,71], may have more muted influence on European vegetation dynamics.

These geographical and climatic factors may explain why in ENA both accumulated and transient vegetation novelty show a strong positive relationship with climate novelty, while in Europe the expression of transient novel ecosystems during the last deglaciation is less pronounced and tends to be strongest at 14.5 ka BP, at the beginning of the time series analysed here (figure 4*a*). This weaker expression of transient ecological novelty in Europe may also explain why the hypothesized positive relationship between climate novelty and ecosystem novelty emerges only for accumulated novelty (figure 5 and table 1), i.e. at short timescales the differences between adjacent time steps are muted and the signals of ecological novelty are relatively weak, whereas as temporal distance increases, the ecological and climatic novelty between time intervals increases and the signals strengthen.

This difference in geographical position and climatic history may also help explain the different emphases in the European and ENA literatures on rates of climate change and vegetation disequilibrium as important drivers of vegetation dynamics. Postglacial rates of climate displacement usually are higher in Europe than in ENA, notably by almost 2.5-fold at 17 ka BP, and nearly 1.8-fold greater at 14.5 ka BP (figure 4*c*). In both regions, the climate displacement rates of the last deglaciation are high even by twenty-first century standards, with past rates peaking between 3 and 5 km/decade between 14.5 and 13.5 ka BP (figure 4*c*), versus projected future global mean displacement rates of 4.2 km/decade (based on temperature alone, [31]). The larger-amplitude mean annual temperature variations (figure 3*b*) and rates of spatial displacement in Western Europe make this region ideal for studying vegetation responses to abrupt warming [14,75]. Individual plant taxa have responded to climatic fluctuations at varying rates owing to their life-history traits and dispersal capabilities. Hence, abrupt millennial-scale climate changes may be a central control on European vegetation community dynamics and structure [34,76]. The literature varies on whether dispersal limitation was an important control on postglacial rates of tree migration in Europe and transient community assembly. Pollen-based maps indicate rates of expansion averaging 4–10 km/decade in Europe, with little evidence for climate limitation [34], while modelling studies that combine environmental niche modelling with migration modelling suggest that expansion of *Fagus sylvatica* in some areas was limited by seed dispersal [47]. In ENA, where millennial-scale temperature variations are more muted (figure 3*b*), vegetation disequilibrium may be less important [8,77], although rates of tree range expansion for some species may be limited by species mutualisms and other factors [78].

This work thus adds new dimensions to intersecting effects of climatic novelty and rates of climate change on ecological novelty and understanding the differences between ENA and Europe in postglacial vegetation dynamics. Traditional explanations for differences between Europe and ENA in postglacial rates of tree expansion have focused on the size and orientation of mountain ranges. In this framework, the European Alps act as a barrier to northwards species range expansion, while the north–south trending Appalachians act as a corridor. More recent work has highlighted the importance of mountainous regions as providing microclimate refugia for species through high topographic and substrate complexity [48,79]. Additionally,

low climate velocities in mountainous areas may allow species to quickly adapt to changing climates by moving upslope or downslope into nearby, thermally suitable, habitats [60]. The work presented here suggests that differences in climatic history and resultant magnitudes of postglacial rates of climate change may be an underappreciated source of differences in drivers of vegetation dynamics and the formation of novel ecosystems. In particular, key factors include the differential position of ENA and Europe on opposite sides of the North Atlantic, the higher continentality and seasonality of ENA climates, and the faster rates of millennial-scale climate change in Europe.

(c) Caveats

An important caveat with these results is their reliance on the CCSM3 SynTrace simulations. All palaeoclimatic simulations carry inaccuracies and biases (as do many inferences based on empirical palaeoclimatic proxies). Comparisons of CCSM3 simulations to chironomid-inferred summer temperature reconstructions in the Mediterranean suggest similar temperatures through the Early Holocene but that the CCSM3 SynTrace experiments underestimate the magnitude of Younger Dryas cooling [80]. Potential inaccuracies in the climate simulations, combined with weaker signals of vegetation novelty together with multiple predictors and interaction terms, may explain why some climatic mechanisms in Europe have negative coefficients in the mixed-effects model (table 1), contrary to expectation. More work is needed here. In particular, there is an urgent need to move beyond palaeoclimatic simulations for understanding the climatic drivers of past vegetation dynamics, but independent palaeotemperature records of the last deglaciation remain scarce, particularly in ENA [81,82]. A key step forward is to build palaeoclimatic data products based on the assimilation of Earth system model simulations with independent palaeoclimatic proxy records to produce global palaeoclimatic data products that are consistent with the available data [83].

A secondary caveat lies in potential limitations in the fossil pollen record. The fossil pollen records in ENA and Europe represent the densest networks available for the last 20 ka. Nonetheless, pollen records offer an incomplete and biased representation of vegetation history, with a variable taxonomic resolution that is typically at the genus level and usually ranges from species to families. This variable taxonomic resolution can cause some aspects of past novel ecosystems to be emphasized and others overlooked [84]. The application of pollen–vegetation models to fossil pollen records may reduce the bias of quantifying past abundance and their changes [85]. Sensitivity analyses suggest that our main findings are not too sensitive to variations in site density (electronic supplementary material, figures S3 and S4). Nonetheless, site density decreases back through time (figure 2c), which underscores the need for additional long-term ecological records during the abrupt climatic and ecological changes of the last deglaciation.

(d) Implications for conservation biology

The last deglaciation (19 000–8000 years ago) is one of the best available model systems for studying broad-scale species responses to climate change: the species involved are nearly all present today, networks of long-term ecological records are dense relative to earlier time periods, and the deglaciation

encompasses large changes in global climates, ice sheets, species distributions and human footprints. A defining ecological characteristic of this time period is its dynamism; species distributions shift as climate changes, and ecosystems show large changes in composition, often including mixtures of species no longer found at present. These records of climate-driven range dynamics and a growing understanding of the driving mechanisms of past novel communities, combined with on-going climate changes at present, are helping shift the conceptual focus of conservation biology to broaden from frameworks primarily focused on resilience and restoration to frameworks that also include efforts to facilitate responses of ecosystems to changing and novel climates [21–23]. A key need in conservation biology is to develop climate metrics that best indicate climate exposure and vulnerability [86,87]. However different metrics, when applied to the historic and projected climate trends for the twenty and twenty-first centuries, show large differences in spatial patterns at continental to global scales, leading to uncertainty about which metrics are best suited for conservation planning [70,72,88]. For example, during the twentieth century and early twenty-first century, climate novelty is globally highest in the tropics, while displacement rates are fastest in the high latitudes and topographically flat areas [27]. The fossil record offers the opportunity to test such metrics against the observed ecological changes in the past, as a way of testing hypotheses about the climatic mechanisms that drive species range dynamics, community turnover and the emergence of novel ecosystems. Of course, other factors besides climate change can produce, and may already have produced in the past [9], novel ecosystems and, as humankind ventures into the Anthropocene, other anthropogenic pressures will be pervasive [89] and should be considered in tandem with the pressures of a changing climate. Nonetheless, by better understanding when and where past novel species assemblages emerged, and the strongest climatic predictors, palaeoecologists and conservation biologists can better understand and predict where novel ecosystems are likely to emerge in the coming decades. Garnering knowledge of the past may thus be critical to facilitating the managed renovation of ecosystems in the coming decades.

Data accessibility. Data associated with our mixed-effects modelling framework, pollen count data and downscaled climate simulations for Europe have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.9w0vt4b9s>) [90]. Downscaled climate simulations for ENA (<https://doi.org/10.5061/dryad.1597g.2>) [91] and Matlab code to calculate novelty (<https://doi.org/10.5061/dryad.0j18k00>) [92] are available in Dryad from their original publications.

Authors' contributions. K.D.B., J.W.W., and A.O. designed the research; K.D.B. performed research; D.J.L. provided downscaled climate simulations for Europe. All authors analysed data and contributed to writing the paper.

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