

Biodiversity across varying environments: accumulation, loss, or stasis?

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Introduction:

Understanding mechanisms and patterns of biodiversity change—and especially transient temporal dynamics of biodiversity patterns—is important given the many factors that may influence biodiversity. To provide a long term context for recent biodiversity changes, we investigate links between local biodiversity and environmental change over the past 21,000 years.

Questions and tentative expectations:

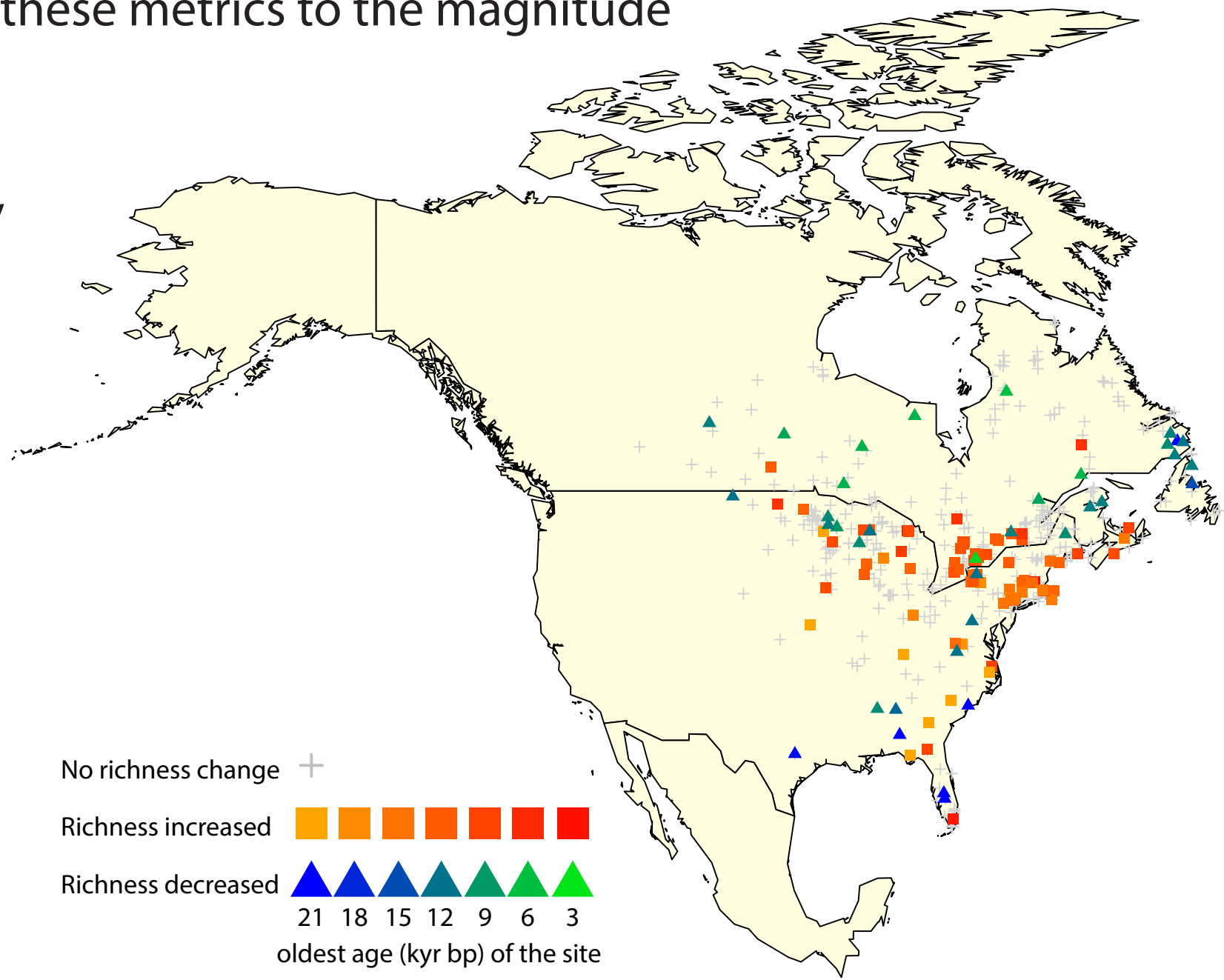
- 1. Is pollen richness stable through time?** Our expectation is that richness will accumulate in the late Pleistocene (at least in glaciated terrain), as taxa respond to environmental change following deglaciation. Whether richness levels off or continues to increase through the Holocene, and whether richness increases or decreases at unglaciated sites, are open questions.
- 2. Are changes in pollen richness related to changes in climate?** If environmental fluctuations pace diversity change, there should be greater changes in richness with greater changes in climate.
- 3. Are there spatial patterns to pollen richness change?** Given the legacy of northern ice sheets, richness should increase more at northern sites than at southern sites. Furthermore, additions of taxa should generally be from taxa with more southerly distributions, while taxa that are extirpated should be centered to the north of sites.

Methods:

Data assembly: We assembled records of fossil pollen genera from lake sediment cores in eastern North America using the Neotoma Paleocology Database (www.neotomadb.org) (Figure 1). Age models for each site were based on Blois et al. (2011). Fossil pollen data were calculated as the abundance of each genus, relative to the total genus sum at each site; these data were then converted to presence-absence if they passed the 5% relative abundance threshold, based on the maximum abundance of the genus across sites in the present day (the optimal pollen abundance threshold determined by Nieto-Lugilde et al. (in revision)).

Richness patterns: We use genus-level richness as a rough proxy for species richness or diversity. We determined mean pollen richness across sites for every 1,000 years from 21,000 years ago to the present (Figure 2), richness change at each site through time, and which specific taxa were added or subtracted from each site at each time step. We compared these metrics to the magnitude of temperature change at each site (Figure 3) based on downscaled CCSM3 paleoclimate simulations (Liu et al. 2009, Lorenz et al. unpub), and to the location of the site relative to the ‘range’ centroid of the genus (Figure 4).

Figure 1. Locations of all sites from all time periods. Sites that show significant increases in richness are indicated in warm colored squares, sites with significant decreases are in cool colored triangles, and sites without significant richness changes are in gray. Significance was determined by a linear model between richness and time at each site. The shading of the icon indicates the oldest age of the time series of pollen richness.



Question 1: Is pollen richness stable through time?

- Yes, the majority of individual sites showed no substantial directional pollen richness changes through time and mean richness across all sites did not significantly change through time (Figure 2a).
- However, some individual sites had significant decreases (36 sites; Figure 2c) or increases (86 sites; Figure 2d) in richness through time. Sites with significant increases through time showed a slight northern bias (Figure 1).

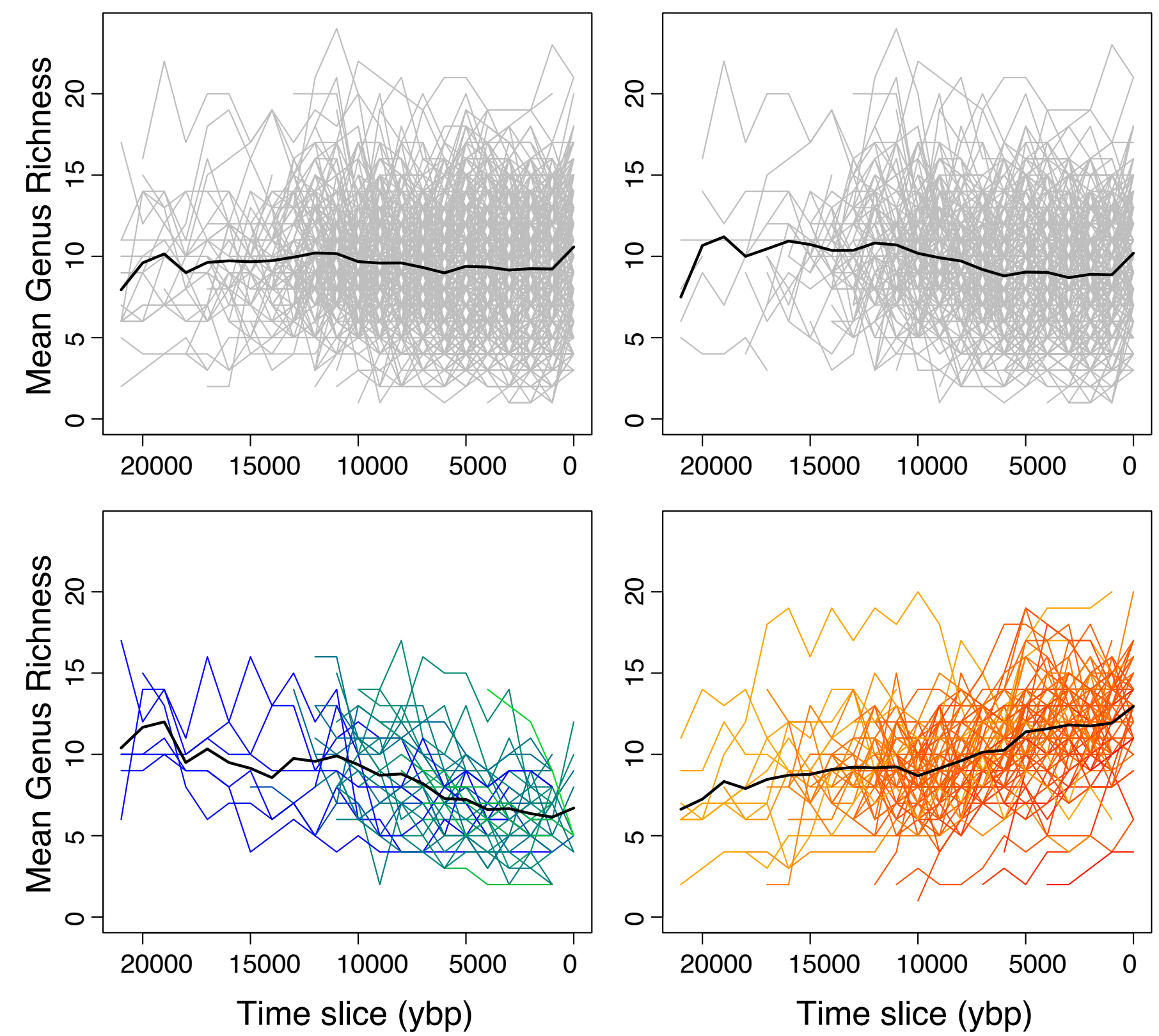


Figure 2. Richness changes through time. Panels show richness change at a) all sites across the dataset; b) sites without significant temporal trends in richness; c) sites with significant decreases in richness through time; d) sites with significant increases through time. In all cases, the thin lines show richness trajectories at individual sites and the thick black line indicates the mean richness across sites.

Question 2: Are changes in pollen richness related to climate changes?

- We examined changes in two ways. First, we compared changes in pollen richness and modeled temperature at a site-by-site level (Figure 3a). Second, we examined mean changes in richness versus mean changes in temperature, for each time step (Figure 3b,c). In each case, there was not a significant relationship between temperature and richness.
- Interestingly, there was a stronger (but still non-significant) pattern in the Holocene (Figure 3c) than in the Pleistocene (Figure 3b), opposite to expectations that diversity should be more strongly affected by larger climate changes.
- Furthermore, there was not a significant relationship with temperature change for sites with significant increases or decreases in richness through time (Figure 1, Figure 2c,d).

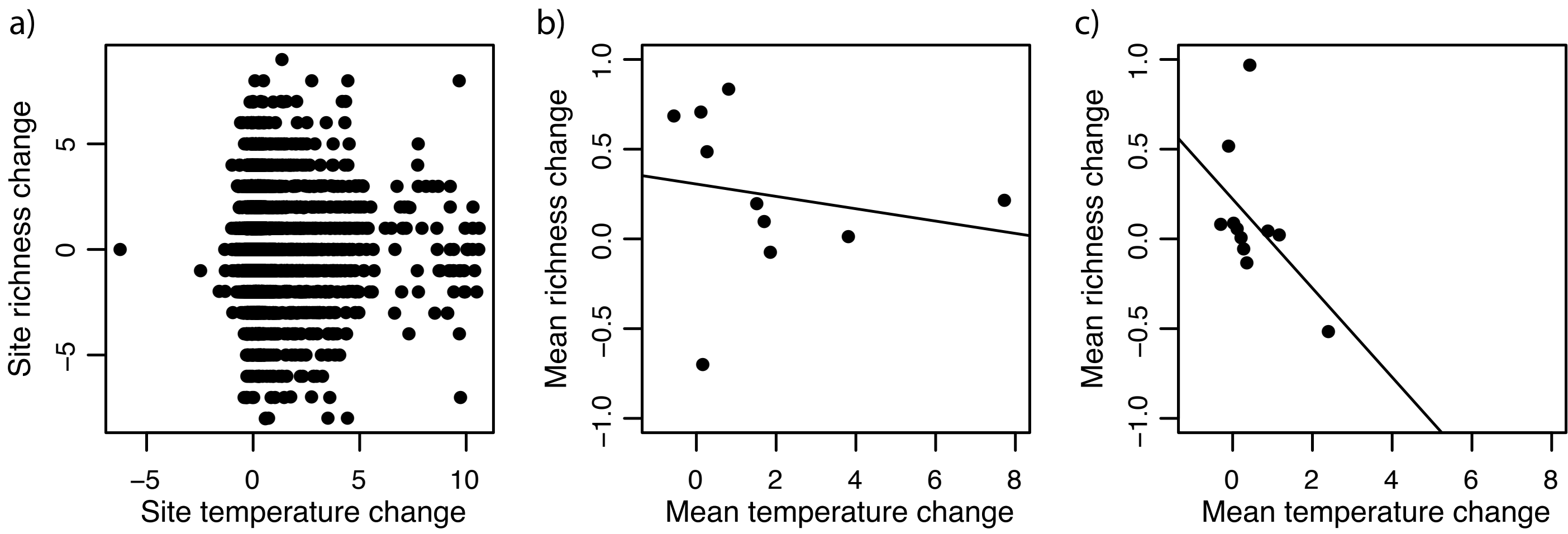


Figure 3. Relationship between richness changes and climate change. There was no significant relationship between the amount of richness change and the amount of temperature change (based on yearly average maximum temperature), either at a) individual sites, b) across sites through the Pleistocene (21,000 to 11,000 ybp), or c) across sites through the Holocene (11,000 ybp to the present).

Question 3: Are there spatial patterns to pollen richness change?

- Most time periods show no spatial patterns of pollen richness change. That is, there was no relationship between richness change and latitude (except for between 13-12,000 ybp and 1,000 ybp to the present) or longitude (except for between 13-12,000 ybp). Richness changes were positively associated with latitude and negatively associated with longitude from 13-12,000 ybp (taxa additions to the north and the west), but negatively associated with latitude from 1,000 ybp to the present (more taxa additions to the south).
- There were no significant differences, between species that were added vs extirpated vs experienced no change, in the overall pattern of direction between the centroids of the taxa ‘ranges’ and local sites (Figure 4).

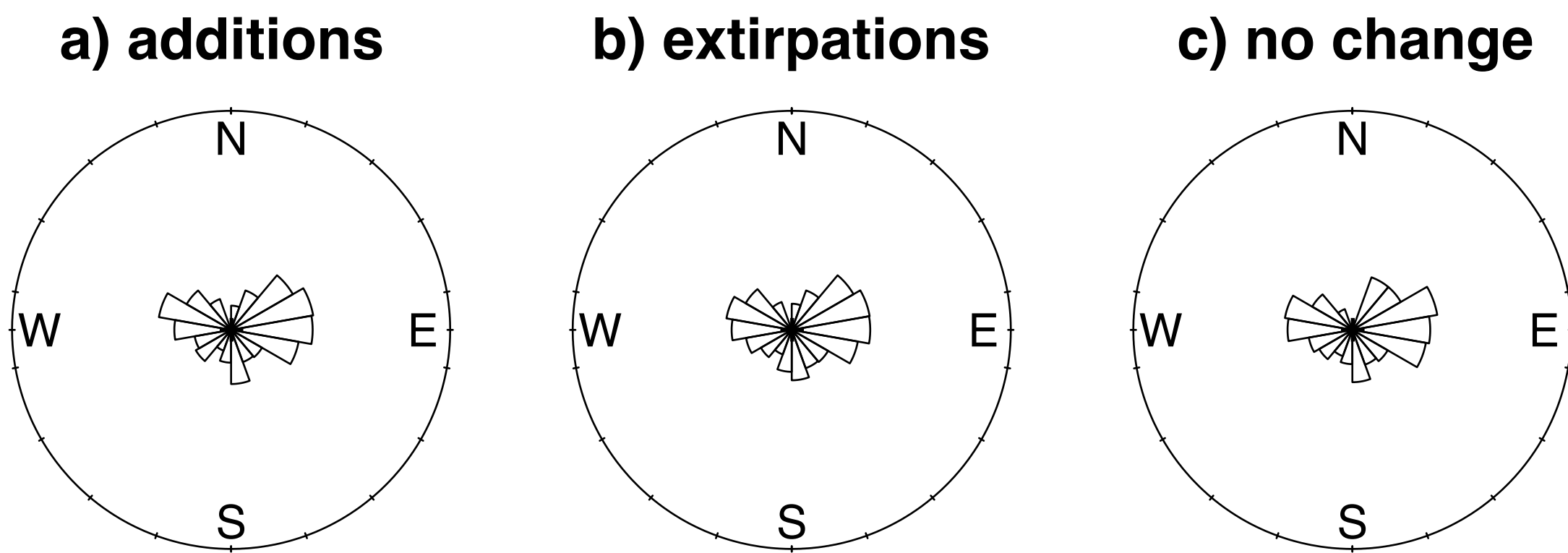


Figure 4. Rose diagrams showing the mean direction of change for taxa that are a) added to a site from one time period to the next; b) extirpated from a site; or c) remain present at a site. The direction depicts the bearing from the centroid of the taxon distribution to the site and thus is only a rough proxy for direction of ‘range’ shift.

Preliminary Conclusions and Next Steps

- While biodiversity at many sites changed substantially through time, there were no mean average changes in pollen richness at sites throughout the late Quaternary: the mean number of genera gained was roughly equal to the mean number of genera lost across all sites, and richness changes at sites were not correlated with changes in climate. These results echo recent findings that alpha diversity has not changed significantly over the past 100 years (Dornelas et. al. 2014), despite compositional change at local sites. They also hint that environmental change maintains diversity in fluctuating environments by influencing colonization and extirpation of different taxa.
- We will next repeat these analyses with other measures of climate besides temperature, with other fossil proxies that may be more sensitive to climate change (e.g., species-level data on plant macrofossils, small mammals), with proportional rather than absolute changes to account for the latitudinal gradient of richness, and within smaller geographic regions such as the Great Basin that may provide more meaningful geographic scales.

Literature Cited: Blois et al. 2011. A methodological framework for assessing & reducing temporal uncertainty in paleovegetation mapping from late-Quaternary pollen records. *Quaternary Science Reviews* 30: 1926-1939; Dornelas et al. 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344: 296-299; Liu et al. 2009. Transient simulation of last deglaciation with a new mechanism for Bolling-Allerod warming. *Science* 325: 310-314; Nieto-Lugilde et al. in revision. Close agreement between pollen-based and forest inventory-based models of vegetation turnover. *Global Ecology and Biogeography*.