Range Mapper: An adaptable process for making and using interactive, animated web maps of Late-Quaternary open paleoecological data

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Abstract

Here, we describe our process of developing Range Mapper, a new set of online interactive and animated visualizations of plant taxon range shifts since the Last Glacial Maximum. These animated maps of taxa distributions since the last deglaciation, based upon spatiotemporal networks of fossil occurrences, offer adaptable visualizations of species range shifts in response to past climate and other environmental changes. They are designed to be useful both for experts for quick-look insights into past patterns and processes at broad scales and for educators and science communicators interested in sharing knowledge about how species adapt to changing climates. Prior generations of animations, such as Pollen Viewer, lacked open-source code and so were not easy to update, and the underlying software no longer complies with internet security standards. Range Mapper maps data from the Neotoma Paleoecology Database using CARTO VL, an open-source JavaScript library for creating dynamic and modifiable web maps that interoperates with CARTO's software-as-a-service platform. Specifically, we downloaded, processed, and temporally interpolated 1204 georeferenced pollen records from Neotoma ranging from 21,000 years ago to present. Then, we created maps for North America, Europe, and Oceania using Carto VL's web mapping features to build the spatiotemporal animated sequences, define visual design parameters, and add interaction controls. Range Mapper illustrates major shifts in taxa distribution over the last 21,000 years on all three continents. All workflows are publicly available on GitHub and Zenodo, allowing interested users to extend this approach to other taxa, regions, and times.

Keywords: animated map, geoinformatics, pollen, Quaternary, range shifts, science communication, software as a service (SaaS), vegetation dynamics

Introduction

Here, we describe our process for developing Range Mapper, a new series of online interactive and animated visualizations of plant taxon range shifts since the Last Glacial Maximum. Open scientific databases have proliferated over the last few decades (Diepenbroek 2018; Peters & McClennen 2016; Uhen et al. 2013; Williams et al. 2018b), offering new opportunities for both research and education. Many of these databases use free and open-source software (FOSS), common data standards, and online cartographic and visualization libraries to allow scientists, educators, and the broader public to explore patterns and trends in the data. For example, Ocean Data View, a tool to visualize large oceanographic data, allows users to upload and store datasets, then create maps and calculate statistics (Schlitzer 2015). The Paleobiology Database Viewer allows users to examine fossil deposits by location, by geologic period, by taxon, and through diversity over time (Peters & McClennen 2016). The Interdisciplinary Earth Data Alliance brings together multiple geochemical and geological databases and allows the creation of multi-layered maps, 3-D models, heat maps, and more (Carter-Orlando et al. 2017).

The Neotoma Paleoecology Database (Neotoma) is an open-access, community-curated data resource (Williams et al. 2018b) composed of a coalition of constituent databases and managed by expert data stewards (Williams et al. 2018a). Neotoma holds a wide range of paleoecology and paleoenvironmental data including pollen, vertebrate fossils, insects, testate amoebae, diatoms, ostracods, and stable isotopes. Neotoma's data collection is growing, with active data mobilization campaigns for the African Pollen Database, European Pollen Database, Latin American Pollen Database and the Indo-Pacific Pollen Database (Flantua et al. 2015; Fyfe et al. 2009; Giesecke et al. 2017; Grimm et al. 2018; Vincens et al. 2007). The Neotoma software stack and its foundational application programming interface (API) services supports a series of user-oriented software, including the *neotoma2* R package

(https://github.com/NeotomaDB/neotoma2/) and Neotoma Explorer, a mapping interface that allows users to filter and view records based on criteria including taxon, geographical extent, and time period (Williams et al., 2018).

Pollen Viewer was a once popular, but now-defunct Java applet for viewing past range shifts in northern and eastern North America (Figure 1, Leduc et al. 1998; Williams et al. 2004), based on data from the North American Pollen Database, now migrated into Neotoma. Even before Pollen Viewer ceased to operate, its underlying maps were increasingly out of date, because the interpolated GIFs were based on mapped data syntheses conducted in the late 1990's and early 2000's (Shuman 2002; Williams et al. 2004) and did not incorporate new sites or advances in age-depth modeling. The *neotoma2* R package uses the Neotoma APIs to support data retrievals from Neotoma and data searches for sites, chronologies, publications, and more that match search parameters – e.g. spatiotemporal boundaries, taxa, or author (Goring et al. 2015). Several third-party applications now use the Neotoma APIs or R package to generate fossil distribution maps for expert and public audiences (Loeffler et al. 2021; Martin & Harvey 2017), but no resource yet supports interactive, dynamic, and modifiable mapping of past species distributions from Neotoma data holdings. Creating visualizations that are readily adaptable to different regions, taxa, and time periods is essential to maximize the potential for open scientific databases to serve broad and diverse user communities.

Further, the increasing number of software-as-a-service (SaaS) web mapping resources have opened new opportunities for both making and using visualizations of open scientific databases (Roth et al. 2014). SaaS describes a model in which a client uses services from a provider's software and receives technical assistance, through direct payment for services or

institutional service licenses (Turner, Budgen & Brereton 2003). Cloud-based resources for geovisualization allow quick views of spatiotemporal patterns contained within large data and also lower barriers to developing high-quality new visualizations by reducing the level of expertise required. The resulting open-source workflows can be readily adapted to support authentic place-based teaching and science communication (Myrbo et al, 2018).

In this article, we describe our reusable and adaptable process for harnessing open source and SaaS web mapping resources to visualize Neotoma paleoecological records in the newly developed Range Mapper (https://geography.wisc.edu/rangemapper/). Specifically, we draw on CARTO (formerly CartoDB), a commercial cloud-computing platform that provides database management, geospatial analysis, and interactive and animated web mapping for large spatiotemporal datasets (https://carto.com/). Range Mapper uses the CARTO Vector Library (VL) to visualize networks of fossil pollen data for three regions—North America, Europe, and Oceania—to show the shifting distributions of selected plant taxa since the last deglaciation. In the following sections, we describe our methods and design considerations, showcase example visualizations, and explain the underlying workflows to support future use and adaptation of Range Mapper and CARTO for other biodiversity and paleodata mapping contexts.

Methods

The creation of Range Mapper followed a two-stage process: data acquisition and processing in R and subsequent web mapping in CARTO. We designed the methods and walkthroughs to be understandable to users with some paleoecology or ecology background and a wide range of experience with coding.

We used the *neotoma2* R package and the underlying Neotoma APIs to download and process pollen data (Figure 2). We downloaded all records from 21 ka before present (BP) to present in bounding boxes for North America, Europe, and Oceania. The total download included 3,432 unique records. We included these North American woody taxa: *Alnus* (alder), *Fagus* (beech), *Picea* (spruce), *Pinus* (pine), *Quercus* (oak), *Tsuga* (hemlock), and *Ulmus* (elm), and herbaceous taxa: *Ambrosia* (ragweed), Cyperacaeae (sedges), and Poaceae (grasses). For Europe, we selected *Alnus* (alder), *Fagus* (beech), *Picea* (spruce), and *Quercus* (oak). We included the Oceanian taxa: *Nothofagus* (Southern Beech), *Callitris* (cypress-pine), *Phyllocladus* (celery pine), *Casuarina* (she-oak), and *Eucalyptus* (eucalyptus). These taxa were chosen because of their widespread abundance and to highlight known past dynamics of interest; other users interested in developing variants of Range Mapper could choose other taxa. In R, we removed records with uncalibrated radiocarbon time series as their default and without the above taxa of interest, resulting in a filtered dataset of 2,635 unique records and 139,720 samples.

We then calculated the percentage of each taxon found at a site at a given time, relative to sums of all upland herbs and trees for that site and time, using Neotoma's ecological groupings, which are ecological and taxonomic sets used when organizing stratigraphic diagrams and taxa lists (Goring 2022). Sites were not shown for a taxon if zero pollen grains of that taxa were reported for the site and timestamp being mapped. Although pollen analysts sometimes use non-zero minimum pollen percentages for each taxon to determine presence/absence, for Range Mapper. a taxon is mapped as 'present' if at least one grain is reported for a given site and time period, but low-abundance sites are visually downweighted relative to high-abundance sites through the proportional symbol size. Then, we did a simple temporal interpolation and binning of the samples in each record, in which we rounded the year of each sample to the nearest 500

years and averaged the pollen percentages for each taxon across all samples in each 500-year time interval. We exported the CSV tables of the interpolated pollen data from R. We provide two R Markdown documents: 1) a simplified walkthrough file for others wishing to make their own variant of these dynamic maps and the methods file for full reproducibility as Supplementary Information and at the Github repository

(https://github.com/NeotomaDB/RangeMapper/tree/master/workflows). Then, we created an account in CARTO and uploaded the CSV tables for each continent to our CARTO account. We also uploaded the publicly available North American and European ice sheet files for the last glacial maximum and deglaciation from Dalton et al. (2020) and Hughes et al. (2016), each of which comprise sets of polygons representing continental ice sheet extents at multiple time periods, to our CARTO account in JSON format (JavaScript Object Notation, a popular data standard for web mapping).

Once the data frames were uploaded to CARTO, we leveraged CARTO VL to create free-to-use, dynamic web maps of pollen fossil pollen abundances for Range Mapper. CARTO VL is a custom, open-source Javascript library that interacts with proprietary CARTO SaaS APIs to build custom maps through in-browser vector rendering, and thus requires free educator/student license or paid commercial license (https://docs.carto.com/faqs/categories/carto-for-education/) to make new maps but not to use hosted maps. We set up a web directory with an HTML file with code to create the map document and widgets, set animation parameters for taxa and ice sheets, and create the map layers (Figure 2). To access our data, we entered our username, API key, and the name of the CSV into the HTML file.

The CARTO VL package enables compact setting of parameters for each animated map visualization. For example, CARTO VL uses the *filter* parameter to animate a map. We set *filter* equal to @animation. Then, we define the @animation variable as an animation that proceeds through the values in the time column of the data frame from -21,000 to 0 years BP. We also input values for the initial animation duration and the fade duration, indicating how long the symbol will appear on the map before and after its timestamp to make a smooth visual transition between timestamps. To create the proportional symbol for the pollen percentage of the taxa, we set the width parameter to be equal to the samples column in the data frame (which holds pollen percentages), multiplying this value by the formula for apparent magnitude scaling, so that users will interpret the proportional symbol size correctly (Flannery 1971). We first implemented the web directory for the North American data frame and later modified the HTML document to integrate the data frames for North America, Europe, and Oceania. We also built a custom user interface using JavaScript for the loaded layers (Figure 3). We modified CARTO VL example code to create the time control and interactive taxa components, and built the continent selection dropdown menu, the proportional symbol legend, and the acknowledgements sidebar from scratch.

All workflows are posted to GitHub (github.com/NeotomaDB/RangeMapper) and Zenodo (https://zenodo.org/record/7600912), so that other interested users can extend this approach to other regions, times, and taxa. The GitHub repository includes the actual workflows used here and the introductory R Markdown and CARTO VL walkthroughs for pollen and mammal data.

Results

The Range Mapper interface includes five component panels: the map, the widget panel with options for animation playback, an interface for continent selection, another interface for taxa selection, and the acknowledgements sidebar (Figure 3). The map, which also includes graphical elements for the proportional symbol legend and interactive zoom bar visualizes the pollen percentage for each taxon and ice sheet extent for each time step. Using the animation playback controls, the user can jump to a selected time period as well as play, pause, slow down, and speed up the animation. Changing the continent selection via the drop-down menu recenters the map on the continent of interest and loads its taxa. The user can add or remove taxa from the map by clicking a taxon's name on the interactive taxa legend. The proportional symbol legend shows the size of a circle for 20, 50, and 100 percent pollen for reference. The user can zoom in/out and pan to different locations using the controls in the bottom left of the screen or directly manipulating the map with the mouse and mouse wheel.

The completed visualizations are interactive and illustrate major shifts in taxa distribution over the last 21 ka years on all three continents. North America's Range Mapper includes western North America, which has had few major mapped syntheses of late-Quaternary plant distributions (Figure 4) (COHMAP Members 1988; Thompson & Anderson 2000). Range Mapper shows the rapid changes during the early to middle Holocene (16-8ka BP), as well as the relative stability of eastern North American vegetation patterns during the full-glacial period and the mid-to-late Holocene (Williams et al. 2004). The unique trajectories of different taxa and different taxa associations over time also are apparent. *Picea* expands northward earlier than other taxa and then declines across the eastern US from 10 to 8 ka BP (Jacobson, Webb & Grimm 1987; Webb 1986). Tsuga expands to the north and west from the east coast, while Ouercus expands northwards across the Northeast and Midwest (Davis 1983). We can see the emergence of mid-Holocene *Ouercus*-Poaceae savannah in the upper Midwest and that the ranges of Fagus and Tsuga did not always overlap as they do today (Williams et al. 2004). The massive deforestation and other land cover changes caused by EuroAmerican colonists during the last 200 to 400 years are less apparent in these maps (Webb 1973), because of the 500-year bins used for the pollen data shown here.

In Europe, other prior mapped syntheses have described the major patterns in vegetation dynamics over the last 20 ka (Brewer et al. 2017; Giesecke et al. 2017; Huntley 1990), which Range Mapper effectively reproduces. Range Mapper shows the rapid northward expansion of *Alnus*, always near the edge of the ice sheet, from the end of the Quaternary onwards (Giesecke et al. 2017). The three main refugial populations of *Quercus* on the Iberian peninsula, Italy, and Turkey/Syria between 15 and 21 ka BP are also clearly visible at the beginning of the visualization (Brewer et al., 2002) (Figure 5). As the animation progresses, Range Mapper depicts the rapid range expansion of *Quercus* at the onset of Holocene warming, and the late Holocene expansions and westward shifts of *Picea* and *Fagus* population centers (Giesecke & Bennett 2004; Saltré et al. 2013). Interested users could readily add additional taxa to the European map to gain a more complete picture of taxa range shifts since 21ka BP.

While Neotoma data for Oceania are still relatively sparse, some important patterns and population changes are visible (Figure 6). As Range Mapper shows, Tasmania has the highest regional density of records currently in Neotoma. Prior to 12 ka BP, Tasmania was connected to Australia, allowing species to disperse more easily between these now disconnected landmasses. While sea level rise is not captured currently by Range Mapper, a user could choose to add the layer relatively easily. Range Mapper clearly shows first the expansion of *Eucalyptus* in

Tasmania between 11.5 and 9.5 ka BP and then the expansion of *Nothofagus* rainforests after ~9 ka BP (Beck et al. 2019). Nothofagus and Phyllocladus pollen often appear together, because they are both wet sclerophyll forest and rainforest taxa (Fletcher et al. 2014; Colhoun & Shimeld 2012). Starting at about 4 ka BP, fire-sensitive taxa, such as Nothofagus, declined in abundance, while fire-resistant taxa like Eucalyptus expanded (Beck et al. 2019; Mariani et al. 2019), which is clear in Range Mapper. The higher values for fire-sensitive Casuarina pollen in northeastern Australia at about 10 ka BP are consistent with previously described vegetation and fire histories in the region (Haberle 2005). Range Mapper will soon support additional ecological research and education in the Oceania region, as a data mobilization campaign for Indo-Pacific pollen data is underway as part of the CABAH project (https://epicaustralia.org.au/). This campaign will allow researchers to do more regional studies on ecological change in the Indo-Pacific, such this recent analysis of vegetation turnover of 24 sites in islands in the Bass Strait, Tasmania, and southeast Australia during the late glacial and early Holocene (Adeleye et al. 2021). This work will also situate these regional trends within global analyses designed to better understand the human, climate, and other drivers of past vegetation change, assess ecological sensitivity to climate change, and integrate pollen data into interdisciplinary research. As this work proceeds, the Range Mapper animations shown here can be readily updated to include new sites and taxa.

Discussion

The Range Mapper visualizations draw upon open data resources for late-Quaternary fossil pollen and ice sheet distributions to provide broad and readily adaptable visualizations of past vegetation dynamics, in which climate change was a primary driver. The open workflows provided here offer increased flexibility in both the creation and use of interactive and animated web maps for displaying paleoecological data. The maps use proportional symbols, a visualization technique first used in palynology by von Post in hand-drawn maps of pollen data (von Post 1924), later were generated by computer, and now, are generated on the fly by the CARTO VL servers.

The data processing by CARTO VL servers simplifies the animation process by removing the need to create individual snapshot images for each time period, as was necessary with Pollen Viewer and other earlier map series (Bernabo & Webb 1977; Jacobson, Webb & Grimm 1987; von Post 1924; Webb III et al. 1993; Williams et al. 2004). Both Pollen Viewer and Range Mapper users select a taxon from a predefined list (Williams et al. 2004), but Range Mapper users can select any combination of taxa within the set of taxa shown, while Pollen Viewer offered a more limited set of pre-built multi-taxa combinations. This additional flexibility is especially useful for scientific hypothesis generation and exploratory exercises in university classrooms and is a major reason we chose proportional symbols over heatmaps or other visualization methods.

Proportional symbols encode information by varying symbol size rather than the symbol shape, color, texture etc. Size is a salient visual variable that is perceived quantitatively (i.e., as a numerical gradient) and therefore enables greater visual discriminability of the symbolized data than maps reliant on the ordinally-read (i.e., as ranked classes without easy numerical estimate) visual variables such as choropleth and heat maps (MacEachren 1994). This perceptual advantage potentially is more important on animated maps that grow in visual complexity and may suffer from "change blindness", or the inability to notice and attend to all important changes

in animated maps (Fish, Goldsberry & Battersby 2011). Animated proportional symbols also evoke a visual metaphor of abundance increases or decreases at specific sites, versus areal spread (as with heat maps) or administrative change (as with choropleth maps) (Kraak et al. 2021), and therefore better showcase the Neotoma dataset for classroom and data-driven exploration. To replicate the ease of adding a Pollen Viewer animation to a presentation, we have created a separate Zenodo upload with MOV videos of selected single taxon and multi-taxa Range Mapper animations (https://zenodo.org/record/7626576).

Users can repeat and adapt the processes outlined in the Range Mapper R and HTML scripts for other regions, time periods, taxa, and paleoecological data types by following the instructions in the walkthrough documents on GitHub (https://github.com/NeotomaDB/RangeMapper/tree/master/workflows) and the guides on the CARTO VL website (https://carto.com/developers/carto-vl/). The scripts are already configured to process and visualize proportional data such as pollen abundance. Hence, users could readily create CARTO animations for other micropaleontological datasets in Neotoma (e.g., ostracod, diatom, and testate amoebae) with few alterations and limited coding knowledge (e.g., Amesbury et al., 2018). Some paleoecological data types may need further preparatory work or minor adjustments to these workflows. For example, one hurdle for mapping diatom data is the disconnect between classic systematics, which grouped species into genera based on characteristics that aided identification, and modern systematics, which arranges species based on phylogenetic relationships (Cox 2009). Reworking the diatom systematics, so that older records can easily be integrated into analyses, is in progress (D. Charles, pers. comm.). Terrestrial vertebrate records could be represented as points if presence-only information is available or proportional symbols for abundance data.

The CARTO zoom and pan interactions allow detailed explorations of past vegetation dynamics at local to global geographic scales. Accordingly, Range Mapper can be readily extended to other regions and spatial resolutions to provide researchers with additional tools for hypothesis generation and conference presentation, while also enabling educators to create place-based and culturally relevant ecological examples for classroom instruction, e.g., mapping common plant taxa in their region. When extending to new regions, the primary need is to choose appropriate lists of taxa and time periods from Neotoma for mapping. We chose the last 21,000 years because there are many records and good radiocarbon dating control. Shorter time domains, e.g., for networks with high-precision chronologies for the last several thousand years, require only minor adjustments to the source code. A longer time domain, such as the last interglacial (Felde et al. 2020), also is feasible, but will result in an animation supported by sparser datasets and often more uncertain age constraints than shown here.

Range Mapper is supported by Neotoma's open and well-vetted datasets. Neotoma follows a community curation model in which expert data stewards check taxonomy, age models, and other key information as they add new datasets into Constituent Databases that comprise Neotoma (Williams et al. 2018a). One potential limitation of Range Mapper is the varying quality of the age models used for the temporal interpolations. Range Mapper simply uses the available default age models in Neotoma, which will vary in the number and precision of their supporting age controls (Blois et al. 2011; Giesecke et al. 2014), the radiocarbon calibration curves chosen, or the choice of age-depth model. There is an on-going effort to generate new and better age-depth models for Neotoma data holdings (Wang, Goring & McGuire 2019). While we removed datasets with only uncalibrated radiocarbon age models, the default age models of some older sites have not all been updated with the most recent radiocarbon

correction curve or preferred method of calculating an age model (e.g., Blaauw & Christen 2011; Parnell et al. 2008). We chose not to calibrate the datasets with uncalibrated radiocarbon models, because the Range Mapper maps are intended primarily for first-pass hypothesis generation, university-level education, and science communication, rather than full scientific analysis. However, as sites are added to or age models are updated in Neotoma, it is straightforward to occasionally run the Range Mapper R scripts and upload new versions of the data frames to Carto to update the map's datasets.

In contrast to Neotoma, which is an open-access database, and Range Mapper, whose scripts are freely available on Github, CARTO VL is proprietary software. All maps are free to use but uploading data and building and hosting maps requires a CARTO license. CARTO offers free licenses to educators and students and discounted licenses to researchers, education professionals, and universities but requires others to purchase an individual or institutional license after a free year-long trial. While CARTO's for-profit model potentially limits the audience for Range Mapper's modifiable workflows, most users wishing to visualize other regions, taxa, or time periods will be university-affiliated and thus have access to a free or discounted license. CARTO and other SaaS, like ESRI's ArcGIS Online, offer stability and support over open-source alternatives and have a lower barrier to access overall but are subject to possibly disruptive updates impacting open-source code written on top of the SaaS. For Range Mapper, the advantages of this proprietary software, including powerful data processing and visualization features and large developer communities, outweighed the concerns. Developers of future modifiable visualizations must consider their audience's technical expertise and software access when deciding whether to use SaaS or open-source software in their workflows.

Conclusions

Range Mapper offers a new set of dynamic and interactive mapped visualizations that shows the changing distributions of plant taxa North America, Europe, and Oceania over the last 21 ka BP. Users can interact with the map using animation controls and the interactive taxa legend. These maps will enable users to integrate up-to-date paleoecological data and mapping methods into their research, teaching, and outreach. The workflows available on GitHub enable interested paleoecologists and biogeographers to make their own maps, to support the extension of these visualizations to undermapped regions or taxa. Because the workflows can be quickly rerun as new data come in, the Range Mapper animations can be regularly albeit asynchronously updated as new datasets are added to Neotoma. The Range Mapper animations, supported by the openly available and curated data available in the Neotoma Paleoecology Database, are available to support research and education for a wide variety of audiences.

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Author Contributions

Adrian George designed and coded Range Mapper, drafted the manuscript and figures, and incorporated revisions from other authors. John Williams and Robert Roth conceptualized the project, offered design suggestions for Range Mapper, and edited the manuscript and figures. Sydney Widell helped design and code Range Mapper and wrote the R Markdown walkthrough file.

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Figure Titles & Legends

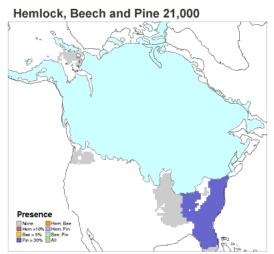


Figure 1: GIF of Pollen Viewer, a now-defunct Java applet, that provided a dynamic visualization of post-glacial range dynamics for various North American plant taxa, based on interpolated surface of fossil pollen data from the North American Pollen Database ca. 1999 (Leduc et al. 1998, Williams et al. 2004).

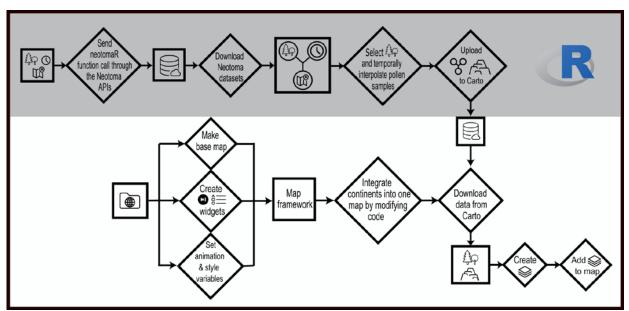


Figure 2: Flowchart showing methods for generating the Range Mapper animated maps; objects are in square boxes while actions are in diamonds. We used the *neotoma2* package in R (top, in gray) to select taxa (trees icon), time period (clock icon), and location (map icon), download datasets (online web services such as the Neotoma database represented by stacked circle icon) from the Neotoma server and process the datasets. We then uploaded the pollen datasets and ice sheets (stepped hill icon) to the CartoDB server and formatted the interactive map using the CARTO VL JavaScript library in an HTML document (bottom, in white). Each

time the Range Mapper page loads, data are downloaded from the remote Carto server, and layers are created and added to the map.

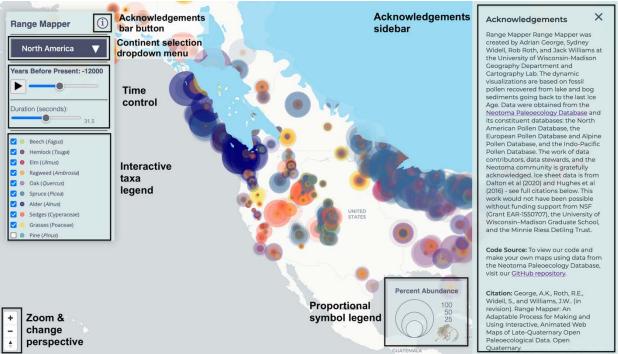


Figure 2: Annotated screenshot of Range Mapper, showing its five panels: the central map, the selector panel for choice of continent, time control panel with buttons and sliders, the interactive taxa legend, and the acknowledgements sidebar. Other graphical elements include the interactive zoom bar and the proportional symbol legend with woodrat icon representing Neotoma. The time control panel allows changes to rate of animation and play/pause, while the interactive taxa legend allows individual selection of taxa for display. Symbol proportion is scaled to pollen percentages calculated as a sum of upland plant taxa. Pollen data are drawn from Neotoma, while ice sheet extents for North America are from Dalton et al. 2020.

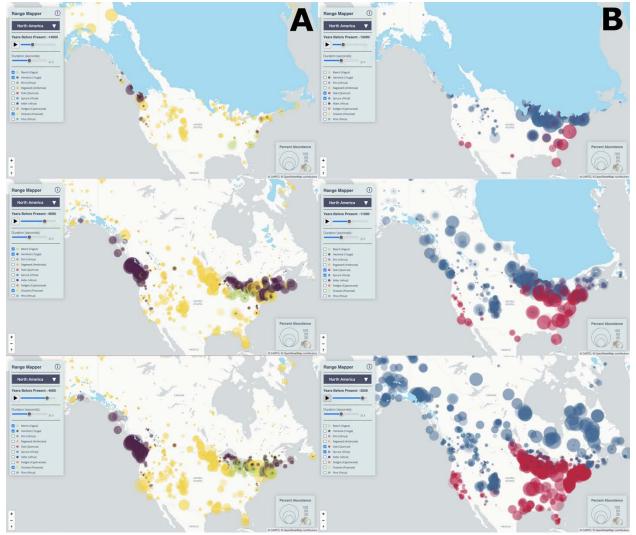


Figure 3: Range Mapper screenshots of North America. 4A) *Tsuga*, *Fagus*, and Poaceae distributions at 14, 6, and 4 ka BP. Vegetation changes shown here include the postglacial expansion of western hemlock (*Tsuga heterophylla*) and mountain hemlock (*T. mertensiana*) in the Pacific Northwest, eastern hemlock (*T. canadensis*) in the northeastern US, the widespread expansion of grass (Poaceae) in the Great Plains, and the beech (*Fagus*) population collapse in the mid Holocene. 4B) Screenshots of *Quercus* and *Picea* distributions at 15, 11, and 2 ka BP show the expansion of oak (*Quercus*) in eastern North America, and the northwards range shift of spruce (*Picea*). Of all the taxa shown here, spruce shows the clearest signals of both leading-edge range exansion into newly suitable habitats and trailing-edge losses of populations at its southern margin.

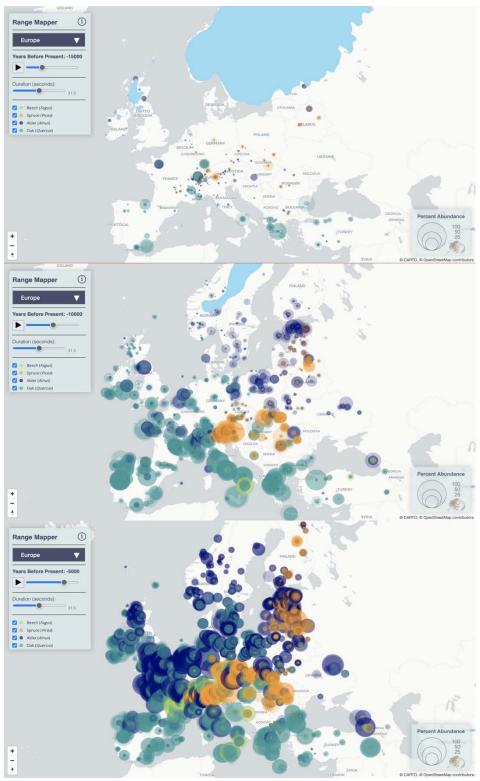


Figure 4: Range Mapper screenshots of Europe from 15, 10, and 5 ka BP. Four iconic tree taxa are shown here: beech (*Fagus*), spruce (*Picea*), alder (*Alnus*) and oak (*Quercus*). Vegetation changes shown by Range Mapper include the known glacial refugia, the post-glacial expansion of beech, rapid range expansion of oak at the onset of Holocene warming, and the late Holocene expansion and westward shifts of spruce and beech population centers.

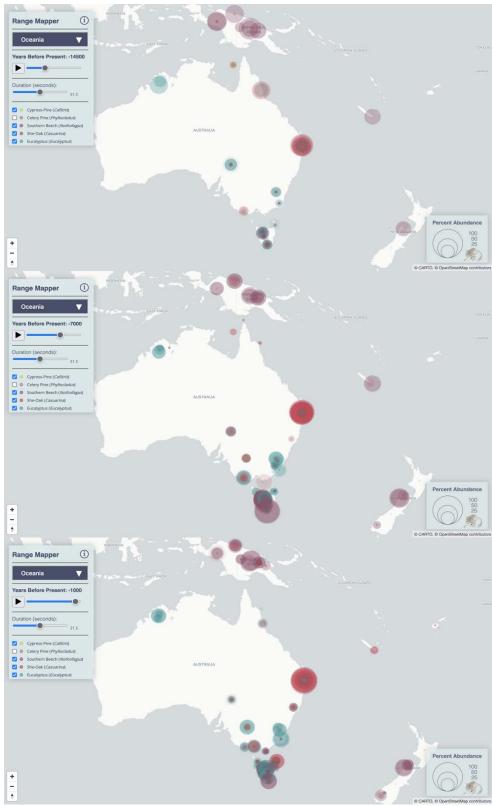


Figure 6: Range Mapper screenshots of Oceania from 14.5, 7, and 1 ka BP. While Neotoma data for Oceania are still relatively sparse, phenomena such as the early Holocene expansion of *Eucalyptus* and *Nothofagus* in Tasmania can be seen.