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RESEARCH ARTICLE

The dynamics of the diversity–energy relationship during the last 21,000 years

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Abstract

Aim: Spatial diversity patterns are linked to energy availability, but how the diversity–energy relationship changes in space and time is unclear. There are three possible scenarios: (a) equilibrium dynamics, where diversity is always positively related to energy availability in both time and space; (b) out-of-equilibrium dynamics, where diversity is determined by energy availability in equilibrium, but diversity variation lags behind changes in energy availability, leading to a mismatch between temporal and spatial diversity–energy relationships; and (c) disequilibrium dynamics where the equilibrium does not exist or is irrelevant. We attempt to distinguish these scenarios using spatio-temporal palaeoecological data.

Location: USA and Canada.

Time period: 21,000–1,000 years before present.

Major taxa studied: Woody plants.

Methods: We tested for the strength and direction of temporal and spatial relationships between pollen type diversity of woody species and energy availability (estimated from temperature and precipitation) in 1,000-year time steps.

Results: Whereas the temporal diversity–energy relationship appears only when energy levels rapidly change, the spatial diversity–energy relationship is pronounced only when these levels stabilize.

Main conclusions: Our findings are consistent with the out-of-equilibrium scenario – diversity equilibria do exist and act as attractors of diversity dynamics, but diversity is often out of equilibrium. Consequently, current rapid climate changes can disrupt spatially consistent diversity–energy relationships. To understand diversity dynamics, it is crucial to simultaneously consider both the spatial and temporal dimensions of diversity variation.

KEYWORDS
diversity-climate relationship, equilibrium dynamics, macroecology, palaeoecology, pollen, species–energy relationship, trees

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1 | INTRODUCTION

The energy available in the environment (hereafter 'energy') is considered a principal factor affecting biological diversity (Bohdalková et al., 2021; Currie et al., 2004; Field et al., 2009; Hawkins et al., 2003; Wright, 1983). Two general forms of energy can be distinguished that drive diversity patterns (Allen et al., 2006; Storch, 2012), namely (a) ambient (thermal) energy that drives the speed of biological processes and sets physiological limits for organisms; and (b) chemical energy of organic compounds of tissue, represented by biomass or biomass production, that limits population sizes. The latter, measured as a combination of temperature or precipitation or net primary productivity (NPP), is known to be, in contrast to thermal energy, a universal correlate of species diversity (Bohdalková et al., 2021). Although specific mechanisms behind the diversity–energy relationship (DER) are not fully clear (Mittelbach et al., 2007; Storch, 2012), there are good reasons to assume that a change in energy levels results in a shift in species diversity (Currie et al., 2004; H-Acevedo & Currie, 2003; Storch & Okie, 2019). Consequently, recent unprecedented human-induced changes in the energy available for natural ecosystems must have an effect on ongoing and future diversity changes (Miko & Storch, 2015; Storch et al., 2022).

Efforts to understand the response of biodiversity to the changes in available energy are typically restricted to projections of the contemporary species distributions using climate models, assuming that species responses to the changing climate are immediate and that spatial and temporal patterns are substitutable. This assumption, however, ignores the known lagged diversity responses or disequilibrium processes (Svenning et al., 2015; Svenning & Sandel, 2013), which potentially cause a mismatch between the temporal and spatial diversity patterns (Gaüzère & Devictor, 2021), challenging the predictability of diversity dynamics in space and time (Blonder et al., 2017). Therefore, a more complex view covering a broader temporal scale is needed to understand diversity dynamics and predict future diversity patterns under current climate change.

Building on the predictions of the Equilibrium Theory of Biodiversity Dynamics (Storch & Okie, 2019), we distinguish three possible types of diversity dynamics concerning the spatio-temporal variation in the DER. First, the diversity dynamic may be strictly equilibrial (Figure 1a), which means that diversity is always in equilibrium determined by the energy level (and potentially other drivers affecting species origination, colonization and extinction rates, see Storch & Okie, 2019). Then, any changes in diversity are driven by shifts in the parameters that drive the equilibrium itself (e.g., shifts in environmental variables that affect the balance between colonization and extinction rate) and not by a movement of diversity from a state out of equilibrium towards the equilibrium. This scenario is similar to the 'no-lag scenario' proposed by Blonder et al. (2017) and the 'fast ecological dynamics' defined in Williams et al. (2021). In such a case, the changes in energy levels should be followed by relatively simultaneous diversity changes leading to a positive DER both in time and space.

Second, diversity changes can lag behind the changes in energy availability, despite the existence of the diversity equilibrium (out-of-equilibrium state, Figure 1b). In such a case, energy availability forms an attractor for diversity, but diversity response to changes in energy levels is slow relative to the changes of energy availability. Possible causes of these lags can be dispersal barriers and limitations (Normand et al., 2011) combined with the distance from glacial refugia (Davis & Shaw, 2001), the decline of megaherbivores (Bakker et al., 2016; Gill, 2014), soil development (Henne et al., 2011) or presence of an ice sheet. Under this scenario, the lags are not constant in time (unlike the constant-lag dynamics, Blonder et al., 2017) and depend on the rate of the change in energy availability. The lags may also vary in space and depend on the distance from source populations, topography, and other site-specific attributes. Under large temporal shifts in energy availability, we expect diversity to change with changing energy levels. Nonetheless, unlike the strict equilibrium state, we expect a weak and variable form of this relationship in space due to non-uniform lags in diversity responses in different localities (Figure 1b: transient state). In contrast, if energy fluctuations diminish and energy level stabilizes, we expect diversity to be closer to equilibrium, resulting in an opposite pattern of a positive spatial and weak positive or negligible temporal DER (Figure 1b: stabilized state). This scenario is similar to the slow ecological dynamics proposed by Williams et al. (2021).

Third, it is possible that available energy does not put any limit on diversity, but that energy drives diversity by promoting its (positive) changes. Indeed, several hypotheses explain the latitudinal diversity gradient by the effect of energy on speciation, colonization or extinction rates without assuming any equilibrium (Pontarp et al., 2019). At temporal scales of tens of thousands of years, energy availability may be associated with higher colonization rates as warmer and more productive environments are physiologically easier to be tolerated than cold and dry conditions (climate tolerance hypothesis sensu Šímová et al., 2011). In such a case, we would expect a positive but highly variable relationship between diversity and energy in time and space (Figure 1c) without any predictable difference between transitive and stabilized states.

In support of the strict equilibrium dynamics scenario, species responses to environmental change have been reported to be relatively fast when focusing on recent temperature changes (Lynn et al., 2021), climate changes across the late Quaternary (Birks & Ammann, 2000; Shuman et al., 2004) and even over longer temporal scales (Willis et al., 2007). Nevertheless, many studies support a lagged diversity response to a changing climate (Butterfield et al., 2019; Ordonez, 2013; Veloz et al., 2012; Woods & Davis, 1989). Moreover, there is evidence for the different abilities of communities to track climate in periods of fast versus slow climate change (Gaüzère et al., 2020; Knight et al., 2019) and for a mismatch between the temporal and spatial variation in community composition patterns in a period of fast climate change (Blois et al., 2013), supporting the out-of-equilibrium scenario. Moreover, a strong imprint of palaeoclimate on current diversity patterns apparent even after the long Holocene climate stability (reviewed by Svenning et al., 2015) seems

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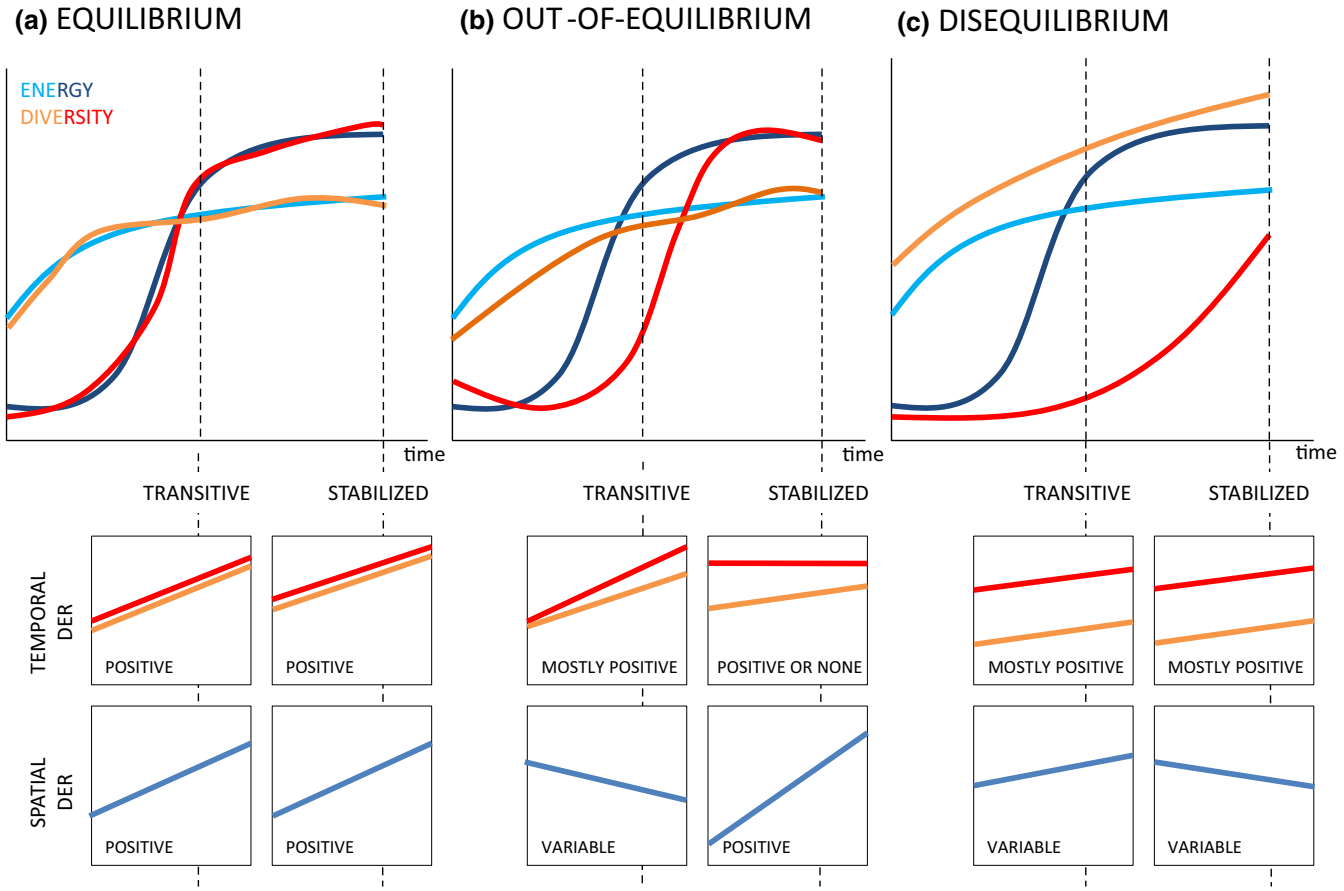

FIGURE 1 Three types of diversity dynamics (equilibrium, out-of-equilibrium, and disequilibrium) related to the changes in available energy, and associated prediction of spatio-temporal diversity–energy relationships (DERs). The three types of dynamics differ in terms of temporal and spatial DERs during two contrasting regimes: (1) transitive regime when energy availability changes relatively rapidly, and (2) stabilized regime characterized by low temporal variation of energy. Each plot shows two regions differing in the trajectory of energy increase and final energy level; one region with a moderate increase in energy and lower final level (light blue for energy and orange for diversity), the other region with a steeper increase in available energy and higher final energy level (dark blue and red, respectively). The temporal DER row shows the temporal relationships between diversity (*y* axis) and energy (*x* axis) for the transitive and stabilized period delimited by the dashed lines. The spatial DER row shows the spatial relationship between diversity (*y* axis) and energy (*x* axis) for particular time slices at the dashed lines. (a) In the case of strictly equilibrium diversity dynamics, we assume that changes in diversity are driven only by changing its equilibrium level given by the instantaneous level of energy; we thus expect diversity to be tightly positively linked to energy in both space and time (even though measured temporal DER can be weak when energy level stabilizes and its variation is thus low). (b) A tendency towards equilibrium, but with various time delays, characterizes the out-of-equilibrium dynamics. Diversity is thus in equilibrium only when there is sufficient time for energy levels to stabilize – a positive spatial DER is then expected. Then, the temporal DER may be weak or absent, as diversity is predicted to fluctuate around its equilibrium level. In contrast, the transitive regime is predicted to be characterized by generally positive temporal and variable (but generally weak) spatial DERs. Due to the time lags, spatial DERs can be even reversed, like in the case depicted in the corresponding panel (dark blue and red lines), where the region with the highest level of available energy had lower diversity than the region of low energy availability, as there was not enough time to track productivity increase. (c) Disequilibrium dynamics scenario assumes that productivity does not drive diversity patterns by setting diversity limits (stable equilibria) but by promoting diversity increase (growth rate). Consequently, we expect positive temporal DERs (although not universally, due to the time lags), while we expect spatial DERs to be variable even in the stabilized regime. Disequilibrium dynamics also mean that diversity levels are universally dependent on history (energy levels in the past), in contrast to the out-of-equilibrium dynamics, where the role of history decreases when the diversity is close to its equilibrium (as its level starts to be determined just by the equilibrium).

to be in accord with the disequilibrium scenario. Still, most of these studies are conducted either over time or space. To understand diversity dynamics, it is crucial to simultaneously consider both these dimensions to identify possible mismatch between the spatial and temporal patterns (Gaüzère & Devictor, 2021). Moreover, given that any such mismatch likely varies with the magnitude of climate change (Figure 1, Blois et al., 2013), it is essential to differentiate between periods of high versus low climate variability.

To distinguish among our proposed scenarios, we explored the spatio-temporal dynamics of the DER using North American pollen data of woody species spanning the last 21,000 years before the present ('yr BP'). We test three predictions associated with the

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proposed scenarios under two regimes characterized by high (transitive regime) and low (stabilized regime) magnitude change of energy availability (Figure 1):

- *Prediction 1*: Under the *strict equilibrium* scenario, diversity should synchronously increase with increasing energy, leading to a positive DER in time and space. Whereas the spatial DER should remain strongly positive over both transitive and stabilized regimes, the temporal relationship should weaken when the energy level stabilizes (Figure 1a).
- *Prediction 2*: Under the *out-of-equilibrium* scenario, we expect temporal DER to be positive, but it should weaken when the energy level stabilizes, similarly to the strict equilibrium scenario. In contrast, a strong positive spatial DER is only expected when diversity approaches the equilibrium (Figure 1b).
- *Prediction 3*: Under the *disequilibrium* scenario, we expect a generally positive temporal DER (although its strength can vary) and a variable spatial DER (Figure 1c) without any predicted difference between transitive and stabilized regimes.

Energy availability can be measured in several ways. The most common surrogate of energy availability that has been demonstrated to be strongly correlated to diversity (Bohdalková et al., 2021) is NPP. However, the situation is more complicated in plants that themselves generate NPP, hence the relationship between NPP and plant diversity may reflect the positive effect of diversity on productivity rather than vice versa (Duffy et al., 2017; O'Connor et al., 2017). For this reason, instead of using realized NPP (for which we do not have historical data anyway), we use potential NPP, estimated using a model based on a combination of temperature and water availability (Lieth, 1975; Šímová & Storch, 2017), which correlates well with the Dynamic Global Vegetation Model (DGVM) of potential biomass production (Fritz et al., 2016). Thus, it is an appropriate measure of energy available to plants, not being itself affected by plant diversity.

2 | METHODS

2.1 | Pollen data

We downloaded data on all pollen cores in the continental USA and Canada from the Neotoma database (Williams et al., 2018). We chose this spatial extent based on relatively dense sampling coverage and the high number of woody species (compared to Europe). We selected only those cores dated at least 12,000 yr BP to obtain a sufficient time-series length for temporal analyses. We grouped the samples in each core into 1,000-year time bins centred on every full 1,000-year time step (i.e., 1,000 yr BP bin contains samples dated between 500–1,499 yr BP). This interval has been considered reasonable for individual species to track the changing climate (Webb, 1986). Also, finer intervals would likely result in more gaps in the data, particularly in the late Pleistocene. We set up the most recent date to 1,000 years BP to restrict the analysis to the pre-Columbian era only. We included occurrences of woody plants only, defined as trees or shrubs that can reach at least 1.5 m in height (see Supporting Information Appendix S1 for details). As most woody plant pollen types were resolved to genus level, we aggregated all pollen types into genera with a few exceptions (e.g., *Ostrya/Carpinus* type, see Supporting Information Appendix S1 for details). We obtained 107 unique pollen types (Table S1.1 in Supporting Information Appendix S1).

To account for the sampling bias, we estimated diversity using individual-based rarefaction with pollen grain counts representing individual abundances (see also Giesecke et al., 2019). For each time bin, we calculated pollen type rarefied diversity for 400 pollen grains using the library *vegan* (Oksanen et al., 2020). The time bins with <400 pollen grains were assigned a missing value, reducing the length of some time series. We restricted our analyses to the cores covering at least 11 time bins, each with more than 400 pollen grains, resulting in 186 pollen cores (Figure S2.1 in Supporting Information Appendix S2).

To validate our diversity estimate, we tested for the correlation between the rarefied 1,000 yr BP woody plant pollen-type diversity (i.e., the most recent period of our analyses) and the diversity of contemporary woody genera and species. We extracted contemporary woody species and genera from the Botanical Information and Ecology Network (BIEN) 3.0 woody species occurrence table (spatial grid of 200 × 200 km^2 resolution, published in Šímová et al., 2018). The Pearson *r* of the resulting relationship was .51 for contemporary species diversity, .52 when considering all contemporary genera, and .58 when focusing only on the subset of genera occurring in pollen data (Figure S3.1 in Supporting Information Appendix S3). This indicates that the rarefied pollen diversity for the time intervals well represents actual diversity patterns, including patterns in species richness.

2.2 | Climate data

We obtained temperature and precipitation data based on the Community Climate System Model ver. 3 (CCSM3) from the tool PaleoView (version 1.5.1, Fordham et al., 2017) at a resolution of 2.5°. We calculated the 1,000-year average temperature and precipitation values as an average from three 100-year windows centred on the 1,000-year step plus and minus 300 years (the software allows the maximum time interval for averaging climate variables to be 100 years). For instance, temperature for 1,000 yr BP was calculated as an average from 100-year intervals centred in 700, 1,000 and 1,300 yr BP. Using the resulting temperature and precipitation values, we estimated energy as potential net primary productivity (NPP) according to the Miami model equation (Supporting Information Appendix S4; Lieth, 1975; see also Fritz et al., 2016). Potential NPP, although calculated using only climate variables, has units of grams of dry matter per square metre per year. Like other climate-based NPP models, it represents potential environmental

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productivity rather than actual plant biomass production (Šímová & Storch, 2017).

2.3 | Statistical analyses

To test for the *temporal* relationship between woody plant pollen-type diversity ('diversity' hereafter) and energy availability within the time series of each core, we first explored the temporal fluctuations in energy levels and diversity separately, and then tested for the effect of energy availability on diversity. For each core (site), we estimated the Spearman's *r* of the energy–time, diversity–time, and DER. We explored the overall trend in the examined relationships across sites by (a) comparing the Spearman's *r* distribution against zero using a one-sample Wilcoxon test and (b) fitting a generalized additive model (GAM). For the GAM, we included site ID as a random factor affecting the intercept and the slope of the explanatory variable. To account for a linear trend, we included the smoothing term 'time' as one of the explanatory variables. The rate and magnitude of the change of energy and diversity were heterogeneous over time (see also Gaüzère et al., 2020; Mottl et al., 2021). Therefore, we repeated all time-series analyses separately for the Holocene (mid/late Holocene, 9,000–1,000 yr BP) and late Pleistocene (late Pleistocene/early Holocene, 21,000–10,000 yr BP) and compared the distribution of site-specific Spearman's *r* of the examined relationships between these two periods using a two-sample Wilcoxon test. Since the split in the two periods reduced the time-series length, we included for the Spearman's *r* distribution only those sites that had at least five data points in a particular period.

To test for the variation in the *spatial* relationship between energy and diversity in different time bins, we estimated the Spearman's *r* of the relationship between diversity and energy across sites for each 1,000-year time bin. We excluded time bins with fewer than five samples. Next, we compared the Spearman's *r* distribution against zero using a one-sample Wilcoxon test for the late Pleistocene and Holocene periods. To account for the decrease in the number of sites with increasing bin age (Figure S2.2 in Supporting Information Appendix S2), we randomly sampled 10 sites per bin to calculate the Spearman's *r* of the relationship between diversity and energy. For each time bin, we repeated this sampling 100 times and estimated the average Spearman's *r*.

Additionally, we explored to what extent was the strength of the examined temporal and spatial relationships affected purely by the magnitude of spatial or temporal change in available energy. We expect that if the magnitude of energy variation is the principal driver of the strength of DERs, we should observe a strong positive relationship between variance in available energy (either in time or space) and the strength of the respective DER.

There was a systematic difference in the temporal fluctuations in diversity and energy levels between the eastern and western parts of the continent (Figure 2c,f). Therefore, we split the sites into eastern (108 sites) and western (78 sites) clusters (Figure S2.1 in Supporting Information Appendix S2) and repeated all analyses for each group separately.

3 | RESULTS

3.1 | Temporal variation in energy, diversity and DER

Energy availability increased towards the present (Figures 2a,b and 3a, Table S5.1 in Supporting Information Appendix S5), and this increase was much stronger during the late Pleistocene than in the Holocene. In the eastern part of the continent ('East' hereafter), this increase was very strong in both periods (Figures 2c and 3a, Supporting Information Table S5.1). In the western part ('West' hereafter), energy weakly increased towards the present in the late Pleistocene, whereas in the Holocene, this relationship was strong, but the opposite (Figures 2c and 3a, Supporting Information Table S5.1). The relationships between diversity and time were similar in form but weaker in strength compared to the energy–time relationships. Diversity increased towards the present more strongly in the late Pleistocene compared to the Holocene (Figures 2d,e and 3b, Supporting Information Table S5.1) and more strongly in the East than in the West (Figures 2f and 3b, Supporting Information Table S5.1).

In agreement with all three scenarios, the temporal relationship between energy and diversity was generally positive (Figure 2h). Nevertheless, whereas in the late Pleistocene this relationship was moderate (median $r = .35$), during the Holocene this increase became very weak (median $r = .14$; Figures 3c and 4a,b, Supporting Information Table S5.1), in agreement with the out-of-equilibrium scenario. When splitting into East and West, the results for the East remained qualitatively the same but stronger than for the entire continent (Figure 3c, Supporting Information Table S5.1). In the West, the strength of the temporal DER ranged from very weak to negligible (Figure 3c, Supporting Information Table S5.1). These results remained qualitatively the same when focusing on GAM (Figure S6.1 in Supporting Information Appendix S6).

When testing for the effect of temporal variance in energy levels on the strength of the DER, both the variance in energy levels and the strength of the DER were generally higher in the late Pleistocene compared to the Holocene (Figure S7.1a,c in Supporting Information Appendix S7). Still, when subsetting the data according to the periods and eastern/western parts of the continent, the time-bin specific relationships between the variance in energy levels and Spearman's *r* were weak or negligible (Supporting Information Figure S7.1b). Therefore, although the magnitude of the change in energy levels seems important for the differences between the periods, the site-specific temporal variation in available energy is unlikely to be the driver of the strength of site-specific temporal DERs.

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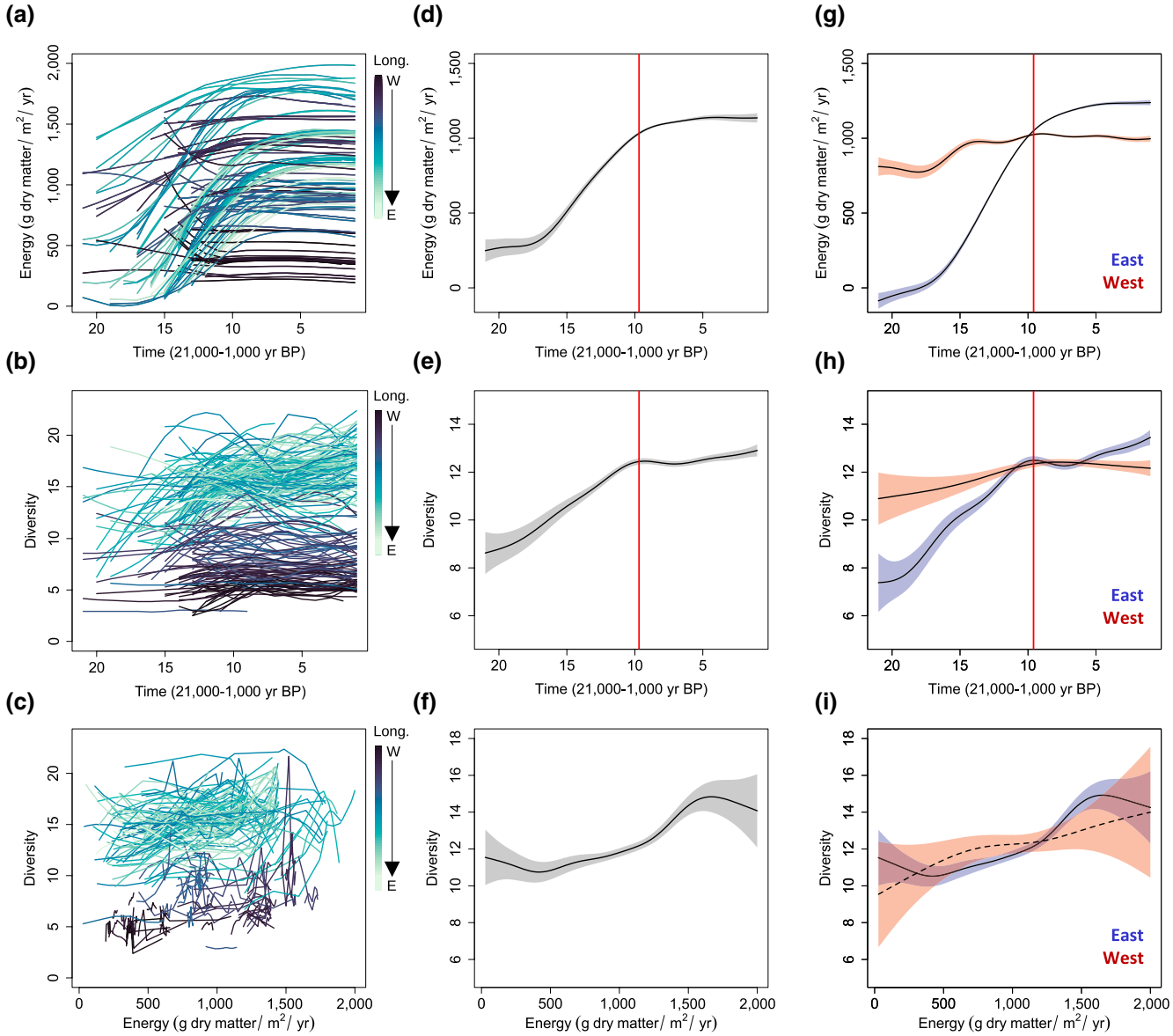

FIGURE 2 Forms of the three types of the temporal relationships explored. Panels (a), (d), (g) represent site-specific LOESS (locally estimated scatterplot smoothing) regression (span = .8) of the relationships between (a) energy and time, (d) diversity and time, and (g) diversity and energy (DER). The lines are coloured according to the longitude of each site. Panels (b), (e) and (h) show the relationships between (b) energy and time, (e) diversity and time, and (h) DER fitted by the generalized additive modes (GAM). The red line represents the split between the late Pleistocene and Holocene periods. Panels (c), (f), (i) show the relationships between (c) energy and time, (f) diversity and time, and (i) DER fitted by the GAM separately for eastern (blue) and western (red) parts of the continent. Energy is a potential biomass production in g dry matter/m^2/yr estimated based on reconstructed temperature and precipitation.

3.2 | Spatial DER in different time bins

The spatial DERs were consistently moderately strong (confidence intervals = .35 and .48, median r = .43) over the Holocene (Figures 4d and 5a, Supporting Information Table S5.1), in line with the strict equilibrium and out-of-equilibrium scenarios. However, in contrast to the strict equilibrium scenario, the strength of this relationship was weak or negative during the late Pleistocene (Figures 4c and 5a; median r = −.20), supporting the out-of-equilibrium scenario. When splitting into the East and West, the West's spatial DER became moderately strong after 13,000 yr BP (Figure 5c, Supporting Information Table S5.1). In the East, however, most DERs were very weak across the entire period (Figure 5b, Supporting Information Table S5.1), apparently supporting the disequilibrium scenario. The results remained qualitatively unchanged when accounting for the decreasing number of sites towards the past (Figure S8.1, Table S8.1 in Supporting Information Appendix S8).

When testing for the effect of spatial variance in energy levels on the strength of the spatial DER, we did not find a strong relationship between these variables (Supporting Information Figure S7.1d–f). The exception was the contrasting patterns in the Holocene, where we observed a stronger spatial DER in the spatially more variable

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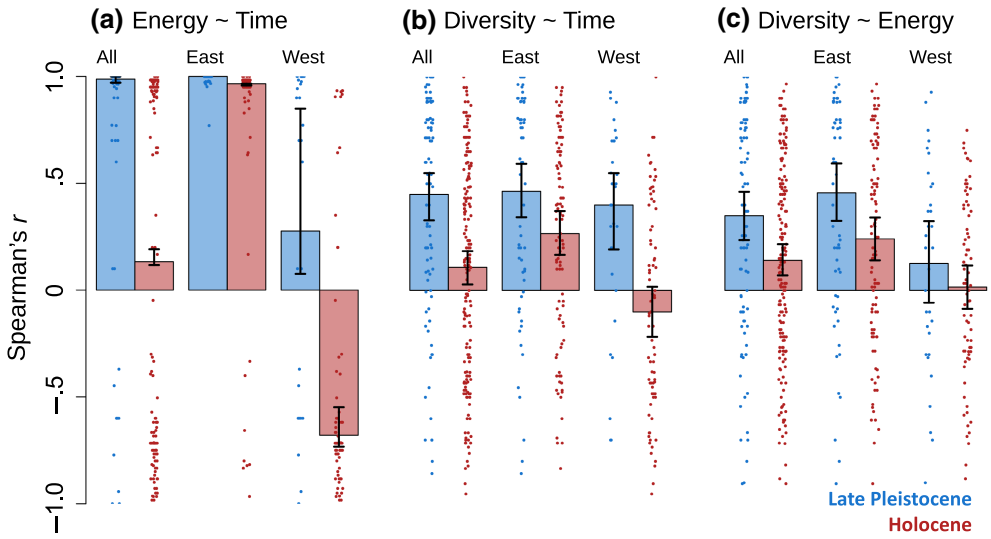

FIGURE 3 Barplots expressing the strength (Spearman's *r*) of the three temporal relationships: (a) energy–time, (b) diversity–time and (c) temporal diversity–energy relationship (DER) for all sites ('All'), and eastern ('East') and western ('West') parts of the continent. The Spearman's *r* is the median from the Wilcoxon test of the distribution of all site-specific Spearman's *r* of a given relationship; the error bars are the 95th confidence intervals of the median; the points are the data from the distribution. See Supporting Information Table S5.1 for summary statistics. Note that time has been coded from 21,000 yr BP (lowest value) to 1,000 yr BP (highest value), leading to a positive *r* when values of the particular variable increase towards the present.

West than in the spatially less variable East. Spatial variation in energy levels per time bin thus seems unlikely to be the primary cause of the variation in the spatial DER.

In summary, diversity increased with increasing available energy either in time or space for a given period and region depending on the magnitude of the temporal change in energy availability. Specifically, during the late Pleistocene, when changes in available energy were large, diversity increased with energy in time but not in space (Figures 4a,c and 6). Conversely, during the climatically stable Holocene, diversity increased with increasing energy in space, but the increase in time was very weak (Figures 4b,d and 6). In the East, where energy increased towards the present during both periods and where the temporal variance in available energy was generally higher, diversity increased with energy in time but not in space (Figure 6). In the West, where the temporal variance in available energy was lower than in the East, diversity increased with energy in both periods in space but not in time (Figure 6). These results agree with the out-of-equilibrium scenario expectations that (a) under the equilibrium state, diversity should increase with energy in space, but only weakly in time, and (b) under the transitive regime characterized by a high magnitude of change in energy level, diversity should increase with energy in time, but not in space.

4 | DISCUSSION

Using North American woody plant pollen data, we observed a relatively strong temporal diversity increase with increasing available energy between the Last Glacial Maximum (~21,000 yr BP) and the onset of the Holocene (~9,000 yr BP). When the climate stabilized during the Holocene, the temporal relationship between diversity and energy became weak, while the spatial relationship strengthened. These patterns are in line with the out-of-equilibrium scenario. According to this scenario, diversity was attracted towards the equilibrium determined by the energy level, but the equilibrium level changed over time. As a result, the equilibrial relationship was never attained during the Pleistocene due to the slow response rate of diversity. Local diversity approached the equilibrium level determined by available energy only when the temporal changes in energy levels weakened. Our results imply that despite the existence of diversity equilibria, diversity may vary in time and be temporarily out-of-equilibrium.

Compared to the existing studies focusing on the temporal dynamics of community composition and climate (Blonder et al., 2017; Gaüzère et al., 2020; Mottl et al., 2021; Williams et al., 2021), our framework highlights two novel aspects that are crucial for the prediction of the diversity dynamics linked to climate changes. First, we should pay separate attention to transient and stabilized regimes. Second, we must simultaneously consider the temporal and spatial dimensions of the diversity–energy relationship to avoid potentially misleading conclusions. Our results correspond to the findings of Gaüzère et al. (2020) and Blois et al. (2013) on the point that under Holocene climate stability, the temporal relationship between vegetation composition and climate was poor and different from the spatial vegetation–climate relationship. Nevertheless, unlike Gaüzère et al. (2020), we contend that this result does not indicate a disequilibrium dynamics. Instead, we argue that diversity can reach an equilibrium level only when temporal variation in environmental variables weakens, that is, during a stabilized regime. Diversity oscillates around the equilibrium level in such a situation, leading to

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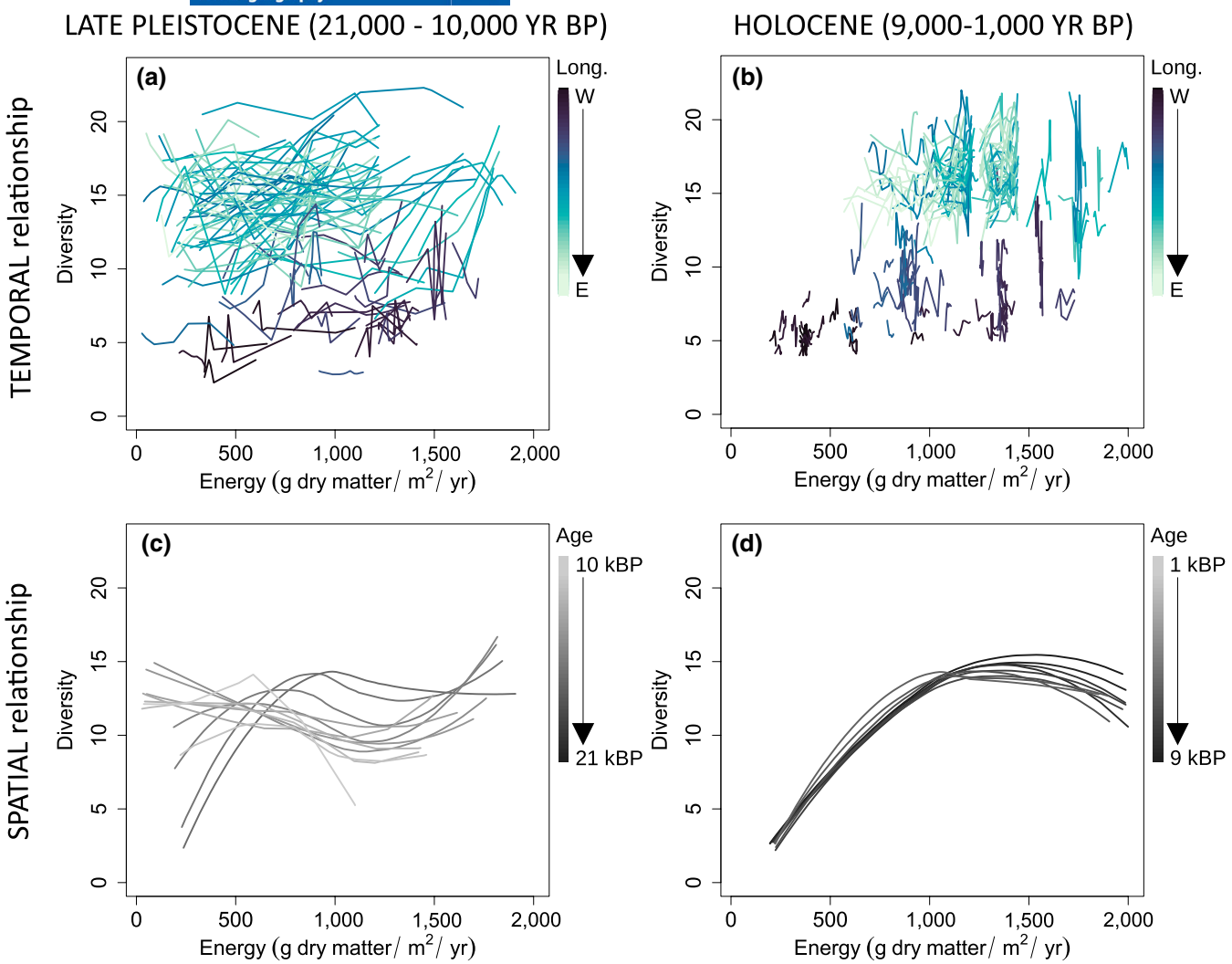

FIGURE 4 Comparison of temporal (top) and spatial (bottom) diversity–energy relationships (DERs) for the Late Pleistocene and the Holocene. Panels (a) and (b) show site-specific LOESS (locally estimated scatterplot smoothing) regressions (span = .8) of the temporal relationships between diversity and energy for (a) the late Pleistocene and (b) the Holocene. The lines are coloured according to the longitude of each site. Only sites with at least five data points are shown. Panels (c) and (d) show the time-bin specific LOESS regressions of the relationships between diversity and energy across sites for (c) 21,000–10,000 year time bin and (d) 9,000–1,000 year time bin. The lines are coloured on a grey scale according to the age of each time bin. Energy is a potential biomass production in g dry matter/m^2/yr estimated based on reconstructed temperature and precipitation.

a poor temporal diversity–environment relationship. Conversely, diversity that tracks temporal changes in energy levels under the transient regime does not necessarily indicate equilibrium dynamics, as Gaüzère et al. (2020) suggested. Our conceptual framework, backed up by our data, highlights that equilibrial dynamics comprise both the oscillation around equilibrium and the tendency towards equilibrium, depending on the rate of environmental changes and the variability of lag-time in diversity responses. Therefore, we must move away from a strict distinction between equilibrium and disequilibrium dynamics to fully acknowledge that even in the presence of diversity equilibria, diversity may change and be temporarily (or even most of the time) out of the equilibrium.

When focusing on the entire continent, the period of the late Pleistocene (21,000–10,000 yr BP) corresponded to the transient regime and the Holocene (9,000–1,000 yr BP) to the stabilized regime. The 10,000 yr BP temporal breakpoint coincides with the fast retreat of the Laurentide Ice Sheet (Dyke & Prest, 1987). However, this pattern did not hold when focusing separately on the eastern and the western sites due to the different climatic histories of these two regions. The steepest increase of diversity with energy during the late Pleistocene took place in the eastern part of the continent, likely due to the rapid warming and fast colonization rates associated with the retreat of the Laurentide Ice Sheet (Williams et al., 2004). Here, cold and dry open coniferous forests moved to the northern area vacant by the ice sheet and were replaced with warm and wet mixed forests colonized by species from the south and west (Williams et al., 2004). The colonization process of the northern, formerly glaciated areas continued over the Holocene (Ordonez & Williams, 2013; Pither et al., 2018; Williams et al., 2001), although the magnitude of the change in

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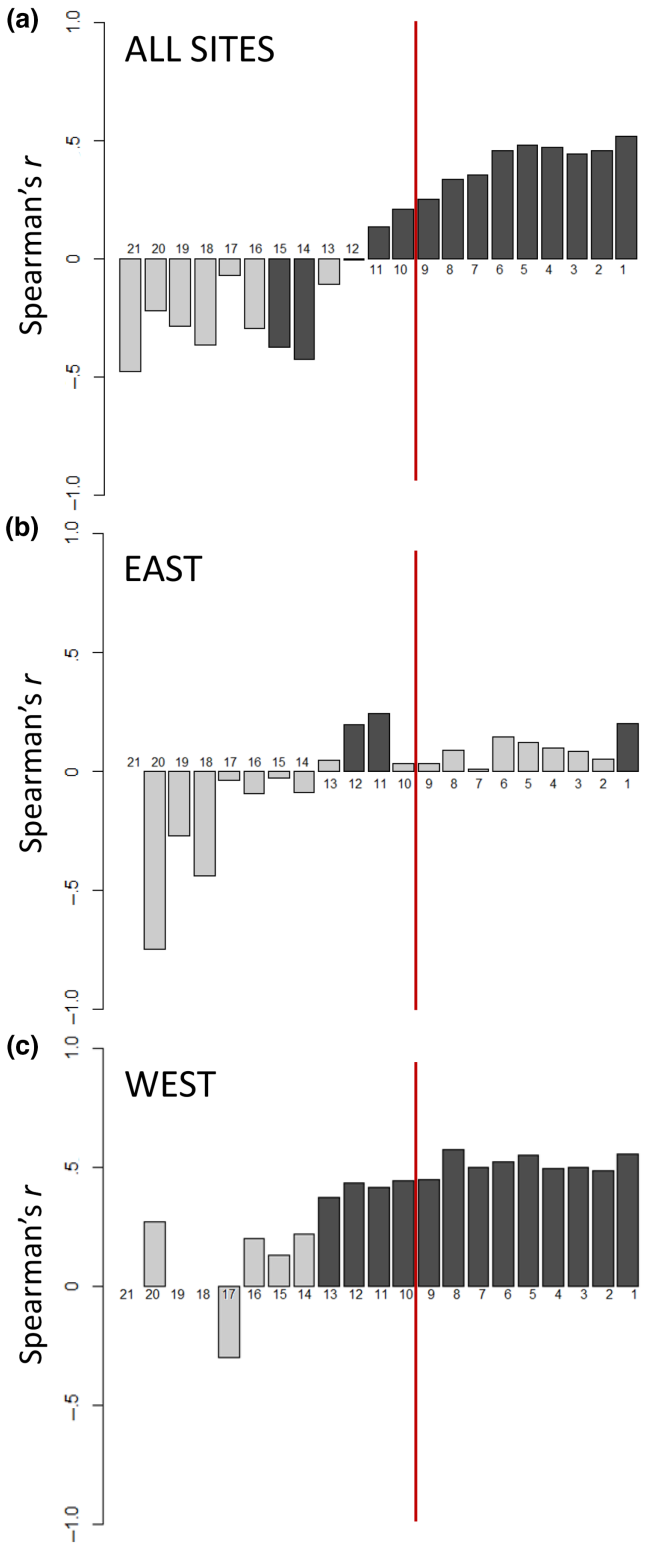

FIGURE 5 Barplots showing the value of the Spearman's *r* of spatial diversity–energy relationships (DERs) in each time bin. The time bins are labelled from 21 to 1, where 21 represents 21,000 years BP and 1 represents 1,000 years BP. The bar is missing for time bins with <5 data points. Significant relationships are highlighted in dark grey. The red vertical line represents the split between the late Pleistocene and the Holocene.

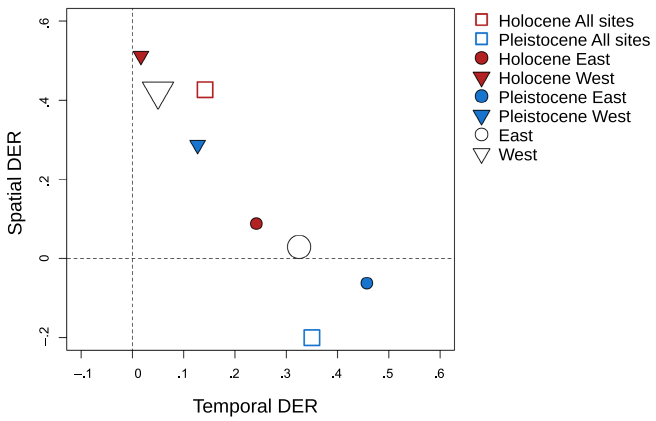

FIGURE 6 Biplot showing the relationship between the strength (Spearman's *r*) of the temporal and spatial diversity–energy relationships (DERs) for all sites, eastern ('East') and western ('West') parts of the continent, further divided into the Holocene and late Pleistocene ('Pleistocene') periods. The Spearman's *r* is the median from the distribution of all site-specific (for temporal relationships) or time-bin specific (for spatial relationships) Spearman's *r*.

energy availability weakened, as did the strength of the temporal DER. In contrast to the results for the entire continent, the spatial DER of the eastern sites remained very weak during the Holocene. Given the continued temporal shifts in energy levels and diversity even after the deglaciation in this region, this result is still consistent with the out-of-equilibrium scenario, indicating that the equilibrium level was not yet approached there.

In contrast to the eastern part, we did not find evidence for a significant temporal increase of diversity with increasing energy availability within the western sites in any studied period. Over the late Pleistocene, the temporal DER was not only much weaker but also highly variable when compared to the eastern sites. Given the poor data available here (32 cores, see Supporting Information Table S5.1), this result should be considered with caution. Nevertheless, after *c.* 13,000 yr BP, coincident with the fast retreat of the Cordilleran Ice Sheet, the fluctuation in available energy stabilized (Figure S9.1b in Supporting Information Appendix S9), and a relatively strong spatial DER emerged, in line with the prediction of the out-of-equilibrium scenario under the stabilized regime. During the Holocene, the energy available at most western sites decreased towards the present, possibly due to the continuing increase in aridity of the southern part (Thompson & Anderson, 2000). Still, this decrease in available energy was small in magnitude (Figure 2c) and did not seem to affect the otherwise strong spatial diversity–energy relationship. Therefore, we consider the western Holocene diversity close to equilibrium.

Although our study covers a comprehensive spatial and temporal gradient, several important limitations exist. First, pollen type diversity provides an imperfect record of species or genera occurrences (Goring et al., 2013). Pollen data are composed mainly of the widespread species, whereas rare and small-ranged

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species are often missing. Rare species form a large fraction of plant species (Enquist et al., 2019), and due to their absence, we may miss some crucial aspects of the diversity patterns and DER. Second, the model behind the climate data may perform poorly in certain periods and regions compared to proxy palaeoenvironmental data and may capture temporal patterns better than spatial ones (Harrison et al., 2014). This model also does not capture site-specific microclimate and edaphic conditions that may be responsible for the high variation in diversity among sites of similar energy levels, such as those in the East. Still, the climate model we used provides the best available estimate of palaeoclimate, and our main result, the contrast between temporal and spatial DERs, is unlikely to be driven by the uncertainty in the modelled climate data. Third, our 1,000-year temporal resolution does not capture short-term climate events such as extreme temperatures or periods of drought, and only roughly represents the periods of rapid warming (Bølling–Allerød) and cooling (Younger Dryas). Therefore, although we believe that our concept is in principle testable at various temporal scales, our results are relevant for a relatively coarse (1,000-year time bins) temporal scale only, and future studies using finer temporal data are needed.

5 | CONCLUSIONS

We tested for three possible scenarios of diversity dynamics: strict equilibrium, out-of-equilibrium, and disequilibrium. In agreement with the out-of-equilibrium scenario, we found that woody plant pollen-type diversity tracked the fluctuations in energy levels in the period of fast climate change, namely the late Pleistocene, but the spatial diversity–energy relationship was poor during that period. This result indicates that although available energy may have constituted an attractor for diversity dynamics, diversity did not reach an equilibrium level determined by energy. The diversity equilibrium then formed during the climatically stable Holocene, when the temporal diversity–energy relationship weakened. Our results show that to understand diversity dynamics related to the changes in available energy, we need to (a) consider temporal and spatial aspects of this relationship simultaneously and (b) consider both the transitive and stabilized regime of environmental change. The conceptual framework we present can be applied more generally to community composition dynamics and environmental fluctuations.

Our results have significant consequences for predicting future diversity dynamics under climate change. The commonly considered scenario of species tracking their climatic niches largely depends on the rate and magnitude of climate change. Assuming that the ongoing changes in available energy are out of the margins of the Holocene stability, we should expect high temporal diversity changes that will only partially track the temporal changes in energy level. Spatial diversity patterns are then predicted to be temporarily decoupled from contemporaneous climate during this period of rapid environmental changes, and their variation may be unpredictable.

AUTHOR CONTRIBUTIONS

IS, DS and AO conceived the study, DS developed the theory, IS performed the analyses, and IS wrote the manuscript with input from DS and AO.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The research is based on publicly available data. The processed data frame table is available at https://figshare.com/articles/dataset/Simova_etal_2023_Global_Ecology_and_Biogeography_Pollen_type_occurrence_table/21908553, including the site IDs, coordinates, climate data, taxa, and rarefied diversity.

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BIOSKETCHES

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SUPPORTING INFORMATION

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

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