

Formation Process of Distribution Pattern and Floristic
Composition of *Betula davurica* Forests in the Japanese
Archipelago and Continental Northeast Asia

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Chapter 1 General Introduction

1.1 Disjunct distribution and climate change

At macro-scales, distributions of many natural plants are primarily determined by climate (Walter 1973; Overpeck *et al.* 1990; Stephenson 1990). Repeated paleoclimate oscillations over glacial and interglacial periods during the Quaternary (over the past 2.6 million years) have caused distribution changes of plants and vegetation worldwide (Council 1995; Comes and Kadereit 1998; Davis and Shaw 2001; Williams *et al.* 2004; Svenning *et al.* 2008). For instance, many species of the northern hemisphere migrated southward during glacial periods and northward during interglacial periods, resulting in local extinctions and range expansions (Wolfe 1997; Comes and Kadereit 1998; Qian and Ricklefs 2000). Such paleoclimate changes during the Quaternary led to present-day disjunct distribution patterns that influence refugia formation, speciation, biodiversity, and floristic composition of vegetation (e. g., Hewitt 1996; Collevatti *et al.* 2009; Qian and Ricklefs 2000; Clarke 2018). Therefore, disjunct distribution has been a major issue in biogeography, and elucidation of the mechanisms of this phenomenon would promote our understanding of macro-level plant diversity and biogeography.

The importance of disjunct distribution of plants is frequently represented by alpine plants, which are also called “alpine glacial relict species”. For example, some alpine species that are distributed in high-latitude regions of the northern hemisphere such as the arctic tundra are disjunctly distributed in high mountain areas of the Japanese archipelago, Europe, and North America (Reisch 2008; Schmitt *et al.* 2010; Hirao 2014). Previous fossil records showed that these species were widely distributed throughout the northern hemisphere during the glacial periods (Birks 2008; Hirao 2014). Thereafter, the distribution ranges of these species shrank during the interglacial periods, whereas some species survived and formed disjunct distribution in cold regions such as high mountains of middle latitude. Therefore, elucidating the formation process of disjunct distribution pattern with climate change would allow the understanding of

the distribution history of plants and could provide useful information in considering the impact on the ecosystems during the future climate changes.

1.2 Cool temperate forests in Northeast Asia

Cool temperate forest is one of the major forest types in northern hemisphere, and three areas of cool temperate forest with large spatial extents occur in eastern North America, Europe, and Northeast Asia (NEA; Frelich *et al.* 2015). In these three areas, the species richness of trees and understory plants of the forest in NEA is the highest, and various forest vegetation types occur (Latham and Ricklefs 1993; Qian 2002; Kolbek *et al.* 2003; Ricklefs *et al.* 2004; Box and Fujiwara 2012). The major reason for this is that many plant species in NEA might have survived through the Quaternary climate change because extensive ice-sheet did not cover this region during the glacial periods (Gray 1878; Clark and Mix 2002; Ehlers and Gibbard 2007; Tang *et al.* 2018). The other reason is that the geographical features of NEA also played a role in providing refugia for many temperate species during the past climate change (Aizawa *et al.* 2012; Bao *et al.* 2016; Chung *et al.* 2017); such refugia include the Korean Peninsula stretching south from the continent, as well as continental islands that run parallel to continental NEA, including Taiwan, the Japanese archipelago, and Sakhalin.

The cool temperate forest of NEA extended across the continental shelf to link the cool temperate forest and many temperate species in eastern China, the Korean Peninsula, and the Japanese archipelago during the Last Glacial Maximum (LGM; *ca.* 21,000 years before present [y BP]; Clark *et al.* 2009; Tang *et al.* 2017), whereas higher sea levels in post-LGM isolated these regions and caused disjunct distribution of them (Qian and Ricklefs 2000; Harrison *et al.* 2001). Moreover, the global warming and the wetting by inflow of ocean current in post-LGM led to distribution change and speciation of Japanese plants and changes in floristic composition of Japanese forest vegetation. Therefore, the Japanese archipelago has been attracting attention as one of the important factors leading to the creation of high plant species richness and various cool

temperate forest vegetation in NEA (e.g., Qian and Ricklefs 2000; Davis and Shaw 2001; Okitsu 2006; Aizawa *et al.* 2012).

1.3 Disjunct distribution of temperate tree species in Northeast Asia

The floristic composition and vegetation types of the present cool temperate forests differs significantly between Japan and continental NEA owing to the difference of climate. The continentality characterized by the increased range of temperatures and dryness is important effective concepts to describe the climatic difference between Japan and continental NEA. Krestov *et al.* (2006) proposed a model of distribution pattern in dominant species, major phytosociological and phytogeographical units of East Asian cool temperate forests in the scheme of vegetation zones and continentality sectors, such as ultracontinental, continental, maritime, suboceanic and oceanic. Continental NEA climate subjected to ultracontinental, continental, and maritime whereas Japanese climate and mostly subjected to suboceanic and oceanic. The cool temperate forests of continental NEA are mainly represented by *Quercus mongolica*–*Betula davurica* forest and various deciduous broadleaved–*Pinus koraiensis* forest adapted to continental or maritime (dry and heavy cold winter) climate and covered widely on the Russian Far East, northeast- to eastern China, and the Korean Peninsula (Kolbek *et al.* 2003). In contrast, the cool temperate forests of Japan are mainly represented by *Fagus crenata* and *Quercus crispula* forests adapted to oceanic (humid and relatively warm winter) climate (Miyawaki 1994).

Despite the fact that climate and vegetation differ remarkably between continental NEA and Japan, several canopy tree species of cool temperate forest in continental NEA are distributed in some regions of Japan, indicating disjunct distribution pattern in NEA. For instance, evergreen coniferous trees *Picea* sect. *Picea* and *Pinus koraiensis* are canopy tree species of mixed broadleaved-coniferous forests in cool and cold temperate zones of continental NEA and are widely distributed in the Russian Far East, northeast China, and mid- to northern

regions of the Korean Peninsula. However, they are also found only in central Honshu of Japan, indicating a disjunct distribution at present. Previous paleobotanical studies reveal macrofossil data for these species obtained throughout Japan during the LGM (Tsukada 1983; Okitsu and Momohara 1997; Morita 2000; Okitsu *et al.* 2016). These data suggest that temperate mixed broadleaved-coniferous forests widely covered Japan during the LGM and have experienced unique distribution history since the LGM (Okitsu and Momohara 1997; Okitsu *et al.* 2016). Therefore, clarifying the distribution history of tree species is an important issue for understanding the process of disjunct distribution of these species and mechanisms of the formation of cool temperate forests in Japan and NEA.

1.4 Distribution *Betula davurica* and phytogeographical features of *B. davurica* forests

The deciduous broadleaf *Betula davurica* Pall. (Betulaceae) is a dominant canopy tree species in NEA. In continental NEA, it is widely and commonly distributed throughout the Russian Far East, eastern Mongolia, northeast China, and mid- to northern part of the Korean Peninsula (Takahashi 1944; Okitsu 2006; Shaw *et al.* 2014); it compose of forest-steppe ecotones under ultracontinental climate or cool to cold temperate deciduous broadleaved forests under continental climate along with *Q. mongolica* (Ermakov 1997; Krestov *et al.* 2006; Okitsu 2006). According to phytosociological studies, temperate forests mixed with *B. davurica* is one of the main forest vegetation in continental NEA, and classified to orders *Lespedeza bicoloris*–*Quercetalia mongolicae* or *Quercu mongolicae*–*Betuletalia davuricae* belong to the class *Quercu mongolicae*–*Betuletea davuricae* (e.g., Ermakov 1997; Krestov *et al.* 2006). In contrast, in Japan, *B. davurica* is found only in the temperate zone of central Honshu and eastern Hokkaido, indicating a disjunct distribution (Takahashi 1944; Okitsu 2006). Even in these regions, the species is main canopy tree species of the cool temperate deciduous broadleaved secondary forests, and these forests classified as associations *Corylo heterophyllae*–*Betuletum davuricae* and *Saso nipponicae*–*Quercetum grosseserratae* in central Honshu and *Carpino*–*Quercetum*

grosseserratae belong to the class *Fagetea crenatae* (Hoshino 1998; Hoshi 2000; Suzuki 2002).

However, few studies exist for comparisons between cool temperate forest vegetation and commonality of flora of the forests between Japan and continental NEA. The comparisons of forest vegetation and flora in these regions would increase our understanding of the relations between cool temperate forests of Japan and continental NEA and importance of *B. davurica* forests in Japan.

1.5 Objectives of this thesis

In this thesis, I focused on the disjunct distribution pattern of *B. davurica* and aimed to clarify the distribution changes of the species with paleoclimate change and the floristic composition relationships of *B. davurica* forests between Japan and continental NEA. To clarify these issues, I conducted the following set of studies:

- 1) To clarify how the present disjunct distribution pattern of *B. davurica* was formed, I statistically evaluated the relationships between climatic factors and the distribution of *B. davurica*, and examined a series of potential habitats in the LGM, the mid-Holocene, and the present by using a species distribution model approach (Chapter 3). This chapter was published in Shitara *et al.* (2018).
- 2) To reveal the distribution change of *B. davurica* associated with the development of oceanic climate in Japan in post-LGM, I projected the potential habitats of *B. davurica*, *F. crenata*, and *Q. crispula* in the LGM, the mid-Holocene, and the present by using a species distribution modeling approach. Thereafter, I discussed the distribution change of cool temperate deciduous broadleaved forests in Japan from the LGM to the present (Chapter 4).
- 3) To clarify the relationship of the floristic composition of *B. davurica* forests between Japan and continental NEA, I compared existing relevés of *B. davurica* forests between Japan and continental NEA by using the Braun–Blanquet approach (Chapter 5).

In the final chapter, I discussed the distribution formation process of *B. davurica* forests in

cool temperate forests of Japan and continental NEA (Chapter 6).

Chapter 2 Materials

2.1 Study species

2.1.1 *Betula davurica*

The genus *Betula* L. is widely distributed primarily in temperate and boreal climate zones in the northern hemisphere and comprises 40–60 species (Furlow 1990; Peiqiong and Skvortsov 1999; Ashburner and McAllister 2013; Nemoto 2016). Approximately 11 species have been identified in Japan (Nakamura *et al.* 2015, Nemoto 2016), and each species has been verified to have a distinct distribution pattern and habitat (e.g., Suzuki 1998; Tsuda and Ide 2005; Okitsu 2006, 2017; Ogawa and Okitsu 2011; Ishida *et al.* 2014; Nakamura *et al.* 2015; Shitara *et al.* 2018).

Betula davurica, that could reach 20 m in height, is a representative tree species characterizing forest-steppe ecotones under ultracontinental climate or in cool to cold temperate deciduous broadleaved forests under continental climate in continental NEA (Ermakov 1997; Krestov *et al.* 2006; Okitsu 2006). The bark is grayish brown to gray and exfoliates with age in distinct, shaggy, paper-like flakes (Fig. 2.1). The hardwood is used in constructing houses, agricultural tools, and furniture in continental NEA (Shaw *et al.* 2014).

In continental NEA, *B. davurica* is widely and commonly distributed throughout the Russian Far East, eastern Mongolia, northeast China, mid- to northern part of the Korean Peninsula (Fig. 2.1a). It occurs in the altitude approximately 400 to 1300 m and is found along with *Q. mongolica* in deciduous broadleaved forests or mixed broadleaved-coniferous forests on dry or moist soils and exposed rocky places or after fire places (Krestov *et al.* 2006; Shaw *et al.* 2014). In Japan, it is disjunctly distributed in central Honshu (Yamanashi, Nagano, Gunma, Saitama, and Tokyo prefectures) and eastern Hokkaido (Fig. 2.1b,c). In addition, this occurs along with *Q. crispula* (synonyms: *Q. grosseserrata* or *Q. mongolica* var. *crispula*) in secondary deciduous broadleaved forests or edge of forests on the stony soil of gentle slopes in the landslide

area (Okitsu 2006; Ogawa and Okitsu 2011). In continental NEA, this species is categorized as LC (“Least Concern”) in IUCN red list; however, the species is categorized as NT (“Near Threatened”) in the Japanese red list (Shaw *et al.* 2014).

2.1.2 *Fagus crenata* and *Quercus crispula*

Fagus crenata Blume (Fagaceae) and *Quercus crispula* Blume (Fagaceae) are both widely distributed species that dominate canopies in the cool temperate forests in Japan. *F. crenata* is a tree species of endemic to Japan and occurs from the southern part of Kyushu to the southern part of Hokkaido (Matsui *et al.* 2004, 2018). The species-dominant forests are established as zonal climax communities of cool temperate forests of Japan and mainly occur particularly in snowy regions in the Sea of Japan side (Miyawaki *et al.* 1994; Hukushima *et al.* 1995; Yagihashi *et al.* 2003; Matsui *et al.* 2018). In contrast, *Q. crispula* mainly occurs in cool temperate forests of southern Sakhalin, the Kuril Islands, and Japan. The populations are dense and continuous in northern Japan but sparse and commonly isolated in small patchy forests at elevations over approximately 800 m in southwestern Japan (Hoshino 1998; Suzuki 2002; Kolbek *et al.* 2003; Krestov *et al.* 2015). *Quercus crispula* forest has a higher tolerance to dry climate condition than *F. crenata* forest (Yagihashi *et al.* 2003). Moreover, *Q. crispula* is more abundant than *F. crenata* in stands with shorter cutting cycles (i.e., more frequent human disturbance; Fujita and Sano 2000; Nagaike *et al.* 2003) because *Q. crispula* has a stronger ability to sprout and a lower minimum fruiting age (*ca.* 10; Kisanuki and Kurahashi 1998) than *F. crenata* (*ca.* 40; Kamitani 1986; Hashizume 1987).

2.2 Figures



Fig. 2.1 Photographs of deciduous broadleaved forests mixed with *Betula davurica* in continental Northeast Asia and Japan. a: Sikhote-Alin (Russia), b: Nagano Pref. (central Honshu, Japan), c: Rikubetsu Town (Hokkaido, Japan).

Chapter 3 Formation process of the disjunct distribution of *Betula davurica* in Northeast Asia using a species distribution model

3.1 Introduction

It is inferred that the primary cause of *B. davurica*'s disjunct distribution was repeated climate change during the Quaternary, most importantly during the LGM and the subsequent Holocene (Okitsu 2006). Such hypothesis has been verified primarily by using traditional paleophytological methods such as analysis of plant macrofossils or pollen fossils. For instance, previous paleophytological studies clarified that *Pinus koraiensis*, which is currently widely distributed in continental NEA but isolated in central Honshu of the Japanese archipelago, had been widely distributed in the Japanese archipelago during the last glacial period, and had decreased with the climate change after the glacial period (Tsukada 1983; Okitsu and Momohara 1997; Morita 2000). To reveal the distributional change of *B. davurica*, past distribution of the species should be examined by the same paleophytological methods. However, macrofossils and pollen fossils of *Betula* are difficult to identify on the species level (Tsuda and Ide 2005; Tsuda *et al.* 2015).

Under such circumstances, species distribution modeling (SDM) has been increasing popularity as an effective alternative method for clarifying past distribution patterns of plant taxa (e.g., Clark *et al.* 2012; Sakaguchi *et al.* 2012; Tsuyama *et al.* 2014; Kimura *et al.* 2014; Zeng *et al.* 2015; Tang *et al.* 2017). SDM is a quantitative method to infer species' environmental requirements from conditions at known occurrences (Wisz *et al.* 2008). This approach can identify climatic controls for target taxa, as well as potential or vulnerable habitats under various climate change scenarios focused in the past, present, or future (Pearson and Dawson 2003; Matsui *et al.* 2004; Thuiller *et al.* 2005; Tsuyama *et al.* 2011, 2014).

Therefore, the objective of this study is to clarify how past climate change influenced the

present disjunct distribution pattern of *B. davurica* in continental NEA and the Japanese archipelago. To do this, I employed SDM to examine the magnitude of the species climatic response and to elucidate historical changes in the potential habitats of *B. davurica* under the climate conditions of the LGM, the mid-Holocene, and the present.

3.2 Materials and Methods

3.2.1 Study area

The study area (between 85–150°E and 25–60°N) in this chapter fully encompassed the actual *B. davurica* distribution (Fig.3.1). The climate in continental NEA is dominated by moist oceanic winds and Asian monsoons during the summer (Krestov *et al.* 2006; Li *et al.* 2015), and by dry continental winds during the winter; in contrast, continental islands including the Japanese archipelago are affected by humid oceanic climate all year around.

3.2.2 Species occurrence data collection

B. davurica occurrence data in Japan were compiled through field surveys using Global Positioning System during 2014–2016. Occurrence data in continental NEA were obtained from various sources such as the Chinese Virtual Herbarium (CVH: www.cvh.ac.cn), the Global Biodiversity Information Facility (GBIF 2016: www.gbif.org), Chang and Kim (2015), Kharkevich (1996), and Ermakov (1997). Because the majority of these sources did not specify latitude and longitude, distribution maps were georeferenced for digitalization of the presence points using the georeference tool available in ArcGIS version 10.4. To preclude spatial autocorrelation, duplicate records were removed within a spatial resolution of 2.5 arcmin (*ca.* 5 km), resulting in 251 occurrences (Fig. 3.1).

3.2.3 Preparation of climate data

Nineteen bioclimatic variables (2.5 arcmin resolution) were obtained from the WorldClim

1.4 dataset (www.worldclim.org; see also Hijmans *et al.* 2005), covering present (*ca.* 1960–1990) *B. davurica* distribution range (and neighboring areas). The model for present potential habitats of *B. davurica* was projected to the following time slices: the LGM (*ca.* 21,000 y BP) and the mid-Holocene (*ca.* 6,000 y BP). Because paleoclimatic layers of high resolution were available only for three General Circulation Models (GCMs), these were the climate scenarios downloaded from WorldClim 1.4 (resolution: 2.5 arcmin), namely, (1) CCSM4 (CCSM: Gent *et al.* 2011), (2) MIROC-ESM (MIROC: Watanabe *et al.* 2011), and (3) MPI-ESM-P (MPI: www.mpimet.mpg.de/en/science/models/mpiesm/).

3.2.4 SDM construction

Maximum entropy principle algorithms (MaxEnt) are often used to project the potential habitats of a given species on the basis of given occurrences and environmental variables (Phillips *et al.* 2006). This has some advantages compared to other SDM approaches including its convenience, its use of presence-only species records, and a generally excellent predictive performance (Elith *et al.* 2006; Hernandez *et al.* 2006; Tang *et al.* 2017). In the present study, I used MaxEnt version 3.3.3 k (www.cs.princeton.edu/~schapire/maxent/) to depict suitable habitats, ranging from 0 to 1 per grid cell (Tang *et al.* 2017).

To select bioclimatic variables, I followed the same method used in the previous study by Tang *et al.* (2017). A correlation analysis was first performed on the 251 occurrence points and a random sample of 10,000 background points within the study area. Next, bioclimatic variables with strong collinearity (Pearson's correlation coefficient $r \geq |0.85|$) were grouped (Table 3.1). All possible combinations of the 19 bioclimatic variables (excluding those with over two parameters from the same group of highly correlated variables) were used to calculate Variance Inflation Factors (VIFs) in R (vif function of usdm package). Datasets with VIFs of > 10 were excluded to avoid multicollinearity. The corrected Akaike information criterion (AICc; Hurvich and Tsai 1989) was used to select the best fit of 3608 combinations, resulting in six variables: annual mean

temperature (AMT; bio1), mean diurnal range (Continental Index; mean of monthly maximum temperature–minimum temperature, MDR; bio2), mean temperature of warmest quarter (MTWQ; bio10), precipitation seasonality (PRS; bio15), precipitation of driest quarter (PRDQ; bio17), and precipitation of warmest quarter (PRWQ; bio18). The best model was then evaluated in MaxEnt with 20-fold cross-validation using area under the curve (AUC) of a receiver operating characteristic (ROC) plot. Maps were generated in ArcGIS version 10.4.

Maxent estimates the importance of the variables with percent contribution and permutation importance values. Percent contribution represents how much the variable contributed to the model based on the path selected for a particular run. Permutation importance is determined by changing the predictors' values between presence and background points and observing how that affects the AUC (Phillips 2006).

3.2.5 Sensitivity analysis for disjunct distribution formation

To examine which climatic variable affected the distribution shift of *B. davurica* with post-LGM climate change, I performed sensitivity analysis using the LGM climate data by changing one of the six climatic variables while retaining the unmodified values of the other five. Firstly, the differences of the average values in temperature and precipitation between the LGM and the present climatic conditions were calculated for all six climatic variables for each GCM (Table 3.3). Secondly, either 50 or 100 % of the calculated differences were separately added to each variable of the LGM for each GCM. The added values for the temperature variables (AMT, MDR, and MTWQ) are shown in degree Celsius, and the precipitation variables (PRS, PRDQ, and PRWQ) are shown as a percentage. Consequently, AMT, MTWQ, PRDQ, and PRWQ were increased by + 3 and + 6 °C, + 2.5 and + 5 °C, + 10 and + 20 %, and + 3 and + 6 %, respectively, whereas MDR and PRS decreased by - 1 and - 2 °C, and - 5 and - 10 %, respectively.

3.3 Results

3.3.1 Model performance and present potential habitats

The model AUC was 0.952 ± 0.013 , considered an excellent fit (Swets 1988). Present potential habitats for *B. davurica* (projected by the threshold of 0.1746) corresponded well with the present occurrence records (Figs. 3.1 and 3.2). Central China, Lake Baikal, Verkhniy Yenisei River, and northern Honshu are identified as potential habitats, but *B. davurica* is presently not recorded there. These “empty habitats” are due to conditions other than climate (Tsuyama *et al.* 2014; Tang *et al.* 2017).

The largest contributing factor in the model was PRWQ, followed by AMT and MTWQ (Table 3.2). The results of the response curve showed that the distribution probability in PRWQ increased sharply at a PRWQ of more than 250 mm, approximately (Fig. 3.3f). The distribution probability in AMT was the highest at approximately 5 °C (Fig. 3.3a). In addition, the distribution probability in MTWQ increased sharply once 14 °C was reached (Fig. 3.3c).

3.3.2 Potential habitats during the LGM

I used three GCMs (CCSM, MIROC, and MPI) to project potential habitats during the LGM period (Fig. 3.4a–c). Each of the projected potential habitats showed expansions in eastern China and Central China, along with complete absence in the Russian Far East and Hokkaido. Potential habitats were also widely and continuously distributed from eastern China and the Korean Peninsula to the Japanese archipelago, excluding Hokkaido.

3.3.3 Potential habitats during the mid-Holocene

I used the same three GCMs to project potential habitats during the mid-Holocene (Fig. 3.4d–f). Compared with the present potential habitats, those in the mid-Holocene period did not differ considerably; they either expanded only slightly northward or retreated into eastern China and west Japan (Fig. 3.4d–f).

3.3.4 Climatic factors contributing to formation of disjunct distributions

The results of the sensitivity analysis showed that increased AMT in each of the three GCMs caused the projected potential habitats to retreat to the north in eastern China and western Japan and formation a disjunct distribution in Japan (Fig. 3.5b). In addition, increased MTWQ in the CCSM and MPI caused the projected potential habitats to expand to the Russian Far East and Hokkaido (Fig. 3.5d). On the other hand, the increase in PRWQ had a minor effect on changes in the potential habitat (Fig. 3.5g).

3.4 Discussion

3.4.1 Potential *B. davurica* habitats under the present climate

Previous studies examining the disjunct distribution formation in NEA plants have been based primarily on macrofossils, pollen fossils, and genetic tools (Note *et al.* 1998; Aizawa *et al.* 2012; Nagamitsu *et al.* 2014). By contrast, this study used the SDM approach to link post-LGM climate change with the disjunct distribution of *B. davurica*. The focus of almost all previous studies about *B. davurica* has been local and ecological; (Hou *et al.* 2004; Okitsu 2006; Kobayashi *et al.* 2007; Ogawa and Okitsu 2011); this is the first biogeographical study for *B. davurica* using the SDM approach. The SDM method is particularly useful to examine historical changes in a species' distribution when the fossil record is inadequate.

The MaxEnt model showed that PRWQ was the major factor contributing to the present distribution of *B. davurica* (Table 3.2). Moreover, the response curves showed that the distribution probability decreased quite sharply at a PRWQ value less than 250 mm (Fig. 3.3f). This suggests that extreme drought in warm seasons is an important limiting factor for the distribution of *B. davurica*. Furthermore, a vast area with PRWQ lower than 200 mm is found in continental inland between 30 and 65 °N where distribution of *B. davurica* is absent (Figs. 3.2 and 3.6b). Thus, PRWQ seems to define the western distribution boundary in continental inland areas

where the warm, moist air blown from the Pacific Ocean during the Asian summer monsoons (Li *et al.* 2015) produces insufficient summer rain.

3.4.2 Empty habitats

The present models projected some empty habitats (Tsuyama *et al.* 2014) on continental NEA (e.g., Central China and around Baikal Lake) and several islands such as Sakhalin and northeastern Honshu (Fig. 3.2). Dispersal limitation appears to be responsible for empty habitats on the continent, as these regions are very far from the main distribution area. In contrast, physical dispersal barriers (i.e., straits) are the likely cause of empty island habitats. Even without physical barriers, interspecific competition, geographical features, and geological history are all factors that could result in the small empty habitats scattered around northeastern Honshu (Okitsu 2006; Ogawa and Okitsu 2011).

3.4.3 Distribution during the LGM

The models projected that potential habitats for *B. davurica* during LGM were continuously distributed around the Korean Peninsula, eastern China, and the Japanese archipelago, excluding Hokkaido (Fig. 3.4a–c). These results are in line with previous SDM studies that projected a continuous distribution of some cool temperate tree species in eastern China, the Korean Peninsula, and the Japanese archipelago under the LGM climate (Harrison *et al.* 2001; Chen *et al.* 2012; Sakaguchi *et al.* 2012). Additionally, the MaxEnt result coincided with results of previous paleophytological studies that showed some species (e.g., *P. koraiensis*) presently having disjunct distribution patterns (like *B. davurica*) were widely distributed in Japan during the LGM (Tsukada 1983; Okitsu and Momohara 1997; Morita 2000).

The Japanese archipelago separated from the Asian continent during the Miocene (*ca.* 23.03 to 5.333 million years ago), but the two became re-connected several times throughout Pleistocene glacial periods (Maruyama *et al.* 1997). *Betula* species probably migrated across

these recurring land bridges. Specifically, a northbound bridge formed between the continent, Sakhalin, and Hokkaido, while the southbound Tsushima Strait land bridge formed between the Korean Peninsula and northern Kyushu (Nakamura *et al.* 2015). Results from the present study indicated that the Japanese population of *B. davurica* in central Honshu migrated via the southbound route.

3.4.4 Distribution change between the LGM and the present

The model in this study projected that potential *B. davurica* habitats shifted dramatically with changing climate between the LGM and the mid-Holocene (Fig. 3.4). Notably, the migration patterns differed between continental NEA and the Japanese archipelago. In the former, potential habitats expanded north (such as to North China and the Russian Far East), whereas in the latter, habitats shrank and formed disjunct distributions. Previous studies using pollen fossil records have indicated that the *Betula* genus was widely distributed in western Japan during the LGM (Hatanaka 1985; Miyoshi 1989; Gotanda *et al.* 2008); however, its distribution was severely reduced in west Japan in post-LGM (Yasuda 1986, 1987). Remarkably, the results in the present study coincided with these studies.

The sensitivity analysis revealed that increase of AMT was a predominant factor causing the retreat of potential habitats in eastern China and western Japan (Figs. 3.5b). In addition, CCSM and MPI scenarios demonstrated that increased MTWQ specifically likely caused an expansion of potential habitats northward (Fig. 3.5d). However, precipitation variables had a lesser effect on the species' migration than that of temperature variables (Fig. 3.5e–g). Interestingly, though PRWQ is the key factor for the present distribution of *B. davurica* (Table 3.2), nonetheless, this variable remained relatively unchanged from the LGM to the present (Fig. 3.6b). Therefore, the variation of temperature (AMT and MTWQ) is considered more important for this species' distribution change from the LGM to the present than that of precipitation (PRWQ). The new findings in the present study corroborate existing views about

plant distribution change: in East Asia, it is more strongly influenced by temperature than by precipitation (Jiang *et al.* 2003; Wang *et al.* 2017).

Potential habitats in the Korean Peninsula and central Honshu remained the same during the mid-Holocene (Fig. 3.4d–f), suggesting that these two regions may be long-term refugia for *B. davurica*. Refugia are areas that remain within a former distribution after range contraction (also called in situ refugia or climate relics), and long-term refugia are populations that persisted through multiple glacial cycles (Tzedakis 1993; Tang *et al.* 2017). In support of the findings in the present study, the northern Korean Peninsula and central Honshu mountains are both known as important refugia for many temperate or boreal tree species of NEA (Aizawa *et al.* 2012; Chung *et al.* 2017). Our present study also demonstrated that these two areas are key locations for the distribution shifts of *B. davurica* during the Quaternary. In the similarly distributed *P. koraiensis*, mtDNA diversity levels among Japanese populations are greater than those among continental populations (Aizawa *et al.* 2012). Extrapolating that pattern to *B. davurica* implies a similarly high genetic diversity in refugia populations. However, more genetic research is necessary to confirm such a possibility.

3.5 Figures

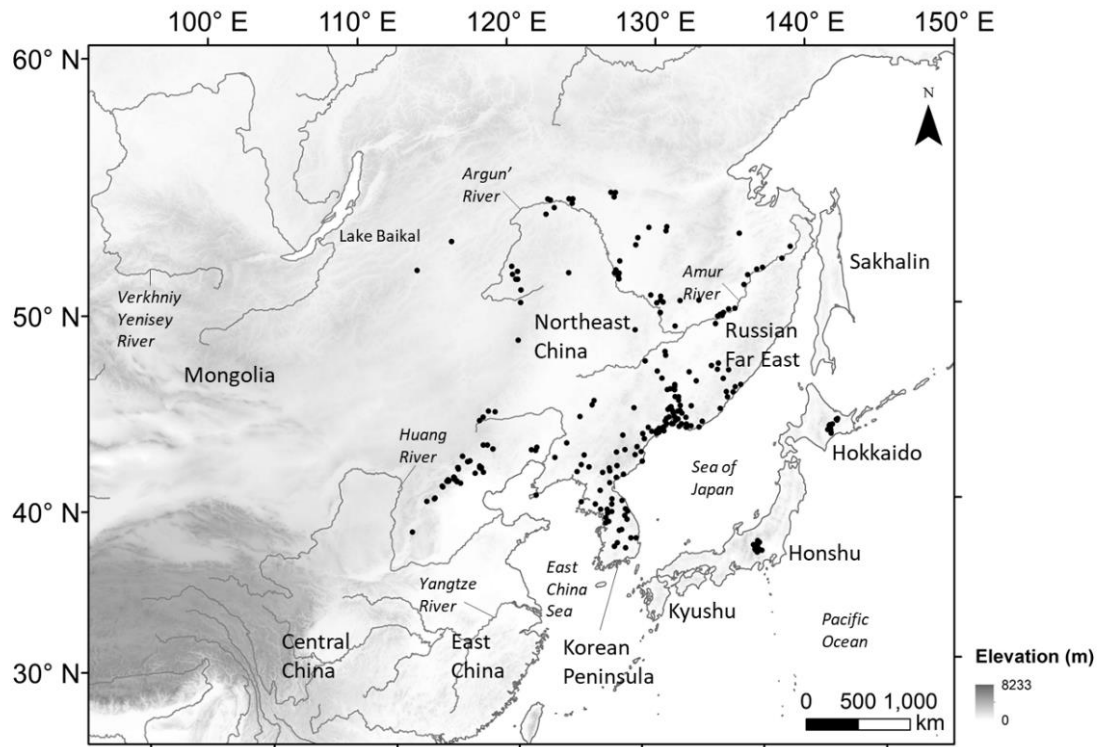


Fig. 3.1 Map of the study area and *Betula davurica* occurrence points (indicated with black circles).

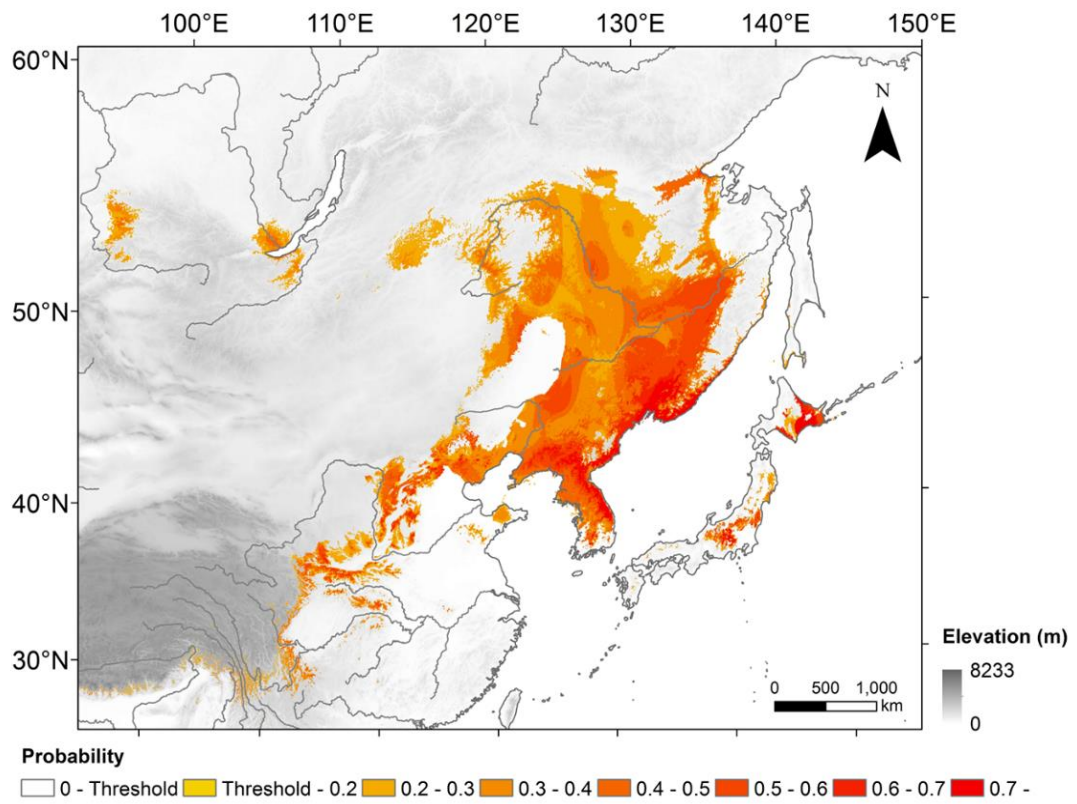


Fig. 3.2 Map of occurrence probabilities of *Betula davurica* under present climate conditions.

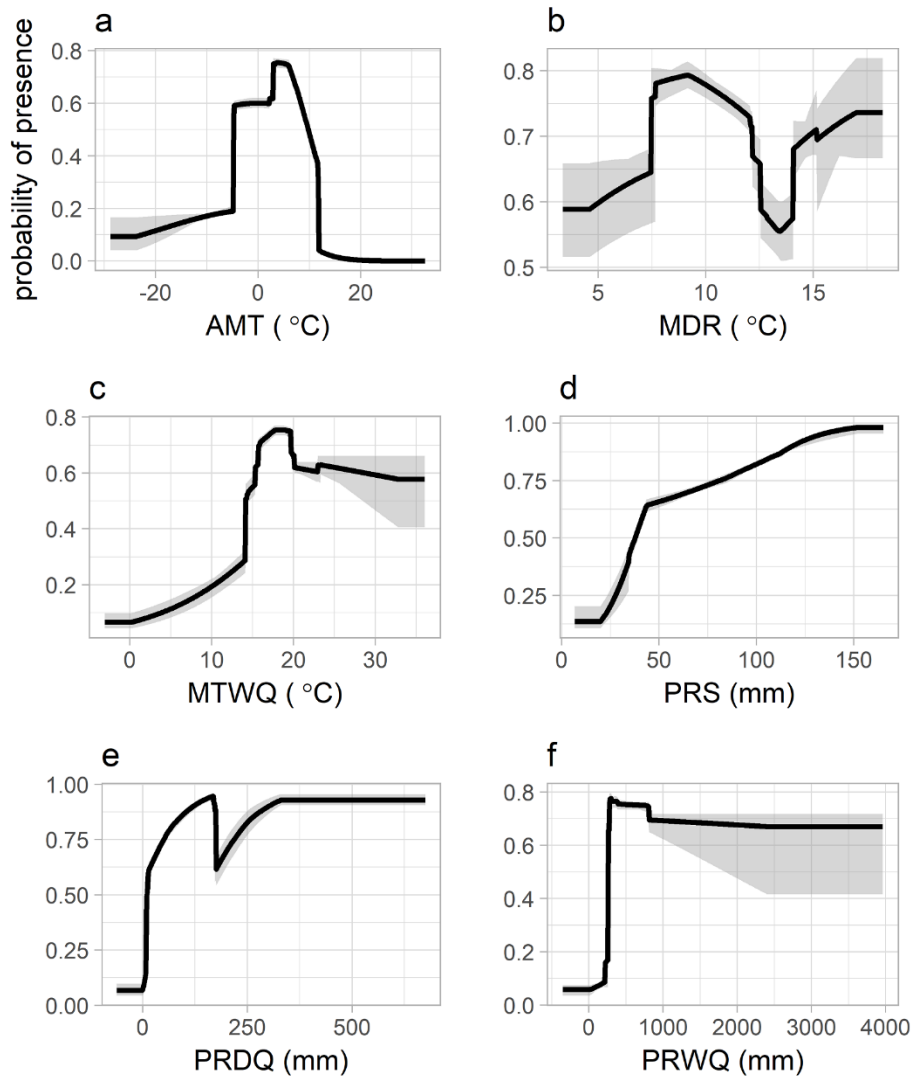


Fig. 3.3 Response curves of MaxEnt models of habitat suitability for *Betula davurica* to predictor variables (bioclimatic variables). These models were constructed by altering every variable while keeping all others at their average values. Response curves presented are means of 20 replicates, and standard deviation is shown in gray. a: Annual mean temperature (AMT), b: Mean diurnal range (MDR), c: Mean temperature of the warmest quarter (MTWQ), d: Precipitation seasonality (PRS), e: Precipitation of the driest quarter (PRDQ), f: Precipitation of the warmest quarter (PRWQ).

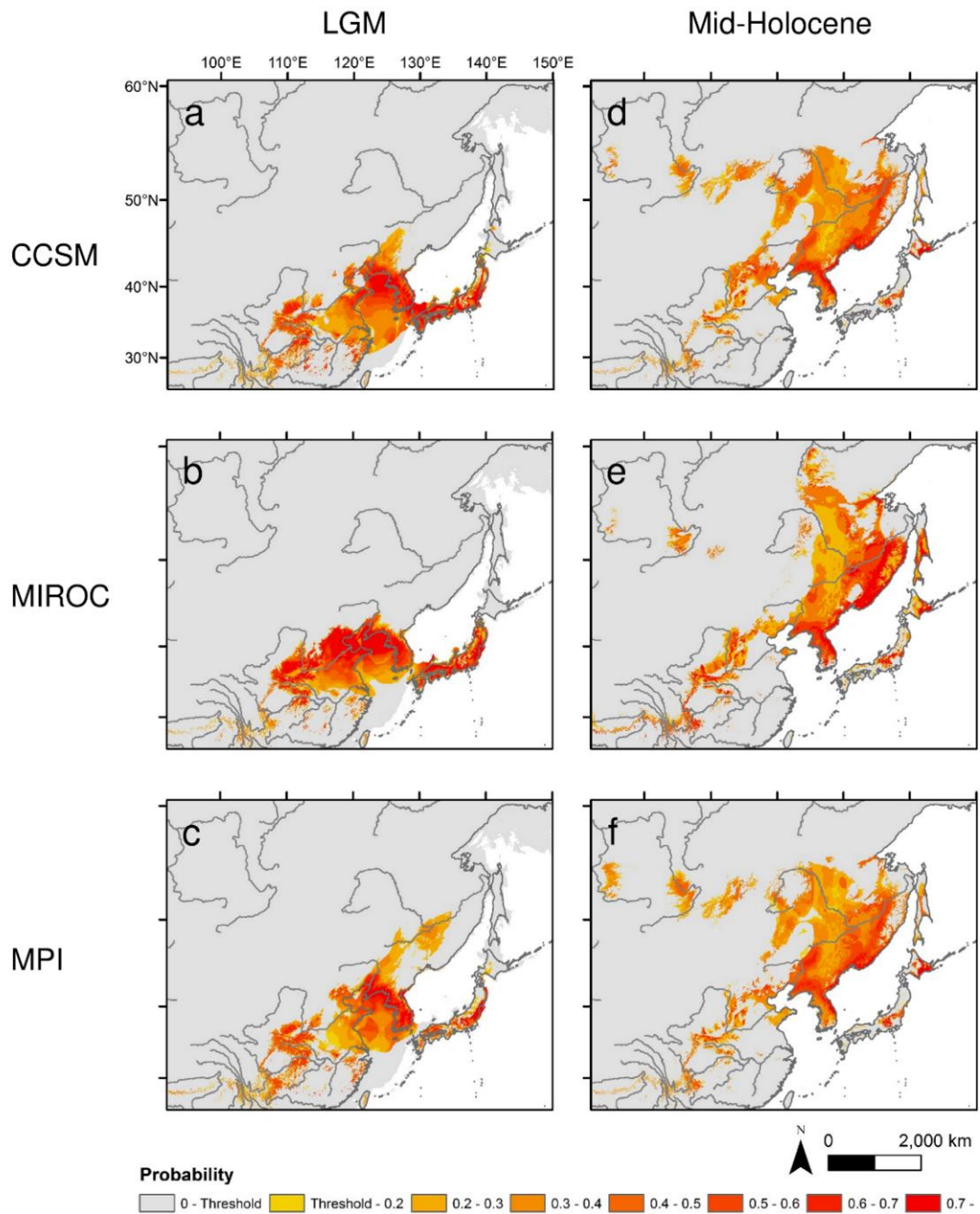


Fig. 3.4 A comparison of potential habitats under three climatic scenarios during the Last Glacial Maximum (LGM) (a–c) and the mid-Holocene (d–f). a, d Potential habitats under the climatic scenario CCSM. b, e Potential habitats under the climatic scenario MIROC. d, f Potential habitats under the climatic scenario MPI.

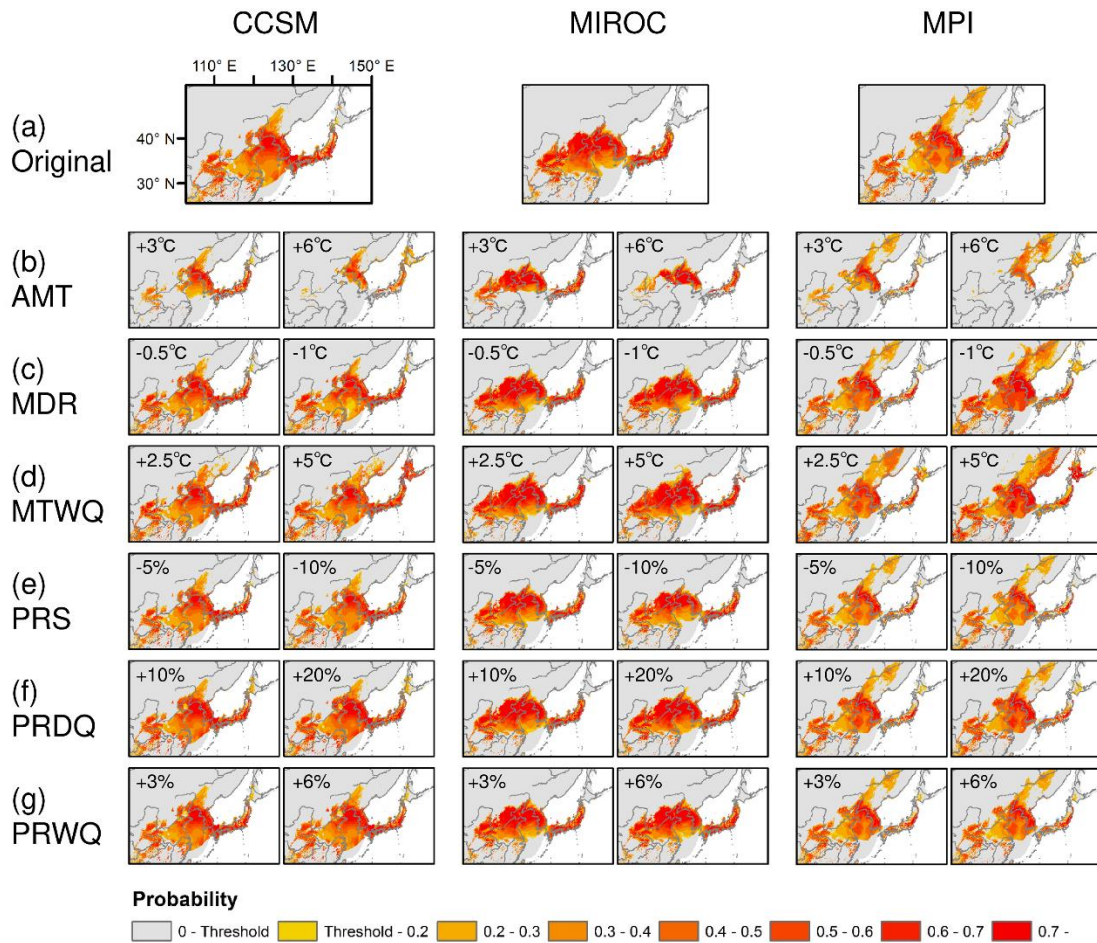


Fig. 3.5 Changes in potential habitat distribution of *Betula davurica* with different conditions of every climatic variable under three General Circulation Model (GCM) simulations for the Last Glacial Maximum (LGM). For details about the changes (increase/decrease) of climate values in each figure, please refer to the “Methods.” a original potential habitats. b Annual mean temperature (AMT). c Mean diurnal range (MDR). d Mean temperature of the warmest quarter (MTWQ). e Precipitation seasonality (PRS). f Precipitation of the driest quarter (PRDQ). g Precipitation of the warmest quarter (PRWQ).

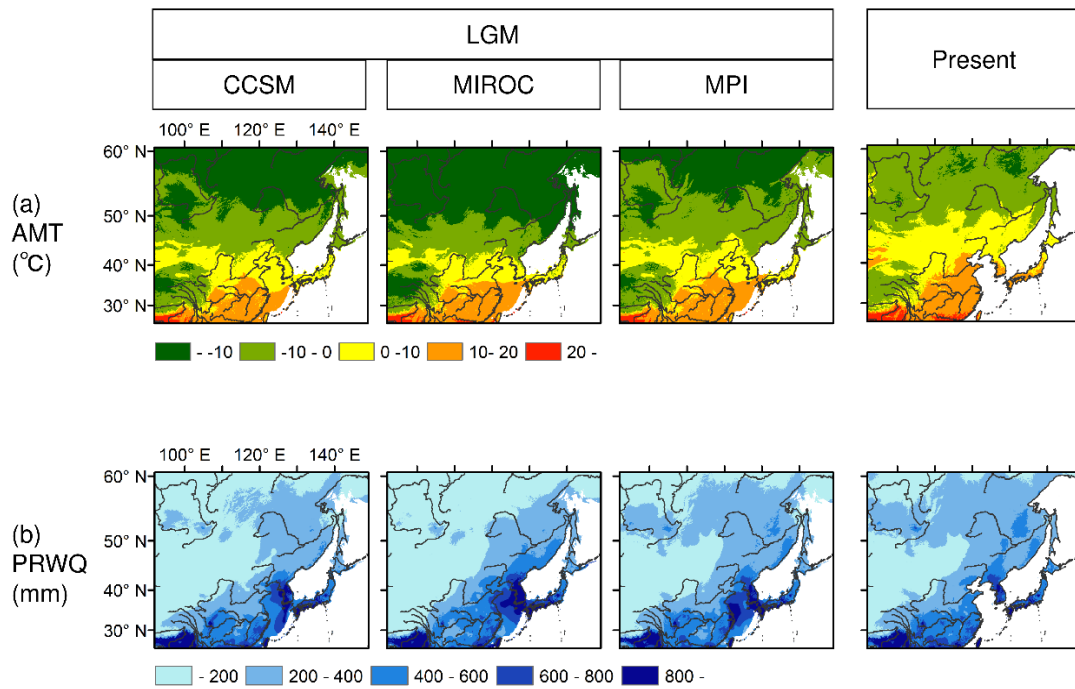


Fig. 3.6 A comparison of climate values of (a) annual mean temperature (ATM) and (b) precipitation of warmest quarter (PRWQ) in the area of study in the Last Glacial Maximum (LGM) and the present.

3.6 Tables

Table 3.1 Pearson's correlations among 19 bioclimatic variables.

	ATM	MDR	ISO	TS	MTWM	MTCM	TAR	MTWetQ	MTDQ	MTWQ	MTCQ	APR	PRWM	PRDM	PRS	PRWetQ	PRDQ	PRWQ	PRCQ	
ATM	1	-0.327	0.639	-0.835	0.777	0.974	-0.845	0.843	0.964	0.874	0.975	0.679	0.679	0.26	0.135	0.677	0.314	0.627	0.286	
MDR		1	0.194	0.211	-0.259	-0.391	0.362	-0.285	-0.344	-0.365	-0.31	-0.624	-0.477	-0.643	0.589	-0.493	-0.671	-0.495	-0.635	
ISO			1	-0.863	0.15	0.703	-0.793	0.274	0.722	0.253	0.749	0.407	0.492	-0.152	0.478	0.497	-0.105	0.463	-0.108	
TS				1	-0.316	-0.92	0.985	-0.436	-0.908	-0.465	-0.935	-0.617	-0.621	-0.189	-0.231	-0.626	-0.238	-0.594	-0.215	
MTWM					1	0.637	-0.333	0.95	0.643	0.975	0.626	0.427	0.416	0.217	-0.043	0.409	0.254	0.339	0.237	
MTCM						1	-0.939	0.723	0.984	0.762	0.995	0.715	0.698	0.311	0.103	0.7	0.365	0.656	0.336	
TAR							1	-0.46	-0.917	-0.497	-0.938	-0.685	-0.668	-0.283	-0.144	-0.674	-0.333	-0.652	-0.305	
MTWetQ								1	0.714	0.971	0.715	0.495	0.516	0.157	0.071	0.505	0.198	0.469	0.159	
MTDQ									1	0.756	0.984	0.699	0.68	0.295	0.096	0.685	0.351	0.632	0.333	
MTWQ										1	0.748	0.55	0.539	0.278	-0.015	0.53	0.321	0.477	0.296	
MTCQ											1	0.687	0.685	0.256	0.165	0.686	0.309	0.64	0.282	
APR												1	0.947	0.562	-0.19	0.96	0.622	0.927	0.591	
PRWM													1	0.33	0.053	0.994	0.395	0.946	0.365	
PRDM														1	-0.624	0.342	0.991	0.372	0.973	
PRS															1	0.016	-0.62	-0.001	-0.609	
PRWetQ																1	0.407	0.946	0.378	
PRDQ																	1	0.428	0.978	
PRWQ																		1	0.39	
PRCQ																				1

Those marked in bold were selected for species distribution modeling (SDM). ATM = annual mean temperature (bio1); MDR = mean diurnal range [mean of monthly (max temp – min temp)] (bio2); ISO = isothermality [(bio2/bio7) × 100] (bio3); TS = temperature seasonality (standard deviation × 100) (bio4); MTWM = maximum temperature of the warmest month (bio5); MTCM = minimum temperature of the coldest month (bio6); TAR = temperature annual range (bio5 – bio6) (bio7); MTWetQ= mean temperature of the wettest quarter (bio8); MTDQ = mean temperature of the driest quarter (bio9); MTWQ = mean temperature of the warmest quarter (bio10); MTCQ = mean temperature of the coldest quarter (bio11); APR = annual precipitation (bio12); PRWM= precipitation of the wettest month (bio13); PRDM= precipitation of the driest month (bio14); PRS = precipitation seasonality (bio15); PRWetQ = precipitation of the wettest quarter (bio16); PRDQ = precipitation of the driest quarter (bio17); PRWQ= precipitation of the warmest quarter (bio18); PRCQ= precipitation of the coldest quarter (bio19).

Table 3.2 Relative contributions of climatic variables to the potential *Betula davurica* habitats in the MaxEnt model.

Variable	Percent contribution (%)	Permutation importance (%)
Precipitation of warmest quarter (PRWQ)	41.3	27.0
Annual mean temperature (AMT)	31.0	41.9
Mean temperature of warmest quarter (MTWQ)	15.9	11.6
Precipitation of driest quarter (PRDQ)	6.6	12.9
Mean diurnal range (MDR)	4.6	2.8
Precipitation seasonality (PRS)	0.7	3.8

Table 3.3 Average of BIOCLIM climatic values in the present and the Last Glacial Maximum (LGM) in the area of study, and the differences of the average of climatic values between the LGM and the present.

Variable	Present	LGM			Average of three GCMs	(the present value) - (average of the LGM values)
		CCSM	MIROC	MPI		
AMT (°C)	-0.4	-6.9	-7.6	-5.2	-6.6	+6.2
MDR (°C)	11.7	12.5	12.4	12.6	12.5	-0.8
MTWQ (°C)	16	10.8	9.8	12.5	11.0	+5
PRS (mm)	77	79.4	85.5	82.3	82.4	-5.4 (-7.0%)
PRDQ (mm)	38.4	28.2	26.9	34.9	30.0	+8.4 (+21.9%)
PRWQ (mm)	284.2	259.7	265.9	274.6	266.7	+17.5 (+6.1%)

Numbers in parentheses show change rates of precipitation.