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Palaeodistribution modelling of European vegetation types at the Last Glacial Maximum using modern analogues from Siberia: Prospects and limitations

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ABSTRACT

We modelled the European distribution of vegetation types at the Last Glacial Maximum (LGM) using present-day data from Siberia, a region hypothesized to be a modern analogue of European glacial climate. Distribution models were calibrated with current climate using 6274 vegetation-plot records surveyed in Siberia. Out of 22 initially used vegetation types, good or moderately good models in terms of statistical validation and expert-based evaluation were computed for 18 types, which were then projected to European climate at the LGM. The resulting distributions were generally consistent with reconstructions based on pollen records and dynamic vegetation models. Spatial predictions were most reliable for steppe, forest-steppe, taiga, tundra, fens and bogs in eastern and central Europe, which had LGM climate more similar to present-day Siberia. The models for western and southern Europe, regions with a lower degree of climatic analogy, were only reliable for mires and steppe vegetation, respectively. Modelling LGM vegetation types for the wetter and warmer regions of Europe would therefore require gathering calibration data from outside Siberia. Our approach adds value to the reconstruction of vegetation at the LGM, which is limited by scarcity of pollen and macrofossil data, suggesting where specific habitats could have occurred. Despite the uncertainties of climatic extrapolations and the difficulty of validating the projections for vegetation types, the integration of palaeodistribution modelling with other approaches has a great potential for improving our understanding of biodiversity patterns during the LGM.

1. Introduction

The Last Glacial Maximum (LGM, ca. 26.5–19 ka BP) was the peak of the last glacial period in the Late Pleistocene when ice sheets were at their maximum extension (Clark et al., 2009). The cold and dry conditions that characterized the LGM in North America and Europe and low concentrations of atmospheric CO_2 (Petit et al., 1999; Otto-Bliesner et al., 2006) strongly restricted the distribution ranges of many species, creating a biogeographic bottleneck with fundamental impact on the present-day distribution of flora and fauna (Newnham et al., 2013; Tzedakis et al., 2013). Our knowledge about the climatic conditions and the vegetation that dominated temperate regions during the LGM in the northern hemisphere is still limited, but new data are continuously contributing new insights to understand vegetation in this critical period (Binney et al., 2017).

Reconstructing palaeoclimate and palaeovegetation for the Quaternary has been traditionally approached by analyzing pollen and macrofossil records (Prentice and Jolly, 2000; Bartlein et al.,

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2011; Feurdean et al., 2014). However these data are geographically sparse for the LGM and restricted to specific sites (Binney et al., 2017). Pollen and macrofossil records are mainly informative for landscape-scale reconstructions around a specific site, but they are insufficient for reconstructing spatial patterns of different vegetation types across broader areas (Huntley and Allen, 2003). Low taxonomic resolution of pollen records (Klerk and Joosten, 2007) coupled with uncertainties related to large variation in pollen productivity and pollen dispersal capacity among species, makes it very difficult to reconstruct the distribution of vegetation at broad spatial scales (but see Gaillard et al., 2008; Sugita, 2007).

A complement to palaeobotanical data is the use of dynamic vegetation models, which are based on the relationships between palaeoclimatic reconstructions, biogeochemistry, hydrology and vegetation formations described through plant functional types (e.g. Allen et al., 2010). These models provide spatially-explicit information about the distribution and productivity of physiognomic vegetation types, most often across large areas such as continents and at a coarse resolution of hundreds to thousands km (Smith et al., 2001). These models are useful for inferring temporal changes in dominant ecosystems and related properties (e.g. productivity), but their applicability for understanding biogeographic patterns is limited due to the coarse nature of the vegetation types used, like biomes, formations or dominant functional types.

Another approach to reconstructing palaeoecological patterns is palaeodistribution modelling (PDM), which assumes the existence of links between species or groups of species and the environment (Svenning et al., 2011; Varela et al., 2011; Franklin et al., 2015). These methods have been proposed for hindcasting the distribution of species by combining present-day data and palaeoclimatic scenarios (Nogués-Bravo, 2009). For example, PDM has provided important insights to understanding the LGM distribution of tree species, suggesting that the general view of central Europe as a treeless landscape should be partly revised (Svenning et al., 2008). Recent modelling studies focusing on individual vegetation types also have suggested the potential of these tools for reconstructing regional habitats in the late Quaternary (Werneck et al., 2011; Potts et al., 2013; Hais et al., 2015). These models are generally calibrated with data on the distribution of vegetation or habitat types defined by species composition or dominant species (Potts et al., 2013). PDM is a promising approach for understanding past distributions of vegetation types that are defined more finely than by dominant plant functional types or biomes. However, it is still rarely applied and needs further development at continental scales and with better spatial resolution (Franklin et al., 2015).

In this study, we use PDM to hindcast the distribution of vegetation types in Europe at the LGM using present-day vegetation data from Siberia. It has been suggested that the European LGM climate has a large overlap with the present-day climate of Siberia (Fløjgaard et al., 2009). There is also biological evidence indicating ecological similarities between present-day Siberia and European regions during the LGM (Kuneš et al., 2008; Meng, 2009; Pelánková and Chytrý, 2009; Horsák et al., 2010, 2015; Magyari et al., 2014; Pavelková Řičánková et al., 2014, 2015). Although these studies suggest that, to a certain degree, present-day Siberian vegetation can be used as a model for understanding European vegetation during the LGM, the climatic analogy between the two periods and regions has not been evaluated yet. Indeed, to our knowledge this is the first attempt at applying PDM to vegetation types that could have occurred during the LGM across the whole European continent. The lack of previous studies is probably due to the difficulty of gathering occurrence data (i.e. present-day distribution of cold- and drought-adapted vegetation types) from areas with a certain similarity to the LGM climates, according to the general assumptions of PDM (Svenning et al., 2011).

We used vegetation-plot data surveyed in the field in Siberia and classified them into finely-defined vegetation types whose distribution is probably driven by climate. We calibrated distribution models for these vegetation types under current climatic conditions in Siberia, and projected the models with a good performance to the climatic conditions in LGM Europe. The reliability of the models was then assessed for different European regions by reviewing the existing literature on palaeovegetation reconstructions based on fossil data and dynamic vegetation models. By considering the uncertainties related to PDM and the assumed similarities in climate and vegetation between the two study regions and periods, we finally discuss the prospects and limitations of PDM for reconstructing European vegetation during the LGM using modern analogues from present-day Siberia.

2. Materials and methods

2.1. Study areas

Siberia occupies an area of 9141 thousand km^2 in the Russian Federation, stretching from the Ural Mountains in the west to the Yablonovyi and Cherskii Range in the east, excluding the Russian Far East (Fig. 1). This region encompasses a broad range of natural conditions, comprising extensive plains, elevated plateaux as well as high mountains. The climate is extremely continental with low winter temperatures throughout the whole region and strong aridity in some areas in the south (Shahgedanova, 2002). According to climatic models (Hijmans et al., 2005), mean July temperature varies between 5 °C in the north and 21 °C in the south, while mean January temperature commonly drops below −20 °C, and in the northeast even below −35 °C. Annual precipitation for most of the region ranges between 150 mm and 700 mm, with a precipitation peak in summer.

LGM Europe corresponds to the extent of Europe during the Last Glacial Maximum (8053 thousand km^2, Fig. 2), considering a decrease in the sea level of 120 m (Peltier, 1994; Yokoyama et al., 2001) and excluding the continental ice-sheet and mountain glaciers (Ehlers and Gibbard, 2004). LGM Europe was characterized by a strong thermal north-south gradient which was strongest in winter (Frenzel, 1992). Mean July temperatures probably ranged from 0 °C in the very north and in the areas adjacent to the ice-sheets, to approximately 20 °C in southern Europe. Mean January temperatures varied between −40 °C in northern Europe and 0 °C in the Mediterranean (Frenzel, 1992; Pollard and Barron, 2003). According to the Community Climate Model System (Gent et al., 2011), annual precipitation showed a strong west-east gradient, being about 1000 mm in western Europe, 500–750 mm in central Europe and 250–500 mm in eastern Europe.

2.2. Vegetation data

Vegetation data were surveyed in the field by recording full species lists of vascular plants in relatively small areas (vegetation plots). Unlike interpreted satellite images or broad-scale vegetation maps, these data make it possible to reliably distinguish different vegetation types that are expected to be largely driven by environmental conditions, especially climate. Vegetation-plot data came from two sources: (1) the Database of Masaryk University's Vegetation Research in Siberia (Chytrý, 2012; GIVD code 00-RU-002, see www.givd.info), sampled from 2003 to 2013 and containing about 1550 vegetation-plot records with GPS coordinates from the Southern Urals, West Siberian Plain, Altai-Sayan Mountains and central Yakutia; and (2) the Database of Siberian Vegetation (Korolyuk and Zverev, 2012; GIVD code AS-RU-002) and related private databases, containing vegetation-plot records with