**Diversity through Time**

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**Introduction**

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

What is the issue? Brown et al. 2001 suggested that environmental change maintains diversity by influencing colonization and extinction of different species, and when environmental change is sufficiently large it could alter diversity by changing species-level carrying capacity.

Does environmental change maintain or disrupt biological diversity?

If EC maintains diversity then:

1. Richness should be stable through time at individual sites

2. This occurs because either: all/most species maintain presence at site OR as many species colonize as are extirpated from a site.

Overall, genus level richness has been maintained in eastern North America for the past 21,000 years, a time which encompasses very different physical environments. So how is this happening?

- Average richness is maintained, but richness increases in some regions and decreases in other regions. Implies that each region has a species-level carrying capacity which is paced/set by climate change.

- Richness changes are site-specific- some sites have increases in richness and some sites have decreases in richness. No overall species-level carrying capacity.

If colonizations == extirpations, are there particular sets of taxa involved in these changes? Or is there a spatial pattern to the changes?

But what about other aspects of “diversity”? A large body of literature shows that it’s not just about whether overall taxonomic richness is maintained- are most taxa maintaining their commonness? Or are taxa becoming more rare?

**Questions and predictions**

Question 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.

Question 2: Are changes in pollen richness related to climate changes? If environmental fluctuations pace diversity change, there should be greater changes in richness with greater changes in climate. But there are two components to climate change: the direction of cc and the magnitude of cc.

a. Related to direction of climate change: Latitudinal diversity gradient, and previous work by Currie paper, shows that, in plants, there are more species in warmer places. Thus, as climate warms, there should be more additions of species than removals. Though Currie paper also shows that changes through time are more strongly related to the local spatial gradient rather than the overall LDG.

b. Related to rate of climate change: General: As climate change happens faster, there should be faster changes in species richness. But, if cc happens too fast, then species may not be able to keep up. So perhaps this leads to a threshold effect, where the rate of changes increases to some threshold, then remains stable despite the changes in climate?

Question 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**

We assembled records of fossil pollen genera from lake sediment cores in eastern North America and determined richness change at each site through time.

Data assembly: We assembled records of fossil pollen genera from lake sediment cores in eastern North America using the Neotoma Paleoecology Database (www.neotomadb.org) (Figure 1). We relied on the dataset of fossil pollen sites assembled by Blois et al. (2013) and further refined by Maguire et al. (in prep). Final sites included in the dataset are given in Appendix X. 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. (2015)). We restricted analyses to sites with at least six pollen samples.

Richness patterns: We use genus-level richness as a rough proxy for species richness or diversity. We first calculated genus richness at each site for each sampled time slice, then calculated mean genus richness across all sites for every 500 years from 21,000 years ago to the present (Figure 2). There was no relationship between genus richness and sample size through time. We then determined the site richness trajectory—that is, whether richness increased or decreased at the site through time. We fit a simple linear model through the richness values and stored both the slope and p-value.

We also calculated proportional richness change at each site through time, based on the number of taxa added or subtracted from a site between time n+1 and n, divided by the number of taxa at the site at time n. We defined strong change as We determined whether there were time periods that consistently showed strong proportional changes across sites.

We determined 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).

Significance of change 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.

Spatial patterns: I then examined the taxa underlying those changes to determine 1) if more compositional change occurred during times of rapid climate change and 2) the spatiotemporal patterns underlying taxonomic changes (i.e., average direction and distance of colonization or extirpation); I compared these changes to similar metrics of climate change.

**Result**

The majority of sites showed no substantial directional changes and the mean richness across all sites did not significantly change through time. However, some individual sites had either significant increases or decreases in richness through time.

**Question 1: Is pollen richness stable through time?**

• Yes, in the aggregate. 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).

**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.

• 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 cli- mate changes.

• 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). 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 ypb (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).

**Discussion**

• 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 environ- ments 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 gra- dient of richness, and within smaller geographic regions such as the Great Basin that may provide more meaningful geographic scales.

These results will illuminate whether environmental change maintains diversity in fluctuating environments by influencing colonization and extirpation of different species.