Latitudinal trends in genus richness of vascular plants in the Eocene and Oligocene of North America

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ABSTRACT

The latitudinal richness gradient is a frequent topic of study on the modern landscape, but its history in deep time is much less well known. Here, we preliminarily evaluated the paleolatitudinal richness gradient of vascular plants for the Eocene (56-33.9 million years ago) and Oligocene (33.9-23 million years ago) epochs of North America north of Mexico using 201 fossil floras. We calculated the direction and shape of the gradient using quadratic regression to detect linear and curvilinear trends. We performed regressions for the Eocene and Oligocene as well as for informal time intervals within the Eocene: early, middle, and middle + late. We found that quadratic models better explain the data than linear models for both epochs as well as for the early Eocene. A roughly linear trend in the middle and middle + late intervals may reflect limited sampling of high latitude floras for those times. The curvilinear relationship was weak for the Eocene and the model showed a peak in richness at 45.5°N. The curvilinear relationship was much stronger for the Oligocene and the peak occurred at 48.5°N. In the Eocene, the mid-latitude peak in richness may be explained by mean annual temperature, which was probably higher at some mid-latitudes than at lower ones. For the Oligocene, the peak in richness at mid-latitudes may be explained by evolutionary diversification within the temperate zone or by increased aridity at low latitudes. We also assessed the latitudinal richness gradient of genera within modern floras in North America north of Mexico and we found a weak, curvilinear trend with a peak in richness at 31.5°N. Our results suggest that the latitudinal genus richness gradient of vascular plants in North America continued to develop into its modern structure following the Oligocene.

von Humboldt (1807) is credited with being the first to describe the latitudinal species richness gradient (hereafter, latitudinal gradient); that is, that species richness generally increases along lines of latitude from the poles to the equator or tropics (Willig et al., 2003; Fuhrman et al., 2008; Archibald et al., 2010; Brown, 2014). The latitudinal gradient is understood to be a strong determinant of biodiversity patterns and is apparent for most taxonomic groups and ranks (e.g., Ricklefs and Renner, 1994; Williams and Gaston, 1994; Balmford et al., 1996; O'Brien et al., 1998; Qian, 1998; Willig et al., 2003; Wagner et al., 2007; Mannion et al., 2011). The latitudinal gradient may result from one or more

evolutionary, ecological, or earth history process, and its causes are widely discussed and debated (reviewed in Willig et al., 2003; Mittelbach et al., 2007).

Extant vascular plants exhibit the general trend of increasing species richness with decreasing latitude (Fischer, 1960; Gentry and Dodson, 1987; Barthlott et al., 1996; Qian, 1998; Ellison, 2002; Mutke and Barthlott, 2005; Barthlott et al., 2007; Qian et al., 2007). This is especially true when richness is measured across geographic extents spanning several degrees of latitude or more (Willig et al., 2003). For example, Gentry and Dodson (1987) showed that the species richness of epiphytic plants decreases from 46 in southern Florida to 41 in central Florida and to two in northern Florida; across an area representing approximately 5° of latitude. Vascular plants also exhibit the typical latitudinal gradient

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at the taxonomic ranks of genus (Qian, 1998) and family (Ricklefs and Renner, 1994).

The latitudinal gradient is well-documented across the modern landscape but is rather poorly understood through deep time, especially for terrestrial organisms (Willig et al., 2003). The latitudinal gradient in deep time has been most often studied among marine organisms, which are much more likely to be preserved in the fossil record than their terrestrial counterparts and which show clear increasing richness with decreasing latitude since at least 500 million years ago (MYA) (Blackburn and Gaston, 1996; Willig et al., 2003; Jablonski et al., 2006; Marshall, 2006; Mannion et al., 2014; Zaffos and Miller, 2014). Investigations of the latitudinal gradient of vascular plants in deep time are very few in number. A pollen-based study by Harrington (2004) used pooled samples representing regional Paleocene/early Eocene (~58-47.8MYA) floras of the Gulf Coast, mid-latitude Rocky Mountains, and Canadian Arctic islands and detected a uniformly declining latitudinal gradient roughly similar to that of the present day. A study of European tree species spanning a time interval of 13 to 1 thousand years ago showed that the species richness gradient was well established in Europe by at least 13 thousand years ago (Silvertown, 1985). Additional studies of the latitudinal gradient of vascular plants in deep time are needed to improve understanding of the evolutionary, ecological, or earth history processes that have facilitated the present day arrangement of botanical diversity (Qian et al., 2007; Powell, 2009; Mannion et al., 2014).

In this study, we conducted an investigation of the latitudinal gradient of vascular plant genera in the Eocene (55-33.9MYA) and Oligocene (33.9-23MYA) epochs of North America north of Mexico by analyzing a large number of fossil floras and by inferring richness from macrofossils. Specifically, we sought to detect a relationship between genus richness and paleolatitudes of Eocene and Oligocene fossil floras within the study region.

1. Materials and methods

1.1. Sampling floras

For purposes of this study, our sampling units were fossil floras within the Eocene and Oligocene epochs. We defined a fossil flora as a list of macrofossil species representing one collection effort for a single well-defined stratum and geographic location (see Greenwood, 1991; DiMichele et al., 2004). Therefore, we treated collections from the same stratum at different geographic locations as representative of different fossil floras. Arguably, this resulted in some lack of independence among our fossil floras, especially among those representing geographically close locations of the same stratum. However, most studies across fossil localities must make similar decisions on what constitutes a sampling unit, and such decisions may run some unavoidable risks of either introducing unwanted autocorrelations or combining geographically distinct, botanically unrelated floras (Barghoorn, 1951; Crane and Lidgard, 1989; Greenwood, 1991).

We obtained lists of published fossil floras representing the Eocene and Oligocene of North America by using four literature sources, because no single literature source provided a comprehensive list (see Wing, 1987; also Powell, 2009 and Alroy et al., 2008 regarding comprehensiveness of the Paleobiology Database at https://paleobiodb.org/#/). Our four sources were: (1) Penhallow (1908), (2) Hollick (1936), (3) Barghoorn (1951), and (4) Wolfe et al. (1998). Each source indexed fossil floras, and for each flora, we assessed the availability of its species list (i.e., digitally or in print; from the original source or reprinted) and its consistency with our definition of a fossil flora. For the fossil floras from Penhallow (1908) and Hollick (1936), we used more recent publications to assign the fossil floras to epochs (namely MacNeil et al., 1961; Nokleberg et al., 2000) and retained only those of Eocene and Oligocene age. For all floras, we verified their geological age using Geolex (http://ngmdb.usgs.gov/Geolex/search) and a survey of the literature, and we assigned each Eocene flora to intervals comprising early, middle or early, which correspond to the Ypresian (56.0-47.9MYA), Lutetian/Bartonin (47.9-37.8MYA), and Priabonian (37.8-33.9MYA) ages, respectively. We performed our downstream analyses using the most current and widely accepted epoch and interval for each flora, but we present date ranges from Geolex or found among the literature in Appendix 1 to show where disagreements currently exist. Notably, future refinements in the geological age of the floras could affect our outcomes and necessitate updates to our analyses. In total, we recovered 201 fossil floras, of which 172 were of Eocene age and 29 represented the Oligocene (Table 1; Appendix 1).

We obtained digitized lists of genera present in the floras from the Paleobiology Database (https://paleobiodb.org/#/), by applying optical character recognition (OCR; online tool at http://www.onlineocr.net/) to .pdf files of species lists, or via manual data entry. We retained the genera as determined by the original authors, and we did not perform taxonomic reconciliation. Taxonomic reconciliation involves standardizing a dataset by applying names from a single source, or a few sources (Isaac et al., 2004). Previously, the effects of taxonomic reconciliation on genus richness were tested by Wagner et al. (2007) on a dataset comprising fossil marine mollusks. The authors obtained data records for mollusks from the Paleobiology Database and reconciled generic names by uniformly applying their own expertise and the most current literature (Wagner et al., 2007). Wagner et al. (2007) found that genus richness based on the raw and reconciled lists were similar for the three geochronological time units included in their study. Similarly, the negligible effects of reconciliation on richness were also demonstrated by comparing studies on trilobites (Foote et al., 2007). Thus, we used the generic names from the original sources to calculate genus richness of each flora.

We obtained the modern geo-coordinates of each fossil flora. Initially, we estimated the geo-coordinates for the floras using GeoLocate software (Rios and Bart, 2010) in its web application mode. GeoLocate works by parsing strings of location information, which we supplied for each flora from the original or a secondary source. In cases where GeoLocate could not resolve geo-coordinates

Table 1
Summary of Eocene and Oligocene fossil floras used in this study.

Age of flora	# of floras	Minimum paleolatitude (°N)	Maximum paleolatitude (°N)	Average genera[a]
Eocene	172	26.3	54.8	15
Early	139	26.3	54.8	12
Middle	29	26.5	53.8	11
Late	4	44.6	48.0	23
Oligocene	29	28.5	68.7	22

[a] Rounded to the nearest integer.