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Origin of the central European steppe flora: insights from palaeodistribution modelling and migration simulations

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The biogeographic origin of the species-rich steppe grasslands in central Europe has long been debated. The alternative hypotheses are long-term species persistence in situ versus immigration from the south-east, either after the last glacial maximum (LGM) or after the Neolithic landscape deforestation. We ask whether macroclimate-based models of habitat suitability support either of these hypotheses and search for macroclimatically suitable 'source areas' from which species could colonise the areas occupied in Europe today. We modelled habitat suitability for 104 species of the central European steppes and projected these models to 10 periods between the LGM and the present using downscaled CCSM3 simulations. By simulating postglacial migration, we identified potential source areas for each species in the LGM and mid-Holocene and examined whether their location differed among three ecological and five chorological species groups.

The central European macroclimate during the cold phases of the Late Pleistocene was suitable for species now typical of Asian desert steppes, whereas the warmer Bølling–Allerød and Holocene macroclimates supported the occurrence of present-day central European steppe flora. The models suggest that the LGM source areas of these species ranged from south-eastern France through the Adriatic region and the Balkan Peninsula to the Black-Sea region but extended to central Europe in the mid-Holocene. Their locations differed considerably among ecological and chorological groups in both periods. Therefore, our models support the hypothesis that during the Pleistocene cold periods, the largest populations of these species occurred in southern and south-eastern Europe and some of them may have later colonised central Europe. If some populations occurred in central Europe during the LGM, as suggested by recent genetic analyses, they were likely restricted to microrefugia embedded in the landscape matrix of species-poor cold steppe. The precipitation-rich mid-Holocene climate had no direct negative impact on the central European steppe flora.

Keywords: CCSM3, central Europe, dry grassland, palaeoclimate, postglacial migration, range expansion, refugium, steppe, vascular plants

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Introduction

Temperate dry and semi-dry grasslands, called steppes in the Palaearctic, represent a zonal vegetation type dominated by grasses and forbs. Steppe occurs naturally in regions where low precipitation, large seasonal variations in temperature and precipitation and other factors such as fires or grazing suppress forest development. Palaeoecological evidence suggests that steppe was the dominant vegetation type in this region during the last glacial period (Binney et al. 2017). In addition to its decline due to forest encroachment in the warm and humid climate of the Holocene, it was subject to severe human impacts, including conversion to cropland and overgrazing (Wesche et al. 2016). As a result, the proportion of pristine and protected habitats is lower than in any other biome (Hoekstra et al. 2005). Nevertheless, steppes and steppe-like temperate grasslands harbour exceptionally species-rich communities (Wilson et al. 2012) of high conservation value (Feurdean et al. 2018).

The Palaearctic steppes extend from central and eastern Europe across Eurasia to north-eastern China (Wesche et al. 2016). Although open and semi-open vegetation was probably present in central Europe throughout the Holocene (Fyfe et al. 2015, Kuneš et al. 2015, Pokorný et al. 2015), the current moderately humid, temperate climate of this region supports the natural dominance of deciduous broadleaved forests (Bohn et al. 2000–2003). Steppe grasslands are therefore confined to lowland areas in the lee of mountains that receive less precipitation. The most extensive areas of this vegetation occur in the Carpathian Basin (also called the Pannonian Basin) and the adjacent hilly landscapes (Wendelberger 1954, Illyés and Bölöni 2007, Dúbravková et al. 2010). In a large part of this region, the natural vegetation mosaics correspond to the forest-steppe biome (Wendelberger 1954, Zólyomi and Fekete 1994, Illyés and Bölöni 2007, Chytrý 2012, Erdős et al. 2018, Chytrý et al. 2022a). Smaller areas of dry grasslands in forest-steppe-like landscape mosaics also occur farther west and north, e.g. in the dry valleys of the Alps (Braun-Blanquet 1961, Magnes et al. 2021), the Rhine valley (Korneck 1974), northern and central Bohemia (Chytrý 2012), Thuringia and Saxony-Anhalt (Mahn 1965), the lower Oder valley, Polish Kujawy and in the uplands of south-eastern Poland (Szafer 1966).

Despite their isolation from the contiguous zonal steppe and forest-steppe areas of eastern Europe (Wesche et al. 2016), central European extrazonal steppes (Kirschner et al. 2020) share many species with eastern European zonal steppes (Willner et al. 2017, 2019, Chytrý et al. 2022b). The origin of these populations in central Europe has puzzled biogeographers since the 19th century (Kerner 1863). Two possible bottlenecks in the history of steppe species in central Europe are considered. The first is related to the Pleistocene glacial periods. In particular, the last Weichselian glaciation significantly influenced the development of present-day communities. Although central Europe was largely unglaciated during the last glacial maximum (LGM), the climate may have been unsuitable for most central European steppe species, although areas with the same macroclimate likely always included sites with more benign microclimates. The second possible bottleneck was in the warm and humid mid-Holocene, which supported the spread of forests, especially in a few centuries before the arrival of Neolithic farmers, who preserved and extended open areas in the landscape. For both periods, early biogeographers hypothesised ain situ survival of steppe species in central Europe.

The 'Ancient Mátra theory' (*Ösmátra-theorie*) proposed by Kerner (1863) and variously modified by later biogeographers (De Soó 1929, Wendelberger 1954) assumed that the mountains in western and northern Hungary contained refugia of steppe flora during periods of pre-Holocene environmental changes. These refugia later served as a source for the recolonization of the lowland areas in the Carpathian Basin. The 'Steppe theory' (*Steppenheidetheorie*) of Gradmann (1933) tried to explain the survival of steppe flora during the period of mid-Holocene forest spread. In this period, the first Neolithic farmers settled in central Europe, and it is assumed that they still found remnants of the early-Holocene forest-steppe in dry lowlands, even on fertile, loess-derived soils. They preferentially settled there and extended the area of open landscape (Fyfe et al. 2015), making it suitable for the continuous persistence of steppe species (Hein 2010, Pokorný et al. 2015). Alternative hypotheses to both the 'Ancient Mátra theory' and the 'Steppe theory' would be the extinction of the steppe biota in central Europe during these critical periods and its recovery by immigration from eastern or south-eastern Europe once favourable environmental conditions were re-established.

Recent genetic analyses (Kajtoch et al. 2016, Kirschner et al. 2020, Willner et al. 2021) demonstrate that several steppe plant and animal species survived in situ in central Europe. The presence of distinct clusters of genetically similar individuals in parts of central Europe suggests an ancient (Pleistocene) origin of these populations. Although long-term local persistence can be a plausible scenario for some species, postglacial or post-mid-Holocene immigration may be a better explanation for other species or infraspecific lineages with different ecological tolerances (Douda et al. 2020).

The steppe grasslands of central Europe comprise several habitat types with different species compositions and environmental affinities (Wendelberger 1954, Willner et al. 2017, 2021, Chytrý et al. 2020). The coarsest classification includes three types: rocky steppe, grass steppe (slope steppe on moderately deep soils over rocky substrates and drier types of loess steppe) and meadow steppe (steppe meadows and mesic types of loess and chernozem steppes). These three types are arranged along a gradient of increasing soil humidity, which is reflected in increasing productivity and a higher proportion of tall forbs. In addition, the latter type is on average more species-rich and contains a higher proportion of species that can occur in both grasslands and forests. We hypothesise that the species characteristic of these types have different tolerances to environmental conditions, resulting in differences in their biogeographic history.

In addition to differences in ecology, plant species of the central European steppe also differ in their biogeographic origins and present-day distribution ranges (Meusel et al. 1965–1992, Chytrý et al. 2022b). They include species with continental distributions (many of them ranging from central Europe to southern Siberia), species with submediterranean (including Mediterranean) distributions reaching their northern limit in central Europe, species with broad temperate ranges from western Europe to eastern Europe or Siberia, and species with narrow central European distribution ranges. We hypothesise that these groups of central European steppe species have different biogeographic histories.

Because steppe-plant remains are poorly preserved in the palaeoecological record or cannot be identified to species or genera, there are currently two main approaches to drawing conclusions about the history of steppe flora. The first approach is phylogeography, i.e. mapping genetic variation in extant populations of steppe species over large areas and using these data to reconstruct possible refugia and migration routes (Kajtoch et al. 2016, Kirschner et al. 2020, Willner et al. 2021). The second approach is habitat suitability modelling (Guisan and Zimmermann 2000), which involves estimating the realised climatic niche of individual species based on their current distribution and projecting the resulting habitat suitability models to past time periods.

Previous projections of climate-based habitat suitability models have been significantly limited by the lack of palaeoclimatic data with high temporal and spatial resolution. These have been developed for the mid-Holocene, LGM and some older periods (e.g. in the WorldClim database), but have been lacking for periods of abrupt climate shifts during the Pleistocene–Holocene transition (Heinrich stadial, Bølling–Allerød and Younger Dryas) and for less pronounced climatic fluctuations during the Holocene. Recently, palaeoclimate simulations from the community climate system model ver. 3 (CCSM3; Collins et al. 2006) have become available with a high temporal resolution of decadal to centennial (100-year) time windows for the last 21 000 years (Fordham et al. 2017). These simulations can be downscaled to more ecologically relevant spatial resolutions useful for creating habitat suitability maps for any period from the LGM to the present.

However, not all areas that were climatically suitable in the past may have served as sources for colonisation of the present-day species distribution ranges due to migration constraints (Svenning and Skov 2004, Normand et al. 2011). Thus, present-day species ranges are determined not only by the availability of suitable habitats but also by species dispersal abilities (Engler and Guisan 2009) and the spatial accessibility of a given site from refugia (Svenning and Skov 2004, Normand et al. 2011). Several process-based models that integrate species-specific dispersal information have been developed to account for constrained migration (e.g. TREEMIG, Lischke et al. 2006, MigClim, Engler et al. 2012), but species migration from potential refugia can also be simulated using a simple iterative algorithm that allows these simulations to be performed over large areas for many species (Nobis and Normand 2014). The key component of these simulations is a series of habitat suitability maps for different periods in the past that are used to simulate the dispersal of species through changing environments (colonizations and extinctions), and to identify source areas from which species are likely to have colonised the currently occupied regions.

Here, we ask whether macroclimate-based models of habitat suitability support either the hypothesis of in-situ persistence of central European steppe species during the LGM and mid-Holocene or the alternative hypothesis of their later immigration from southern and south-eastern refugia. We used data on the current distribution ranges of 104 species of this flora and developed a habitat suitability model for each of them. We also created a dataset of downscaled and debiased CCSM3 simulations and used them to produce a series of habitat suitability maps for each species during the most critical periods of the Late Pleistocene and Holocene. These map series were then used in simulations of species migration from the areas with suitable macroclimate to identify those that may have acted as 'source areas' (i.e. potential refugia). Specifically, we asked the following questions:

1) Was the macroclimate of central Europe in critical periods of the last 21 000 years suitable for vascular plants that now occur in the steppe vegetation of this region?
2) Which areas with suitable macroclimate in the LGM and mid-Holocene likely served as sources for colonisation of present-day species ranges after these time periods?
3) Does the distribution of potential source areas differ among ecological types of steppe vegetation (rocky steppe, grass steppe and meadow steppe) and groups of species with similar present-day distribution ranges (chorotypes)?

Methods

Studied species and distribution data

Based on dry-grassland species lists from large syntheses of vegetation-plot data (Dúbravková et al. 2010, Willner et al. 2017, 2019, Chytrý et al. 2020) and available species distribution data, we selected 104 vascular plant species typical of central European steppe grasslands (Supporting information). Digitised distribution data (point occurrences and range polygons) were obtained from the Chorological Database Halle (CDH). These data were based on the published maps from Meusel et al. (1965–1992), which were revised and updated by E. Welk and collaborators. This update was based on floristic data, i.e. mainly regional to national distribution atlases, and regional Red Books of Russian provinces and regions, published since the release of the respective maps in Meusel et al. (1965–1992). Depending on the map scale of the published data, the positional uncertainty of the digitised occurrence data ranges between 10 and 50 km. The largest amount of original occurrence data was collected between 1950 and 2010. A list of sources is provided in Supporting information. The CDH dataset was furthermore supplemented with occurrence records from the GBIF database (<https://doi.org/10.15468/

dl.xeczz3>). We considered only those records marked as PRESERVED_SPECIMEN, most of which were from herbarium collections. All occurrences were no older than 1940 and had a location uncertainty of less than 5 km. Species occurrence maps were then critically revised and non-native or unlikely occurrences were discarded. Because habitat suitability modelling requires point occurrences, but these did not cover entire species ranges, we converted range polygons to points by a prior random sampling of 20 000 points throughout the Palaearctic region. The random points within each range polygon were considered pseudo-occurrences (163 418 in total) and merged with the true occurrence records from the CDH and GBIF databases (640 707 in total) to form a single dataset. According to our preliminary models, random sampling appears to be an acceptable solution when some parts of a species range are missing from its occurrence data. The number of records ranged from 48 for *Astragalus exscapus* to 126 908 for *Ranunculus bulbosus,* and the average number of occurrences per species was 7732. The species distribution maps are available in the Zenodo repository (<http://doi.org/10.5281/zenodo.5907271>), and the numbers of occurrences for each species are listed in the Supporting information.

We classified species into ecological and chorological (biogeographic) groups (Supporting information). Based on phytosociological and habitat-related literature (Willner et al. 2017, Chytrý et al. 2020), we selected species characteristic of three ecological types of central European steppes: 1) rocky steppe (16 species), 2) grass steppe (30) and 3) meadow steppe (37). These groups correspond to the phytosociological orders *Stipo pulcherrimae-Festucetalia pallentis*, *Festucetalia valesiacae* and *Brometalia erecti* (Mucina et al. 2016) and EUNIS habitat types R15, R1B and R1A (Chytrý et al. 2020). Twenty-one species that frequently occur in more than one type were not considered in this classification.

The classification of species into chorological groups was based on a cluster analysis. We first assigned species occurrences in Europe to UTM grid cells of 50 × 50 km and calculated the pairwise dissimilarity of species distributions using the Sørensen dissimilarity measure. The square-rooted dissimilarity matrix was then clustered using Ward's algorithm. After inspecting the resulting dendrogram, a partition with five clusters was accepted. In a few cases where the range of a particular species differed considerably from the other ranges in the same cluster, the species was moved to a more appropriate cluster. Examples of different distribution ranges with overlaid occurrence records are shown in the Supporting information. The following types of distribution ranges (chorotypes) were defined:

1) Temperate continental species (ranging from central Europe to southern parts of eastern Europe or Siberia; 23 species).
2) Subatlantic–submediterranean–continental species (ranging from western and southern through central to eastern Europe; 23 species).
3) Central European and submediterranean species (species from southern and central Europe that are largely absent in north-western and eastern Europe; 26 species).
4) Broad-range species (ranging from western to eastern Europe or Siberia, and from southern Europe to the hemiboreal zone of northern Europe; 23 species).
5) Narrow-range central European species (9 species).

Habitat suitability modelling

We used Maxent ver. 3.4.1 (Phillips and Dudík 2008) to calculate the habitat suitability model for each species. Models were calibrated using 20 000 randomly distributed background points and species occurrence records from across the Palearctic and adjacent areas (32.5°W–180.0°E, 16.0°N–82.5°N). Climatic and topographic variables with a spatial resolution of 2.5 arc-min were used as predictors. Based on monthly temperature and precipitation grids from the CHELSA database for 1940–1989 (Karger et al. 2017), we calculated 19 bioclimatic and 16 ENVIREM variables as described by Title and Bemmels (2018). These variables were supplemented by the two topographic indices from the ENVIREM database (Title and Bemmels 2018). To avoid collinearity issues, we reduced this set to only 11 variables whose pairwise Pearson correlations were lower than 0.7. This subset included mean annual temperature (bio1), mean diurnal temperature range (bio2), temperature seasonality (bio4), mean temperature of the wettest quarter (bio8), mean temperature of the warmest quarter (bio10), annual precipitation (bio12), precipitation seasonality (bio15), precipitation of the wettest quarter (bio16), Thornthwaite aridity index, seasonality of potential evapotranspiration (PET) and topographic ruggedness index.

To avoid possible biases in the habitat suitability models caused by the uneven density of occurrence records, we resampled species occurrences using an environmental filtering procedure (Varela et al. 2014). For each species with more than 100 occurrence points (97%), we plotted each point in the multidimensional environmental space defined by the standardised environmental variables and projected geographical coordinates. We then divided this space into equal-sized bins, each spanning 0.3 SD, and randomly selected one occurrence point from each bin. If the bin contained both true and pseudo-occurrence, the true occurrence was selected. This procedure resulted in a subset of 300 529 occurrence records that evenly covered species environmental niches and all occupied areas (of them 51.4% were true occurrences and 48.6% were pseudo-occurrences). Their numbers ranged from 48 for *A. exscapus* to 17 989 for *Filipendula vulgaris*, and the average number of filtered occurrences per species was 2890 (Supporting information). This dataset is available in the Zenodo repository (<http://doi.org/10.5281/zenodo.5907271>). According to the cross-validation results, models calibrated with the filtered data showed higher predictive power. Maxent models were calculated using the 'dismo' R package (Hijmans et al. 2021).

Each model was evaluated using a spatially blocked 5-fold cross-validation (Roberts et al. 2017). The size of spatial blocks was set to 1/10 of the species distribution range in longitudinal or latitudinal direction, whichever was larger. Blocks were randomly assigned into folds using the *spatialBlock* function in the 'blockCV' R package (Valavi et al. 2019). Model evaluation was based on the following three statistical metrics averaged over five cross-validation runs: 1) area under the ROC curve (cvAUC); 2) overfitting, i.e. the difference between training and test AUC (Warren and Seifert 2011); 3) continuous Boyce index (Hirzel et al. 2006). Details of the modelling procedure are provided in the ODMAP protocol in the Supporting information.

Projection of the models

Habitat suitability models were projected onto the European climates of the following periods, given in thousands of years before the present (ka BP): 21 ka BP (last glacial maximum, LGM), 17.1 ka BP (Heinrich stadial), 14.3 ka BP (Bølling–Allerød interstadial), 12.2 ka BP (Younger Dryas stadial), 9.9 ka BP (early Holocene, Greenlandian), 8.2 ka BP ('8.2 ka' event), 6.2 ka BP (mid-Holocene, Northgrippian), 4.2 ka BP ('4.2 ka event'), 2.1 ka BP (late Holocene, Meghalayan), present (1940–1989 CE). Pleistocene maps account for the presence of ice sheets as documented by Peltier et al. (2015). For all maps, eustatic sea level change was estimated based on data published by Lambeck et al. (2014).

To characterise European climate conditions during the Late Pleistocene and Holocene, we used gridded palaeoclimate simulations of the CCSM3 (Collins et al. 2006) as provided by the PaleoView software (Fordham et al. 2017). Using the delta-change method (Ramirez Villejas and Jarvis 2010) and baseline climatic data from the CHELSA database (Karger et al. 2017), we debiased and downscaled CCSM3 simulations of monthly minimum, mean and maximum temperatures and precipitation amounts to 2.5 arc-minute resolution for each centennial (100-year) time window up to 21 000 BP. Based on these data, we calculated a set of bioclimatic and ENVIREM variables that we then used to project habitat suitability models to past climates. A detailed description of these data and the downscaling procedure is available in the Zenodo repository (Divíšek 2021; <http://doi.org/10.5281/zenodo.5119958>). The repository contains bioclimatic and ENVIREM grids at finer spatial resolution of 30 arc-seconds allowing aggregation to any coarser resolution.

Identification of source areas

For each species, we used habitat suitability projections to identify 'source areas' in the LGM (21 ka BP) and mid-Holocene (6.2 ka BP), i.e. areas with suitable climate that likely contributed to the establishment of the species' current distribution range through postglacial migration. First, we delineated all climatically suitable areas in the LGM (potential source areas) by applying the '10th percentile of training presence' threshold provided by Maxent to the LGM suitability map (Fig. 1b; glaciated areas were defined as unsuitable). This threshold classifies all map pixels with a suitability value higher than the lowest 10% of the occurrence records as climatically suitable. We then simulated migration from each isolated, spatially contiguous area larger than 1000 km^2 using KISSMig, a migration model that generates maps of the accessibility of each potential source area (Fig. 1c, d; Nobis and Normand 2014). KISSMig started from each climatically suitable area in the LGM and iteratively simulated the spatial dispersal of species. During a single iteration step, all pixels were colonised or remained colonised according to a probability that increases with the suitability value of the pixel and the number of occupied pixels within the 3 × 3 neighbourhood of the previous step (Nobis and Normand 2014). Iterations were performed for each of 10 squared habitat suitability maps (for the periods described above) to simulate colonisations and extinctions in changing environments. Because the migration ability of each species was not known a priori, KISSMig used 10–200 iterations (with step 10) for each ~2100-year step, corresponding to an average migration rate of 23–466 m year^{-1}. For each potential source area, KISSMig produces a map of first occurrences (FOC), i.e. values from the first iteration step in which a raster cell was colonised. Early colonised cells have low values while late colonised cells have high values. To obtain an accessibility map, each FOC map was rescaled by calculating the difference from max(FOC) + 1 (Fig. 1c, d). Simulations were performed in the Lambert azimuthal equal-area projection with a resolution of 4.9 × 4.9 km. For details on this procedure, see Nobis and Normand (2014).

To test whether simulated accessibility of each potential source area (in addition to environmental factors) significantly contributed to explaining current species distributions in Europe, we used a generalized linear model (GLM) with a binomial response distribution and logit link. In these models, species presence–absence records in 50 × 50 km UTM grid cells were used as a dependent variable, and explanatory variables included mean values of environmental variables (those used in Maxent models) and accessibility of potential source areas. The explanatory variables were standardised to zero mean and unit variance. We calibrated a series of GLM models for accessibility patterns simulated using each migration rate considered from each potential source area (Fig. 1e). Then we checked which migration rate reduced the residual deviance of the model (D_{diff}) the most. We considered 'source area' to be any area whose accessibility under the most efficient migration rate had a significant ($p < 0.05$) positive effect ($\beta > 0$) on the current species distribution (Fig. 1e, f). Finally, we also identified mid-Holocene source areas, i.e. climatically suitable areas that were accessible from the LGM and whose accessibility significantly contributed to explaining the current species distributions. Alternatively, we ran all simulations and tests for climatically suitable areas delineated based on the '5th percentile training presence' threshold to check the sensitivity of the resulting patterns, but the results were very similar and did not change our conclusions.

Finally, to test whether the distribution of source areas in the LGM and mid-Holocene differed significantly among ecological and chorological types of steppe vegetation, we assigned source areas to UTM grid cells and

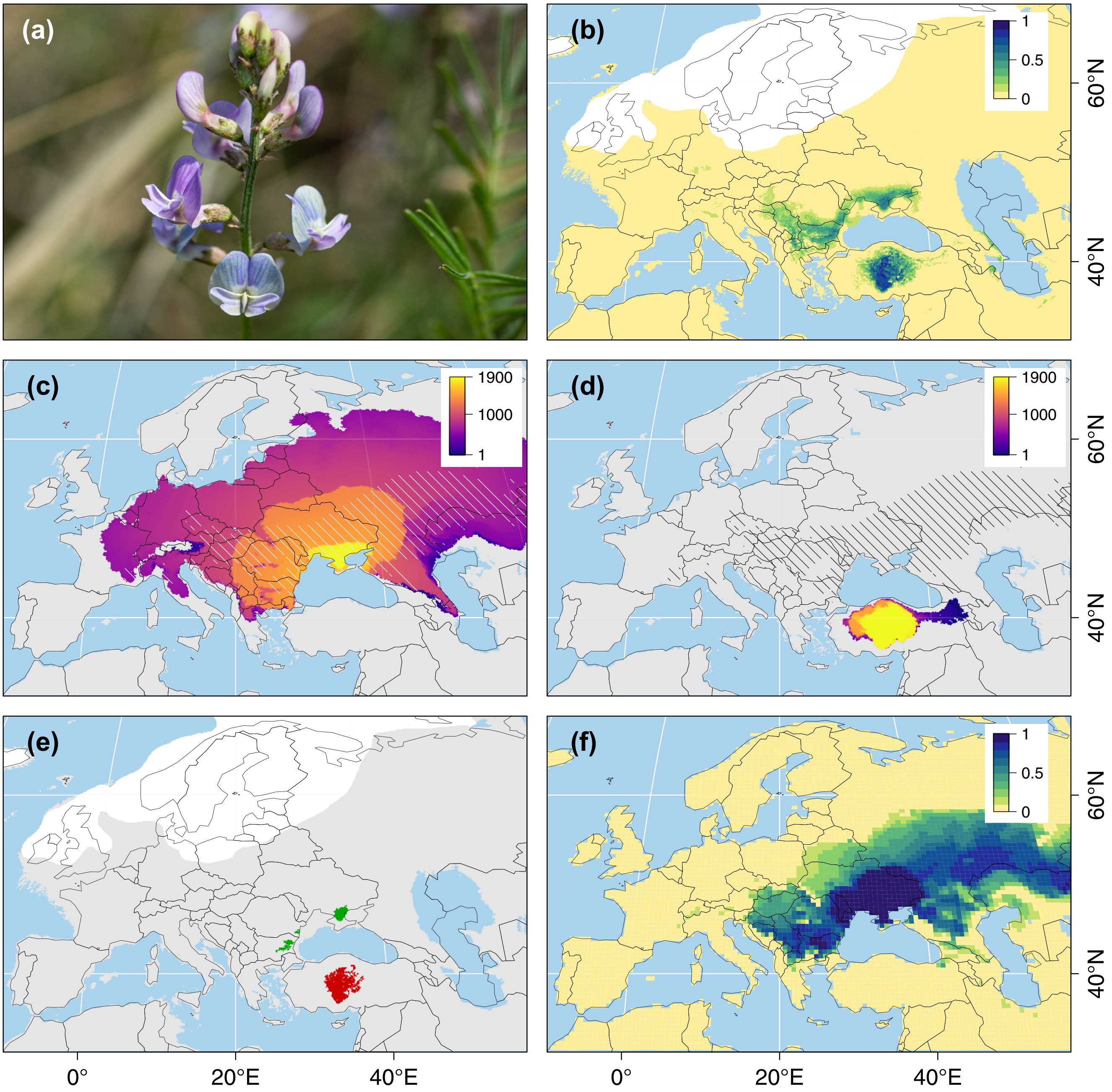

Figure 1. Illustration of migration simulations and LGM source area identification for *Astragalus austriacus*. (a) Photo by Kryštof Chytrý. (b) Habitat suitability in the LGM predicted by the Maxent model with 11 environmental variables. (c) Accessibility from the potential source area in southern Ukraine derived from the KISSMig simulation with 190 iterations (corresponding to an average migration rate of 443.3 m year^{-1}) on each of the 10 habitat suitability maps from the LGM to present. High values represent high accessibility, and low values represent low accessibility. Inaccessible areas are in grey. The present species range in Europe is hatched. Using the accessibility from southern Ukraine as an additional predictor (along with environmental variables) in the GLM model of the present distribution of *A. austriacus* in Europe reduced the residual deviance (D_{diff}) of the model by 33.7% ($\beta = 2.3$; $p < 0.001$). (d) Accessibility from the potential source area in Anatolia ($D_{diff} = 0.1\%$; $\beta = -1289.8$; $p = 0.968$). (e) Source areas in the LGM identified by the GLM models. Green colour indicates source areas whose accessibility had a positive ($\beta > 0$) and statistically significant ($p < 0.05$) effect on current species distribution in GLM models that included environmental variables. Red colour indicates areas with negative and/or insignificant effect. (f) Probability of *A. austriacus* present-day occurrence in 50 × 50 km UTM grid cells as predicted by the GLM model with 11 environmental variables and accessibility from all significant source areas.

then calculated the dissimilarity of source-area location for each species pair using the Sørensen dissimilarity measure. Differences among groups were tested by permutational analysis of variance using distance matrices (Anderson 2001) with 9999 permutations. Statistical significance was considered at $\alpha = 0.05$. The square-rooted dissimilarity matrix was then visualised in 2-dimensional space using principal coordinate analysis (PCoA). We then passively projected geographical coordinates (longitude and longitude) onto ordination space using the *envfit* function (with default settings) in the 'vegan' package (Oksanen et al. 2022). All analyses were performed using R software ver. 4.0.2 (<www.r-project.org>).

Results

We developed habitat suitability models for 104 species of central European steppe grasslands. The cross-validation AUC of these models ranged between 0.647 (*Galium verum*) and 0.996 (*Galium austriacum*), with 78% of the models having an AUC > 0.8. Overfitting ranged from 0.001 (*G. austriacum*) to 0.157 (*Bothriochloa ischaemum*), and 88% of the models had an overfitting of less than 0.1. The Boyce index ranged from −0.140 (*Anemone sylvestris*) to 0.971 (*Draba lasiocarpa*), and 75% of the models had a Boyce index value > 0.5. As few models had poor predictive performance with respect to all three evaluation indices, we used all models to project habitat suitability in past time periods. The evaluation scores for each model can be found in the Supporting information.

The 104 species studied showed specific patterns of habitat suitability across Europe. For most of them, the area of suitable habitats extended in the warm periods of the late Pleistocene (Bølling–Allerød interstadial) and Holocene, but retreated during the cold periods (LGM, Heinrich stadial and Younger Dryas stadial). In the cold periods, the most suitable areas were suggested to be in central Anatolia, Crimea and lowlands along the Black-Sea coast, the Balkan Peninsula including the Dinaric Mountains and the southern Carpathian Basin, the northern Italian Peninsula and southern France (Fig. 2). In warmer periods, climatically suitable areas extended northward to central Europe (Bølling–Allerød, early Holocene), to the hemiboreal zone in southern Sweden (mid-Holocene), and to more continental areas in the east (late Holocene).

Two species in our dataset, *Ephedra distachya* and *Krascheninnikovia ceratoides*, are typical of desert steppes of central Asia (Wendelberger 1954, Mucina et al. 2016). These species were notable exceptions to the pattern described above. Both had the most suitable habitats in the LGM in the lowlands north of the Black Sea and east of the Caspian Sea, not in warmer Anatolia like most other species (Fig. 3). They both found suitable conditions in central Europe during the cold and dry periods of the Heinrich stadial and Younger Dryas, while their suitable climate was restricted to the continental areas of eastern Europe during the warmer periods of the Bølling–Allerød interstadial and Holocene. Such a pattern contrasts with all other species, which were generally favoured by warmer and wetter climates.

By integrating habitat suitability models with simulations of species migration, we identified significant source areas for 96 species in the LGM and for 95 species in the mid-Holocene. Based on our criteria, we found no LGM source area for eight species, mostly those with narrow current ranges. For nine species, climatically suitable areas in the mid-Holocene were either inaccessible from the LGM source areas or their accessibility did not contribute significantly to explaining the current species distribution in Europe. All maps resulting from habitat suitability modelling and migration simulations are available in the Zenodo repository. The size and number of identified source areas for each species can be found in the Supporting information.

For most species, current climatic conditions explained slightly more deviance (~44%) in species distribution than did accessibility from the LGM source areas (~40%), but less than accessibility from the mid-Holocene source areas (~47%; Table 1; Supporting information). Accessibility from the LGM source areas explained the greatest deviance in the distribution of the broad-range species (chorotype 4; 50%), but that from the mid-Holocene source areas explained the greatest deviance in the central European and submediterranean species (chorotype 3; 53%). Including accessibility from the LGM source areas into the models with climate resulted, on average, in ~57% of the explained deviance and the highest proportion of deviance was explained in the distributions of broad-range species (chorotype 4; 61%). The joint effect of climate and accessibility from the mid-Holocene source areas was on average ~59%, being the highest for the central European and submediterranean species (chorotype 3; 64%).

We obtained constrasting patterns by stacking the source areas for specialists of the three ecological types of central European steppes (Fig. 4). For most of the rocky-steppe species, LGM source areas were suggested to be in northern Italy, especially in the southern foothills of the Alps and northern Apennines. For the grass-steppe species, source areas were on the western and northern coasts of the Black Sea, and for the meadow-steppe species, the source areas were in the Po Valley, but also in south-eastern France (Rhône valley), on the southern margin of the Carpathian Basin, and on the western Black-Sea coast. Stacking of the mid-Holocene source areas showed that most of the rocky-steppe species were likely distributed from western France and southern Germany through the southern foothills of the Alps to the Dinaric Mountains. For the grass-steppe species, source areas were suggested from the Balkan Peninsula (eastern Bulgaria and Romania) to Moldova and southern Ukraine. The source areas for the meadow-steppe species were likely located from central France to western Germany and from northern Italy to the Dinaric Mountains. Differences among ecological groups in the localization of source areas were statistically significant ($p = 0.046$ for the LGM and $p < 0.001$ for the mid-Holocene; Fig. 6a, b).

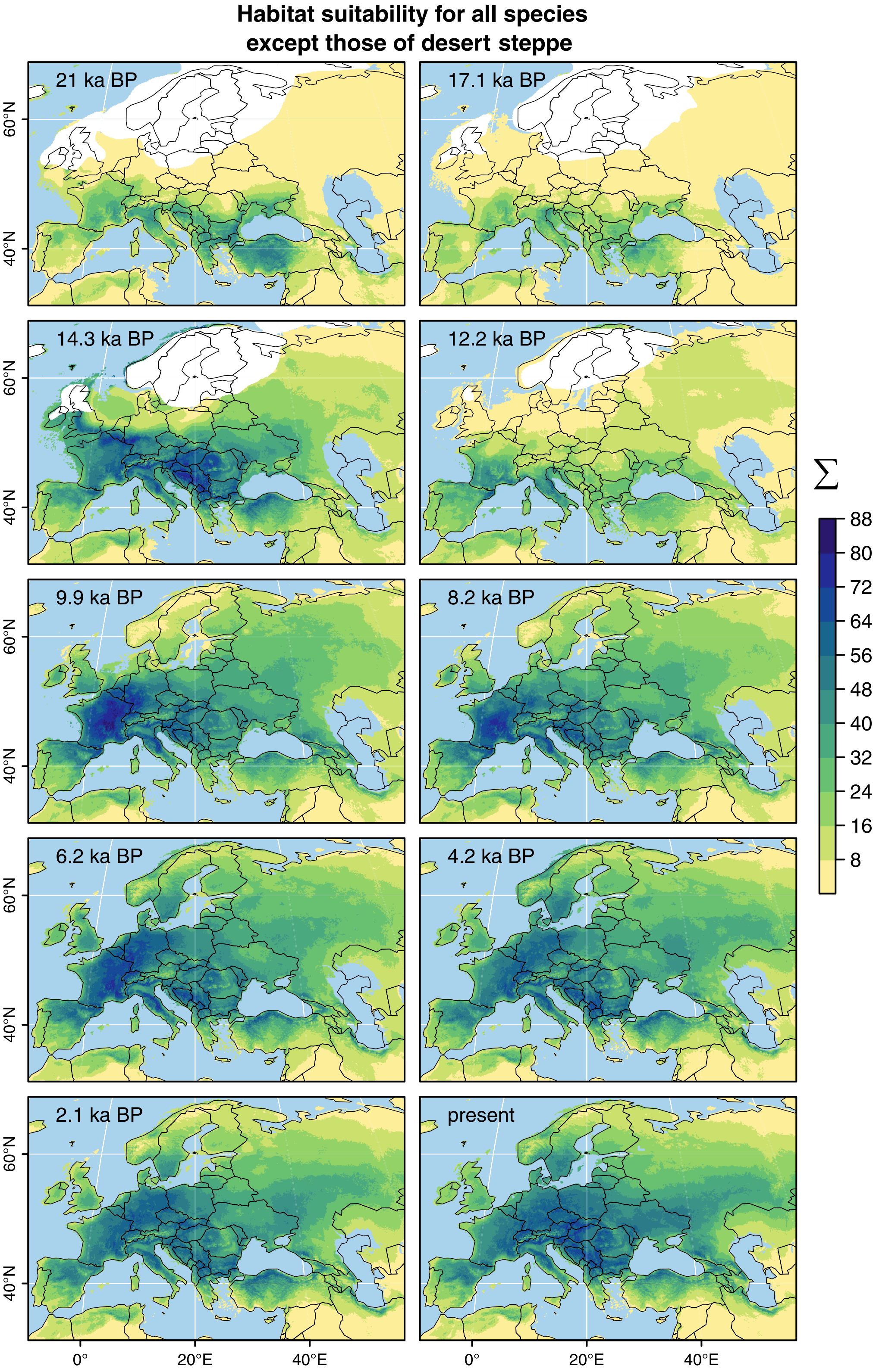

Figure 2. Stacked maps of habitat suitability for all species except those of desert steppe (102 species). The sum of habitat suitability values (∑), expressed by the colour scale, shows the hypothetical number of species present. The extent of the continental ice-sheet (white) was estimated based on Peltier et al. (2015).

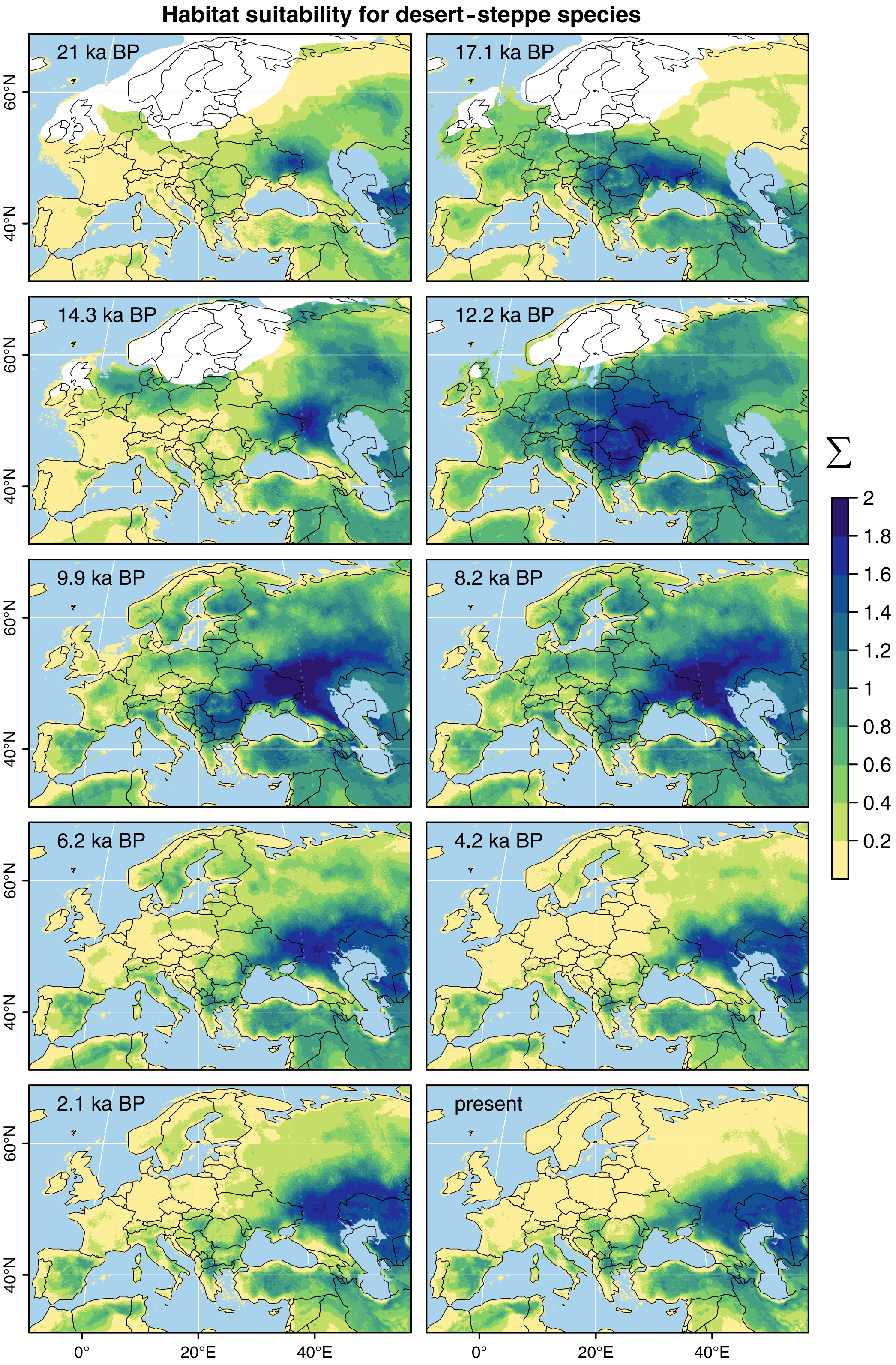

Figure 3. Stacked maps of habitat suitability for two species of desert steppes, *Ephedra distachya* and *Krascheninnikovia ceratoides*. For details, see Fig. 2.

Table 1. Importance of climate and accessibility from the LGM and mid-Holocene source areas for explaining present-day species distributions in Europe. Mean percentage deviance (± SD) explained by climate and/or accessibility of source areas is shown. Chorotype 1 – temperate continental species, chorotype 2 – subatlantic–submediterranean–continental species, chorotype 3 – central European and submediterranean species, chorotype 4 – broad-range species and chorotype, chorotype 5 – narrow-range central European species.

		LGM source areas		Mid-Holocene source areas	
	Climate only	Accessibility only	Climate + accessibility	Accessibility only	Climate + accessibility
All species	43.9 ± 10.1	40.0 ± 18.0	56.9 ± 10.6	46.7 ± 13.5	59.3 ± 9.7
Rocky steppe	46.5 ± 9.4	39.8 ± 20.9	57.4 ± 10.0	45.6 ± 14.7	59.4 ± 8.6
Grass steppe	36.4 ± 8.6	39.0 ± 14.9	53.7 ± 10.5	41.8 ± 13.8	54.0 ± 10.6
Meadow steppe	47.4 ± 8.9	42.5 ± 17.6	58.6 ± 10.2	50.4 ± 11.5	62.3 ± 8.7
Chorotype 1	39.1 ± 11.0	31.1 ± 15.4	53.1 ± 9.8	36.8 ± 13.0	54.8 ± 8.5
Chorotype 2	40.2 ± 9.1	37.1 ± 22.8	54.8 ± 13.4	47.4 ± 13.8	58.0 ± 10.7
Chorotype 3	49.3 ± 7.8	46.4 ± 14.1	60.5 ± 8.4	53.0 ± 7.6	63.6 ± 8.0
Chorotype 4	47.8 ± 8.4	49.7 ± 7.2	60.9 ± 6.7	51.4 ± 11.8	62.0 ± 8.2
Chorotype 5	38.7 ± 10.3	19.4 ± 20.4	47.9 ± 13.8	37.7 ± 17.6	53.0 ± 13.9

Chorotypes also differed considerably in the localization of their source areas in the LGM (Fig. 5). The temperate continental species (chorotype 1) had their source areas situated north of the Black Sea (southern Ukraine), while the subatlantic–submediterranean–continental species (chorotype 2) had them mainly in eastern Bulgaria and Romania along the Black-Sea coast. For the central European and submediterranean species (chorotype 3) and broad-range species (chorotype 4), source areas ranged from south-eastern France through northern Italy and the southern Carpathian Basin to eastern Bulgaria, Anatolia and southern Ukraine (broad-range species only). For the narrow-range species (chorotype 5), LGM source areas were suggested to be in the north-western and southern foothills of the Alps. Similar differences were found for the mid-Holocene. Most of the temperate continental species had source areas situated north and north-west of the Black Sea, but for most subatlantic–submediterranean–continental

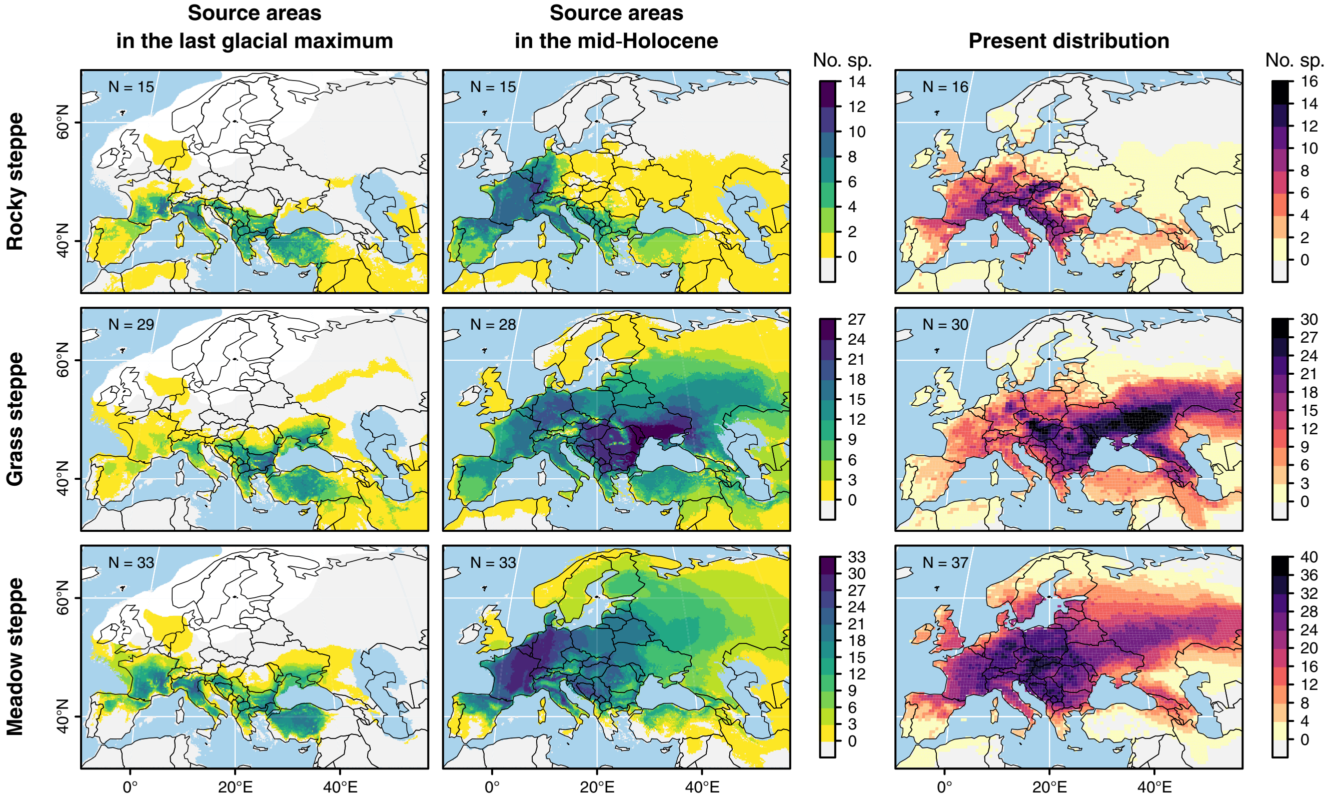

Figure 4. Stacked source areas and present distribution ranges for specialists of three ecological types of the central European steppes. The colour scales show the number of species present. Source areas were defined as environmentally suitable areas whose accessibility under the most efficient migration rate contributed significantly to explaining the current species distribution ranges (Methods). N is the number of species included in each map. In the present distribution maps, N is the total number of species in the group, whereas in the source-area maps, it is the number of species for which we identified at least one source area.

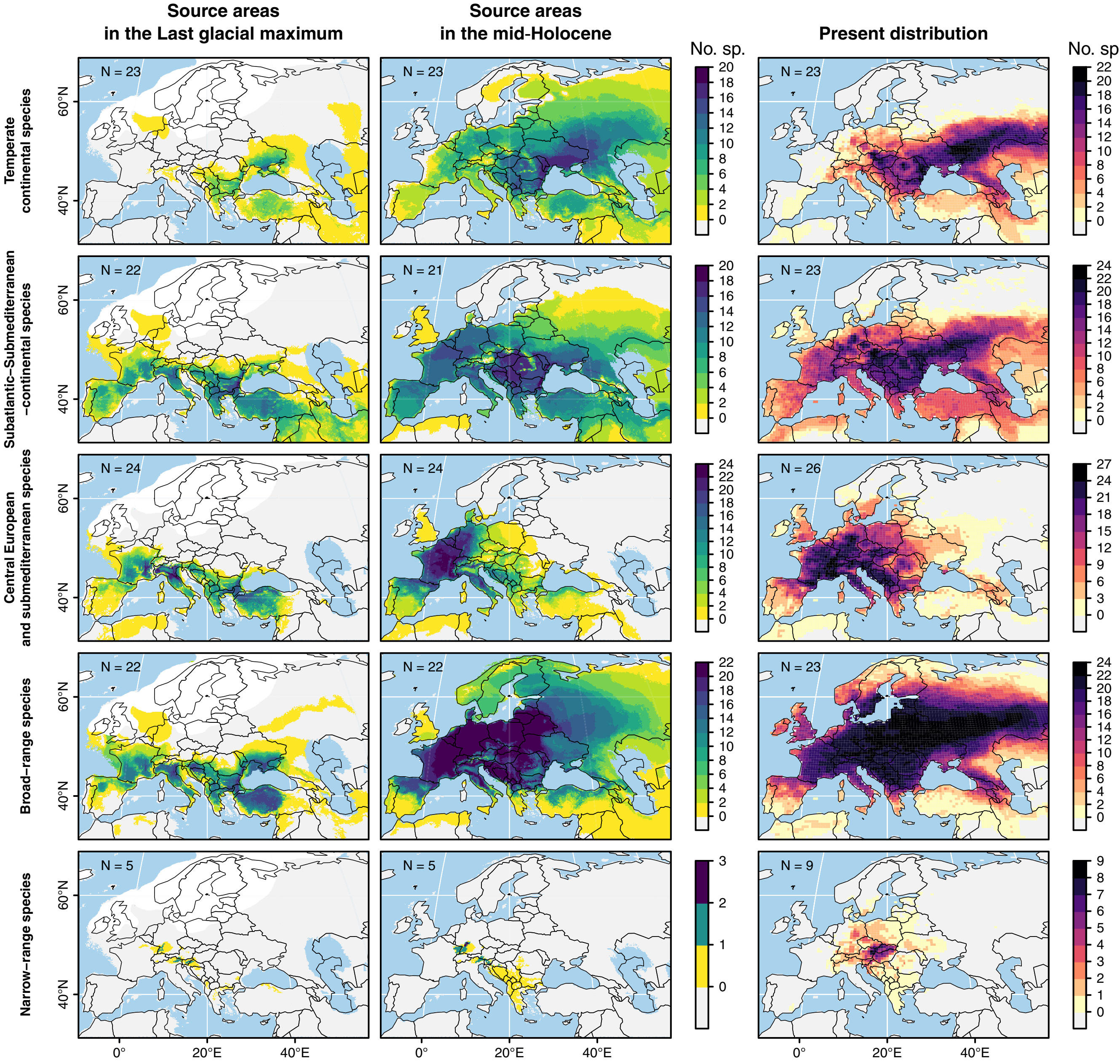

Figure 5. Stacked source areas and present distribution ranges of species belonging to five chorotypes of the central European steppes. For details, see Fig. 4.

species, source areas were distributed from eastern France through central Europe and Carpathian Basin to the eastern Balkan Peninsula. The central European and submediterranean species had source areas mainly in southern and central France but those of broad-range species extended from central France through central Europe to the Baltic countries and the Balkan Peninsula. The narrow-range species showed a similar pattern as in the LGM. Differences among chorological groups in source area localization were statistically significant ($p < 0.001$ for both the LGM and mid-Holocene; Fig. 6c, d). The distribution of source areas across 11 selected regions in Europe can be found in the Supporting information.

Discussion

We demonstrated that the abrupt climatic shifts at the Pleistocene–Holocene transition considerably affected the climatic suitability and potential distribution of steppe species in central Europe. Our models suggest that during the cold periods of the Late Pleistocene (LGM, Heinrich stadial and Younger Dryas), the macroclimate in most parts of central Europe was generally unsuitable for most species that now occur in the zonal steppes of this region. Suitable macroclimates were found farther south and south-east, particularly in the Adriatic region, the Balkan Peninsula (southern margins of the Carpathian Basin and the Dinarides) and

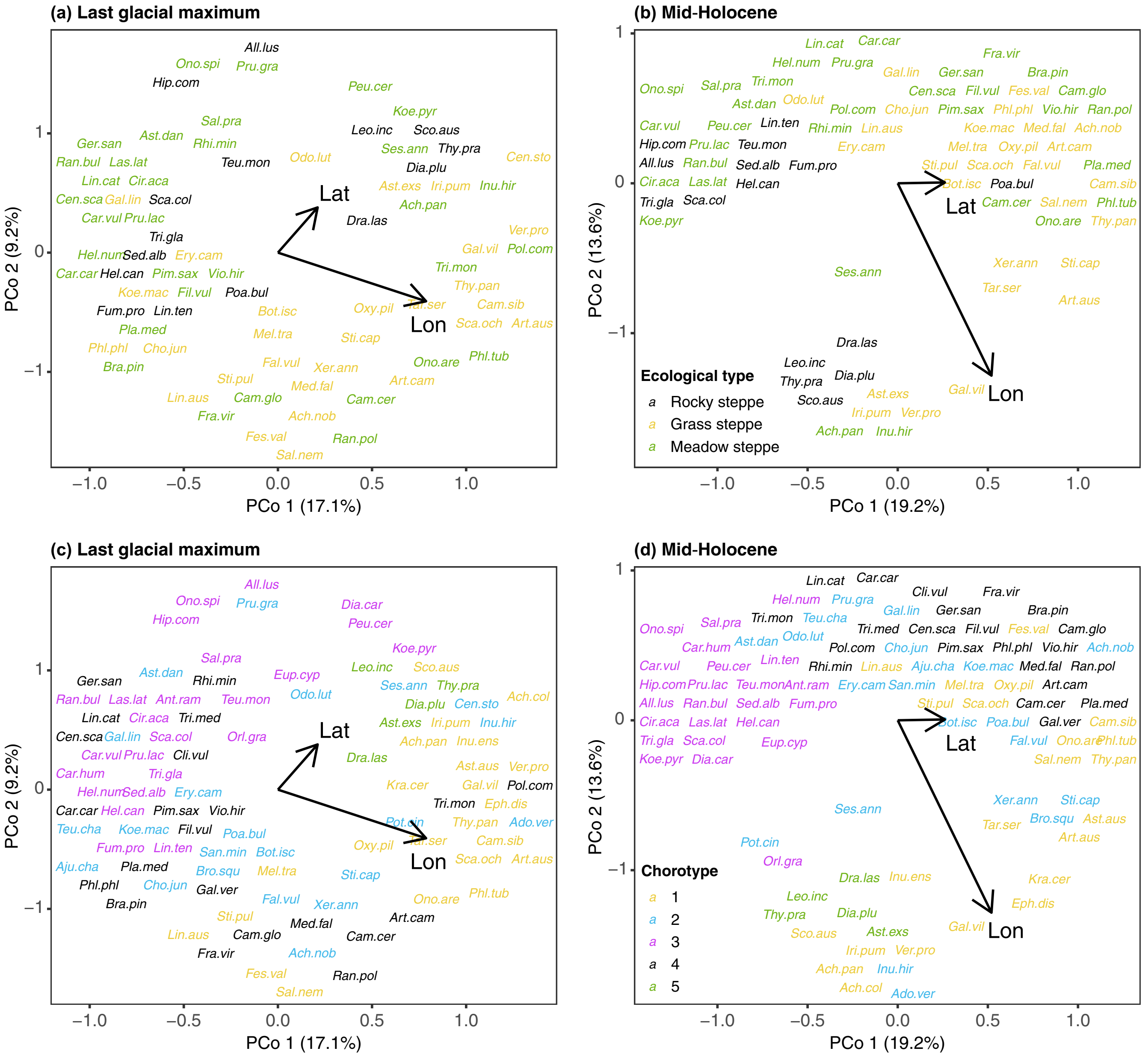

Figure 6. Similarity in source area location visualised using principal coordinates analysis of square-rooted Sørensen dissimilarity matrices. Differences among ecological and chorological groups of species (shown in colours) were tested by permutational analysis of variance using distance matrices: (a) F = 1.564, p = 0.046; (b) F = 3.163, p < 0.001; (c) F = 3.933, p < 0.001; (d) F = 4.302, p < 0.001. Chorotype 1 – temperate continental species, chorotype 2 – subatlantic–submediterranean–continental species, chorotype 3 – central European and submediterranean species, chorotype 4 – broad-range species and chorotype, chorotype 5 – narrow-range central European species. Longitude and latitude were passively projected onto the ordination diagram using the *envfit* function of the 'vegan' R package (Oksanen et al. 2022). For abbreviated species names, see Supporting information. Note that the abbreviations in the ordination diagrams may be slightly shifted for better readability.

the Black Sea region including Crimea, eastern Bulgaria and central Anatolia. Central Europe became generally suitable for these species only during the warmer and wetter Bølling–Allerød interstadial and the Holocene, when the Carpathian Basin and (south-)western Germany were the most suitable regions.

This result supports the hypothesis of a postglacial immigration of steppe species to central Europe, which is consistent with interpretations of genetic patterns in some phylogeographic studies of dry grassland species. For example, immigration from (south-)western Europe was suggested for *Hippocrepis comosa* (Leipold et al. 2017) and *Sanguisorba minor* (Tausch et al. 2017). However, these studies also support the existence of northern refugia that have contributed to genetic variation in the present-day populations of these species. Evidence for glacial refugia in central Europe also comes from other phylogeographic studies of both steppe plants and animals (Kajtoch et al. 2016, Plenk et al. 2017, Kirschner et al. 2020). These studies revealed the existence of infraspecific lineages restricted to different regions of central Europe, suggesting a pre-LGM separation of populations of eastern zonal steppes and central European extrazonal steppes and, consequently, long-term in situ persistence in central Europe. Although habitat suitability models suggest that the central European macroclimate of the cold Pleistocene periods was unsuitable for most of the dry grassland species studied on a coarse scale, these species could have survived in microrefugia, especially in topographically heterogeneous areas (Willner et al. 2021). The same mechanism is thought to be the cause of the presence of full-glacial forest patches in this region (Willis and van Andel 2004, Birks 2008, Kuneš et al. 2008, Magyari et al. 2014, Feurdean et al. 2015). The complex genetic structure of some species suggesting northern refugia can thus be attributed to species' local adaptations and differential success in survival and dispersal of individual genetic lineages during the Pleistocene–Holocene transition. For example, Douda et al. (2020) found that a cold-tolerant genetic lineage of *Atriplex tatarica* that occurred at the periphery of the species' range during the last glacial period did not spread to the north in the Holocene. Further north (in Poland), it was replaced by a less cold-tolerant lineage that originally occurred in more suitable areas of the Balkan Peninsula and south-eastern Europe during the LGM. Consequently, the less cold-tolerant lineage now occurs at the northern edge of the species range. This implies that some cold-adapted populations may have survived the last glacial period in microrefugia in central Europe, while individuals from less cold-tolerant populations may have immigrated from the south with climate warming during the Holocene.

Indeed, our macroclimate-based models were unable to identify sites that may have served as microrefugia for steppe species in central Europe during Pleistocene cold periods (so-called cryptic refugia). However, by integrating habitat suitability models with simulations of postglacial migration, we identified macroclimatically suitable areas farther south that could have harboured large populations of these species. Willner et al. (2021) summarised species-distribution and genetic data for several species occurring in the Carpathian Basin and adjacent regions and concluded that most of these species have been present there since at least the early Holocene. They found the greatest diversity of meadow-steppe specialists on the margins of the Carpathian Basin and on the northern Balkan Peninsula, the greatest diversity of grass-steppe specialists in the steppe zone of Ukraine and along the western coast of the Black Sea, and that of rocky-steppe specialists along the western margins of the Carpathian Basin, in the Dinaric Mountains and on the Balkan Peninsula. These patterns are consistent with the LGM and mid-Holocene source areas we have identified for individual steppe types and chorotypes. The distributions of haplotype groups for some species given by Willner et al. (2021) are also consistent with the source areas suggested by our models.

The current distribution ranges of most of the species considered in this study span a wide range of climatic conditions, from the humid climates of central Europe to the dry continental climates of central Asia. Only *Epherda distachya* and *Krascheninnikovia ceratoides* avoid moderately humid climates and are restricted to dry and extremely continental climates comparable to those of the Late Pleistocene cold periods. A comparable climate is currently found in some areas of Siberia, and models based on Siberian vegetation-plot data suggest the presence of steppe in central Europe during the LGM (Janská et al. 2017). The existence of steppe in this region during the cold and dry periods of the Pleistocene is also supported by fossil pollen data (Magyari et al. 2014, Feurdean et al. 2015). However, the full-glacial steppe was likely much less species-rich than the Holocene steppe, as suggested by our models and a comparative analysis of grassland species richness between adjacent areas in Siberia with LGM-like and Holocene-like climates (Chytrý et al. 2017). Our models suggest that some species now common in the middle and central Asian steppes may have spread to central Europe during each cold period and retreated during warmer periods. One of these, *K. ceratoides*, is traditionally considered a relict of the Pleistocene loess steppe in central Europe (Wendelberger 1954, Horsák et al. 2015, Seidl et al. 2020, 2021). Some other species, now restricted to continental areas of eastern Europe and middle/central Asia, may also have occurred in the Pleistocene steppes of central Europe (e.g. *Artemisia laciniata* and *A. rupestris*; Jäger 1987), but we did not consider them in this study because we focused on species typical of the present-day central European steppes. However, the Pleistocene cold steppe should not be considered as one large area with a homogeneous habitat. Most likely, it contained various habitats, including different steppe types that occurred in a mosaic with patches of tundra, dry and wet scrub, and taiga, similar to the present-day steppe-tundra in Siberia (Yurtsev 2001, Chytrý et al. 2019). More sensitive steppe species were probably not common but could have survived in small patches of warmer or moderately humid habitats that functioned as glacial microrefugia. Other species or less cold-tolerant genetic lineages may have gone extinct, returning only during warm periods by migrating from southern or south-eastern refugia (Magyari et al. 2010). These were probably located at the margins of the Carpathian Basin (Willner et al. 2021), in the Dinaric Mountains and other mountain systems of the Balkan Peninsula, and along the Black-Sea coast.

For the warm and humid period of the mid-Holocene, our models do not suggest a climatically driven retreat of the central European steppe species. On the contrary, the area of suitable climate was most extensive for many of the studied species during this period, and the models suggest that they were present, and probably abundant, in the central European landscape, as suggested by other studies (Kuneš et al. 2015, Pokorný et al. 2015, Feurdean et al. 2018, Willner et al. 2021). Thus, if steppe species were suppressed during this period, it was due to forest expansion rather than the direct effect of climate on steppe plants. We intentionally did not include forest cover in the models to downweight suitability for steppe species because, based on fossil pollen data (Magyari et al. 2010, Feurdean et al. 2015, Kuneš et al. 2015, Pokorný et al. 2015), we assume that there were always some open patches in low-elevation areas of central Europe (Gradmann 1933) that could not be captured by our models. They were located either on dry, south-facing slopes in hilly landscapes or in areas disturbed by wild herbivores or humans and their livestock (Chytrý et al. 2022a). Many species now typical of steppe may have also occurred in the herb layers of open-canopy forests of the mid-Holocene (Chytrý et al. 2010) or in woodland–grassland mosaic landscapes (Fyfe et al. 2015). Moreover, during most of the Holocene, central European lowlands were settled by people who may have kept parts of the landscape more open so that light-demanding species could survive (Jamrichová et al. 2017, Pokorný et al. 2022). After the arrival of the first Neolithic farmers and the subsequent expansion of grasslands, these species probably spread from several small refugia scattered across central Europe and formed their current distribution ranges.

Although our habitat suitability models and migration simulations were unable to identify 'true refugia', i.e. areas where a species survived unfavourable climatic conditions and from which it expanded into its present range, they suggested likely source areas from which colonization of currently occupied regions was possible. Based on migration simulations, the spread of central European steppe species from potential source areas with suitable macroclimates and large populations (macrorefugia) appears to be considerably limited, as the accessibility of only some of these areas had a significant effect on the current species distributions. This is consistent with other studies showing that not all refugia contributed equally to postglacial dispersal (Magri et al. 2006, Tzedakis et al. 2013). As a result of limited migration from past refugia, many European plants, including trees, do not currently occupy all climatic conditions suitable for them and thus do not fill the full extent of their potential ranges (Svenning and Skov 2004, Normand et al. 2011). These species also have different biogeographic affinities that likely reflect their different biogeographic histories, including localization, size and number of past refugia, and migration rates.

Unlike in present-day central Europe, where all modelled species co-occur in the same landscapes, our models showed that we can recognize species groups with different potential source areas. Surprisingly, species with similar distribution ranges showed better patterning than species with similar ecological requirements, although there is some overlap between these two groupings. This suggests that present-day species assemblages may be partly of recent origin, composed of species with different LGM-Holocene histories, rather than synchronized postglacial migrations of entire communities.

Conclusions

The central European macroclimate during the Pleistocene cold periods does not seem to have been suitable for most species of the present-day extrazonal steppes in this region. Steppe probably existed in the dry lowland and hilly landscapes, but it was likely generally species-poor and dominated by continental species that have most of their present range in desert steppes of middle and central Asia. Nevertheless, there may have been patches of locally warmer and wetter habitats that served as microrefugia for many species of the present-day steppe. This long-term persistence of some species or infraspecific cold-tolerant lineages is supported by genetic evidence. For other species or lineages, late-glacial or postglacial immigration from southern and south-eastern refugia remains a plausible scenario. These refugia probably ranged from south-eastern France through the Adriatic region and the Balkan Peninsula to the western Black-Sea coast and Crimea. However, their localization probably differed according to both chorological and ecological types of central European steppe vegetation. The warm and humid climate of the mid-Holocene had no direct negative impact on these species. If some of them reduced their populations during this period, it was due to forest expansion and not to the climate per se. However, these species likely remained present in the central European landscape and expanded after the Neolithic farmers promoted the expansion of open vegetation.

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Author contributions

Jan Divíšek: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead). **Martin Večeřa**: Conceptualization (lead); Data curation (equal); Formal analysis (supporting); Writing – original draft (supporting). **Erik Welk**: Data curation (lead); Methodology (supporting); Writing – original draft (supporting). **Jiří Danihelka**: Data curation (lead). **Kryštof Chytrý**: Visualization (equal); Writing – original draft (equal). **Jan Douda**: Validation (equal); Writing – original draft (supporting). **Milan Chytrý**: Conceptualization (lead); Data curation (supporting); Funding acquisition (lead); Writing – original draft (lead).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06293>.

Data availability statement

Species distribution maps, coordinates of species occurrences used for calibration of Maxent models, and all maps produced in this study are available in the Zenodo repository (<http://doi.org/10.5281/zenodo.5907271>).

Supporting information

The Supporting information associated with this article is available with the online version.

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