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Distribution of *Betula* species in Japan

– Nakamura, Y., T. Shitara, P. Krestov, Y. Ishida and S. Suziki –

Betula species in Japan

Approximately 40 species of the genus *Betula* occur in the northern hemisphere, primarily in temperate and boreal areas. The 12 species of *Betula* found in Japan are composed of shrub, subtree, and tree species. Of the 12 species, 6 are endemic to Japan and 6 are also found in continental northeast Asia (Tab. 1).

Betula species belong to different community types and occur in different habitats, and different distribution areas. The Japanese Archipelago is located in the climatic zone of subtropical to cool temperate, and most of the *Betula* species of the region grow in the montane to subalpine belts of the temperate zone (Fig. 1).

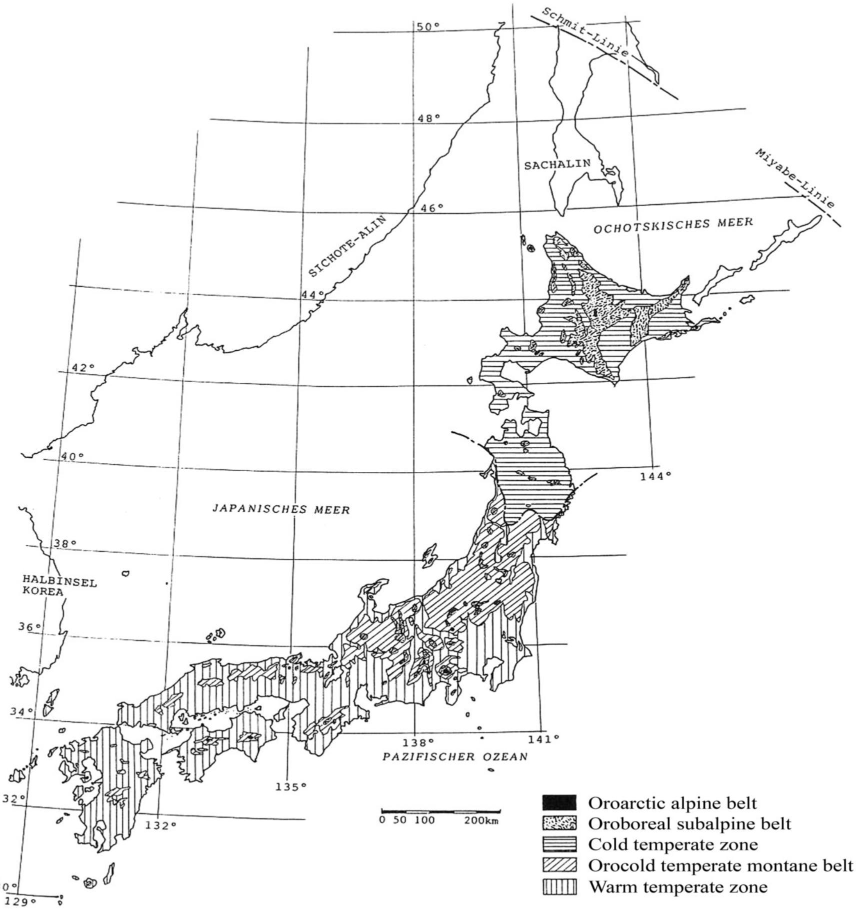

Fig. 1. Bioclimatic vegetation zones in Japan (MIYAWAKI & NAKAMURA 1988).

Tab. 1. Japanese Betula species and its attribution (NAKAMURA et al. RTG-Symposium 2015)

Species	Life form	Habitat	Clima zone	Vertical belt	Endemism
Betula apoiensis	shrub	ultrabasic rock	northern temperate	montane	endemic
Betula chichibuensis	subtree	basic rock	cool temperate	montane	endemic
Betula globispica	tree	edaphic stand	cool temperate	upper montane	endemic
Betula maximowicziana	tree	pioneer stand	cool temperate	montane	endemic
Betula grossa	tree	pioneer stand	cool temperate	montane	endemic
Betula corylifolia	tree	pioneer stand	cool temperate	subalpine	endemic
Betula ovalifolia	shrub	swamp	northern temperate to boreal	colline	northbound
Betula ermanii	tree	edaphic & pioneer stands	cool temperate to boreal	subalpine	north-southbound
Betula platyphylla	tree	pioneer stand	cool temperate to boreal	montane	north-southbound
Betula davurica	tree	pioneer stand	cool temperate to boreal	montane	north-southbound
Betula costata	tree	edaphic stand	cool temperate	montane	southbound
Betula schmidtii	tree	edaphic stand	cool temperate	montane	southbound

Edaphic climax and pioneer features of *Betula* species

Betula species are often pioneer species and compose single-storied stands following wildfires or logging, but some species may occur as edaphic climax forests on rocky cliffs and ridges. Forest vegetation that includes *Betula* species should also be described in order to clarify the Japanese *Betula*.

Pioneer plant communities of the Fagetea crenatae region include the *Betula maximowicziana*, Corylo heterophyllae-Betuletum davuricae, and Rhododendro-Betuletum platyphyllae communities, while Betuletum corylifolio-ermanii is the pioneer plant community of the Vaccinio-Piceetea region.

Edaphic climax plant communities are composed of the Rhododendro quinquefolii-Betuletum globispicae community in the Fagetea crenatae region and Betuletum ermanii and Calamagrostio-Betuletum ermanii communities in the Betulo-Ranunculetea region.

Fagetea crenatae Miyawaki, Ohba et Murase 1964
  Tsugetalia sieboldii Suz.-Tok. 1966
    Pruno maximowiczii-Quercion crispulae Wada 1982
      Rhododendro-Betuletum platyphyllae Yamazaki et Uematsu 1963
      Rhododendro quinquefolii-Betuletum globispicae Suzuki 1998
      Corylo heterophyllae-Betuletum davuricae Hoshi 2000

Betulo ermanii-Ranunculetea acris japonicae Ohba 1968
  Streptopo-Alnetalia maximowiczii Ohba 1973
    Smilacino yezoensis-Betulion ermanii Ohba 1973
      Betuletum ermanii Suz.-Tok., Okamoto et Honda 1964
      Calamagrostio-Betuletum ermanii Yamazaki et Uematsu 1963 em. Ohba 1973
    Athyrio brevifrondis-Weigelion middendorffianae Ohba 1973
      Weigelo middendorffianae-Betuletum ermanii Nakamura 1988

Climate zone and *Betula* species

In terms of climate, the Japanese Archipelago is generally classified as subtropical to cool temperate in the oceanic sector. Yakushima Island, at E 130^0 30’ longitude and N 30^0 28’ latitude, is often identified as the boundary between the subtropical and the warm temperate zone. Japanese *Betula* species are distributed mainly within the cool temperate zones. The boundary between warm and cool temperate zones is typically drawn at the northern latitude of 38 degrees, where zonal evergreen broad-leaved forests meet summergreen broad-leaved forests (MIYAWAKI & NAKAMURA 1988; Fig. 1). *Betula platyphylla*, *B. schmidtii, B. davurica*, *B. globispica*, *B. maximowicziana*, *B. chichibuensis*, *B. grossa,* and *B. costata* occur in the montane belt of Fagetea crenatae that occurs in the cool temperate zone, where mean temperatures average between 6–13. *B. platyphylla*, *B. davurica,* and *B. maximowicziana* are also found on the island of Hokkaido.

The Vaccinio-Piccetea region of Japan is located in the upper montane to subalpine belts within the cool temperate zone. Mean temperatures for this class of forest range from 0–6 °C, a range similar to that of the boreal zone. *B. ermanii, B. corylifolia, B. ovalifolia,* and *B. apoiensis* are found in this forest region; *B. corylifolia* is found in Honshu while *B. ovalifolia* and *B. apoiensis* are found in Hokkaido.

Endemic *Betula* species and their vegetation types

Endemic *B. apoiensis* grows along with *B. ovalifolia* and *B. ermanii* on the extremely basic soils of the slopes of Mt. Apoi (Fig. 2). *B. chichibuensis* occurs in two widely-separated areas with numerous limestone outcrops (Fig. 2). *B. apoiensis* and *B. chichibuensis* are new endemic species. *B. globispica, B. maximowicziana*, and *B. grossa* primarily inhabit the Fagetea crenatae region within the cool temperate zone (Figs. 3-5). *B. globispica* is an edaphic species that grows along mountainous ridges. Rhododendro quinquefolii-Betuletum globispicae is distributed throughout eastern Chubu and northern Kanto, and in the montane to upper montane belts (SUZUKI 1998). *B. maximowicziana* is a pioneer species of the Fraxino-Ulmetalia and occurs in the Fagetea crenatae montane and upper montane zones of central Honshu. *B. grossa* is a pioneer species of the Tsugetalia sieboldii belt, located below the Fagetea crenatae belt. Although *B. maximowicziana* and *B. grossa* are pioneers, they may reach 1m DBH and live for more than 300 years.

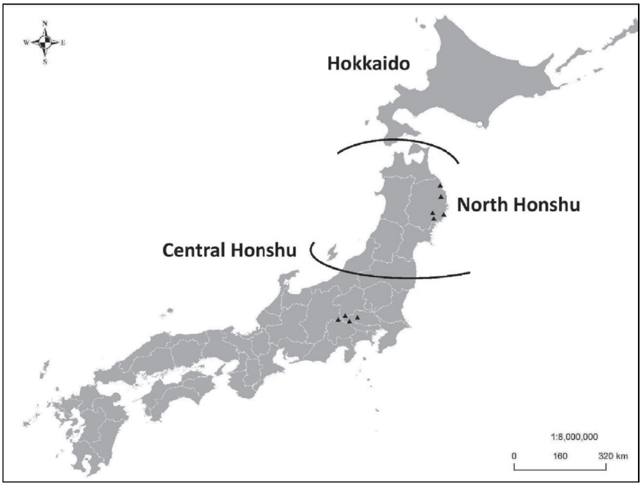

Fig. 2. Distribution of *Betula apoiensis (*○*)*and (▲*) B. chichibuensis*.

Fig. 3. Distribution of *Betula globispica*.

Fig. 4. Distribution of *Betula maximowicziana*.

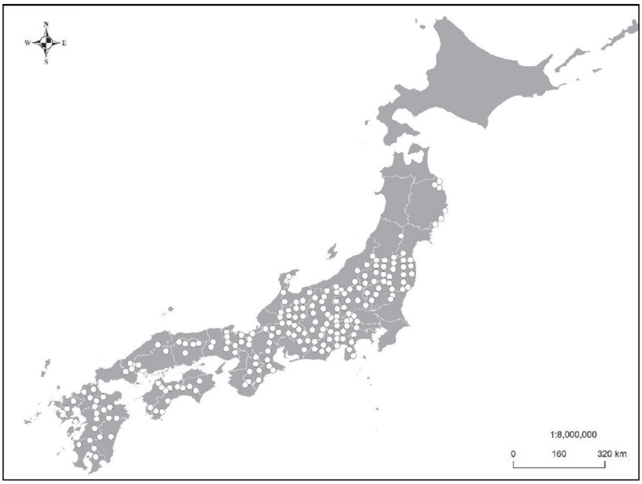

Fig. 5. Distribution of *Betula grossa*.

B. corylifolia is a species characteristic of Betuletum corylifolio-ermanii, the secondary forest of Abieti-Piceetalia that is found in the subalpine belt (Fig. 6). Those three species; *B. maximowicziana*, *B. grossa*, and *B. corylifolia* do not have relatives outside of Japan, although *B. chinensis*, a close relative of *B. globispica*, can be found in China and Korea. There is little information available regarding relatives of an additional three species from neighbouring countries.

The remaining six species of *Betula* are found in continental Northeast Asia as well as Japan. The distribution pattern and species combinations of these communities are interesting in terms of vegetation history.

Fig. 6. Distribution of *Betula corylifolia*.

The vegetation types of *Betula* species common to both Japan and continental Asia

The Japanese Archipelago separated from continental Asia during the Miocene Epoch (15–20 million years ago), but Japan was reconnected to the mainland several times throughout the glacial periods of the Pleistocene, allowing *Betula* species to move across land bridges. One bridge was formed between the continent and the islands of Sakhalin and Hokkaido, while another bridge connected the Korean Peninsula with Honshu; these are termed the "northbound" and "southbound" routes, respectively (Fig. 7).

B. ovalifolia is a dwarf shrub that grows in wet habitas. It is common in the boreal zone and isolated in the wetland of eastern Hokkaida (Fig. 8.)

B. ermanii is a common species of the edaphic climax forests in the subalpine belt of Japan's cool temperate zone, as well as a dominant species in the climax forests of the oceanic sector of the boreal zone of Northeast Asia (Fig. 9), and is a characteristic species of Betulo-Ranunculetea acris japonici. In the subalpine belt, *B. ermanii* forests are often found in avalanche zones, despite the presence of Vaccinio-Pinetum pumilae on nearby ridges.

Vegetation maps of Mt. Kita-dake depict the climatic climax Abietetum veitchio-mariesii forests as being located in the upper montane belt (ISHIDA et al. 2014; Fig. 10). The vegetation within avalanche paths is represented by Calamagrostio-Betuletum ermanii and the all accumulated snow avalanche by tall forbs, Cirsio senjoensis-Angelicetum pubescentis matsumurae.

Fig. 7. Japanese flora connected with continental Asia during the LGM: northbound and southbound routes.

Fig. 8. Distribution of *Betula ovalifolia*.

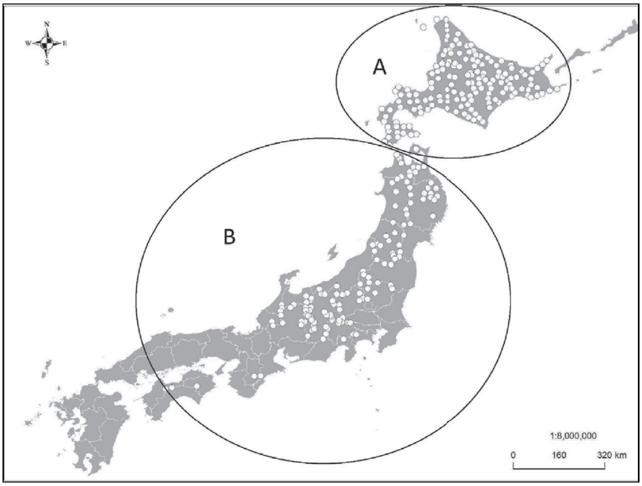

Fig. 9. Distribution of *Betula ermanii*.
A: Athyro brevifrondis-Weigelion middendorffianae;
B: Smilacino yezoensis-Betulion ermanii

Table 2. Streptopo-Alnetalia maximowiczii Ohba 1973

District:	Hokkaido					Tohoku			Chubu													
Running Nr.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Nr. of releves	9	10	26	7	6	6	4	5	11	10	8	7	16	3	5	14	4	7	12	6	19	7
Average of species nr.	24	27	26	20	16	29	13	23	20	17	21	21	23	33	40	27	34	32	22	33	37	24
Ch. Species of Athyrio brevifrondis-Weigelion middendorffianae Ohba 1973																						
Cirsium pectinellum	III	I	IV	IV	IV	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Coelopleurum lucidum var. *gmelinii*	II	III	IV	I	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Athyrium pterorachis	IV	II	IV	·	II	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·
Spiraea betulifolia var. *aemiliana*	II	·	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Corydalis ambigua	V	III	II	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Angelica anomala	IV	+	I	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Betula maximowicziana	V	IV	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rubus idaeus var. *aculeatissimus*	IV	I	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Epipactis papillosa	III	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Anemone yezoensis	IV	·	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Euonymus oxyphyllus var. *magnus*	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Urtica platyphylla	III	·	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cardamine yezoensis	II	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Aconitum sachalinense	II	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vaccinium praestans	·	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Athyrium sinense	·	·	II	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lonicera alpigena var. *glehnii*	·	·	I	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Arabis serrata var. *glauca*	·	I	IV	III	III	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Aegopodium alpestre	I	·	·	II	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Weigela middendorffiana	V	IV	V	·	I	I	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Angelica ursina	I	II	·	·	·	·	1	II	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Angelica edulis	·	·	III	II	III	·	·	I	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Ch. Species of Smilacino yesoensis-Betulion ermanii Ohba 1973																						
Streptopus streptopoides var. *japonicus*	·	·	·	·	·	IV	2	III	II	II	I	II	IV	2	I	IV	2	V	·	I	·	II
Smilacina yesoensis	·	·	·	·	·	III	·	IV	+	II	I	III	I	3	V	I	2	III	II	V	II	·
Prunus nipponica	·	·	·	·	·	II	1	II	·	·	I	III	II	1	III	I	2	II	I	IV	IV	I
Lonicera tschonoskii	·	·	·	·	·	·	·	·	II	V	IV	IV	IV	2	III	IV	4	II	III	IV	I	·
Athyrium melanolepis	·	·	·	·	·	II	·	IV	IV	III	IV	IV	II	3	IV	IV	2	III	V	IV	III	·
Rubus ikenoensis	·	·	·	·	·	III	2	II	·	·	I	·	·	·	·	II	3	III	II	·	I	·
Paris japonica	·	·	·	·	·	·	·	I	II	·	·	I	·	2	I	II	1	I	·	·	·	·
Coelopleurum multisectum	·	·	·	·	·	·	·	·	I	II	II	III	I	1	·	·	·	I	II	III	·	I
Smilacina hondoensis	·	·	·	·	·	·	·	·	+	+	·	·	I	·	·	II	·	·	+	·	·	·
Ch. species of Streptopo-Alnetalia maximowiczii Ohba 1973:																						
Betula ermanii	·	·	I	IV	I	V	·	I	·	·	II	III	V	1	V	IV	4	V	III	V	V	V
Alnus maximowiczii	·	I	·	·	·	V	·	IV	IV	·	V	V	IV	2	IV	IV	3	V	V	V	I	V
Sorbus matsumurana	·	·	II	·	·	I	·	I	V	V	IV	V	IV	2	III	V	4	I	V	V	IV	·
Rubus vernus	·	·	I	·	·	·	4	I	V	·	I	V	·	2	II	IV	3	II	·	·	·	·
Thelypteris quelpaertensis	·	·	r	I	·	IV	2	III	II	+	I	I	III	2	·	III	1	V	+	V	IV	·
Diphylleia grayi	·	·	·	·	I	I	1	III	II	I	·	III	II	3	I	II	2	III	I	II	I	·
Galium kamtschaticum	·	·	II	III	IV	IV	·	·	II	·	·	III	v	2	IV	III	1	III	·	I	I	I

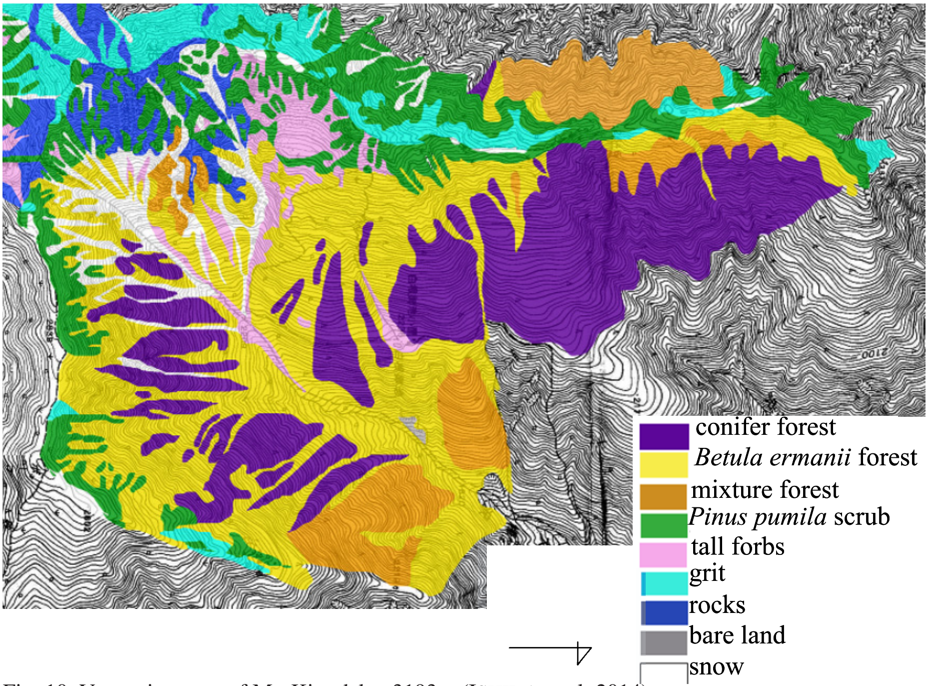

Fig. 10. Vegetation map of Mt. Kita-dake, 3193m (ISHIDA et al. 2014).

Athyri brevifrondis-Weigelion middendorffii occur in Hokkaido, Sikhote-Alin and the Kamtchatka Peninsula, while Smilcino yesoensis-Betulion ermanii is found in Honshu. However, the Smilcino yesoensis-Betulion ermanii of Tohoku is influenced by elements of northern. Athyri brevifrondis-Weigelion middendorffii (Tab. 2). In the map of *Betula ermanii*, circle A shows the distribution of Athyro brevifrondis-Weigelion middendorffii and circle B shows the distribution of Smilacino yesoensis-Betulion ermanii (Fig. 9). Weigelo middendorffii-Betuletum ermanii is also found on the island of Sakhalin.

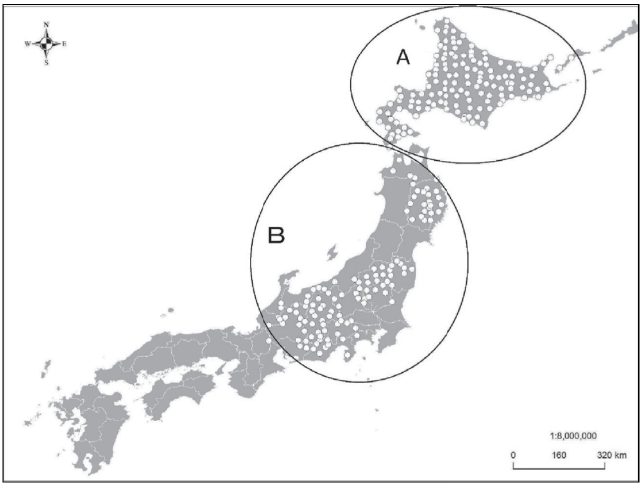

Fig. 11. Distribution of *Betula platyphylla*.
A: *Betula platyphylla-Quercus crispula* community;
B: Rhododendro-Betuletum platyphyllae

Table 3. Temperate *Betula* communities in Japan and Russia

1: Rhododenndro quinquefolii-Betuletum globispicae
2: *Betula schmidtii* community
3: Colyro heterophyllae-Betuletum davuricae
4: Betula davurica-Quercus mongolica community
5: Ulmo japonicae-Pinetum koraiensis
6: Athyro crenati-Pinetum koraiensis

	Japan				Russia			
Community Nr.:	Ii	Iii	2	3	4	5i	8i	6
Number of releves:	6	5	8	13	5	2	2	2
Average of species number:	29	49	24,5	40	57,3	44	52,5	44
Betula globispica	V(2-5)	V(1-4)	.	.	.	.	.	.
Rhododendron quinquefolium	V(+-2)	IV(+-2)	.	.	.	.	.	.
Viburnum urceolatum var. *procumbens*	IV(+-1)	II(+)	.	.	.	.	.	.
Euonymus macropterus	III(+)	IV(+)	.	.	.	.	.	.
Hydrangea paniculata	IV(+)	III(+)	.	.	.	.	.	.
Sorbus commixta	IV(+)	I(+)	.	.	.	.	.	.
Menziesia pentandra	IV(+-2)	II(+)	.	.	.	.	.	.
Betula schmidtii	.	.	V(1-4)	.	I(+)	.	.	.
Fagus japonica	.	.	III(+-3)	.	.	.	.	.
Sorbus commixta var. *rufoferruginea*	.	.	II(+-2)	.	.	.	.	.
Tsuga sieboldii	.	.	II(1-3)	.	.	.	.	.
Rhododendron wadanum	V(1-3)	V(+-2)	IV(+-3)	.	.	.	.	.
Clethra barbinervis	V(+-2)	V(+-1)	V(+-2)	.	.	.	.	.
Viburnum furcatum	V(+)	V(+-1)	I(+)	.	.	.	.	.
Calamagrostis hakonensis	V(+-1)	V(+-3)	IV(+-1)	.	.	.	.	.
Hydrangea hirta	V(+-2)	IV(+-2)	II(+)	.	.	.	.	.
Rhododendron tschonoskii	V(+-3)	IV(+-3)	I(+)	.	.	.	.	.
Acer micranthum	IV(+)	II(+-1)	II(+-1)	.	.	.	.	.
Stewartia pseudocamellia	II(+-1)	I(+)	II(1)	.	.	.	.	.
Betula davurica	.	.	.	V(1-4)	IV(+-3)	2(1)	1(3)	.
Betula platyphylla	.	.	.	V(1-2)	I(+)	1(+)	1(2)	.
Dioscorea nipponica	.	.	.	IV(+-1)	III(+)	2(+)	1(+)	.
Maackia amurensis	.	.	.	I(+-1)	IV(+)	2(2)	2(1)	1(+)
Populus sieboldii	.	.	.	I(+-1)	II(+)	2(+)	1(+)	1(+)
Acer mono	.	.	.	I(+)	V(1-2)	2(2-3)	2(2)	2(2-3)
Viburnum sargentii	.	.	.	IV(+-1)	I(+)	2(+-1)	.	1(+)
Corylus heterophylla var. *thunbergii*	.	.	.	V(+-3)	IV(+-1)	.	.	1(2)
Syringa reticulata	.	.	.	+(+)	1(+)	1(1)	.	.
Schisandra chinensis	.	.	.	+(+)	.	.	2(+)	2(1-2)
Quercus mongolica var. *grosseserrata*	V(+-4)	IV(+-2)	III(+-2)	V(+-4)	.	.	.	.
Enkianthus campanulatus	V(+-1)	V(+-4)	II(1-2)	+(+)	.	.	.	.
Acer sieboldianum	III(+)	I(+)	III(+-2)	I(+-1)	.	.	.	.
Fraxinus lanuginosa	I(+)	II(+-1)	III(+-1)	II(+-2)	.	.	.	.
Abies homolepis	I(+)	II(+)	I(+)	II(+-1)	.	.	.	.
Prunus maximowiczii	I(+)	II(+)	.	V(+-2)	.	.	.	.
Quercus mongolica	.	.	.	.	V(2-5)	2(4-5)	2(1-2)	.
Thalictrum filamentosum	.	.	.	.	V(+-2)	2(+-1)	1(1)	2(+-1)
Tilia amurensis	.	.	.	.	IV(+-1)	2(2)	2(1)	2(+-1)
Pinus koraiensis	.	.	II(1-3)	.	III(1-3)	2(1)	2(2)	2(1-3)
Vitis amurensis	.	.	.	.	IV(+)	1(+)	2(+-1)	2(+)
Euonymus pauciflora	.	.	.	.	III(+)	2(1-2)	2(1)	2(1)
Abies nephrolepis	.	.	.	.	I(+)	2(+-1)	1(1)	2(2)
Corylus mandshurica	.	.	.	.	I(+)	2(2)	2(2)	2(+-2)

Betula platyphylla is pioneer species that creates secondary forests in the upper belt of Fagetea crenatae, and ranges from the cool temperate zone to the southern part of the boreal (Fig. 11). The *Quercus crispula-Betula platyphylla* community composes the secondary forests of Carpino-Quercion crispulae in Hokkaido and northern Honshu, while Rhododendro-Betuletum platyphyllae composes the secondary forest of Pruno maximowiczii-Quercion crispulae in Honshu. Carpino- Quercion crispulae and Pruno maximowiczii-Quercion crispulae grow under inland climatic conditions where there is no beach forest.

Fig. 12 illustrates the distributions of *B. davurica, B. costata,* and *B. schumdtii*. Representative temperate *Betula* forests are shown in Table 3. Endemic *B. globispica* is the distin-

Fig. 12. Distribution of *B. davurica* (■), *B. costata* (▲), and *B. schmidtii* (○).

guishing species of Rhododendro quinquefolii-Betuletum globispicae, which belongs to Pruno maximowiczii-Quercion crispulae. *B. schmidtii*, which also occurs in Korea, northeast China and Russia, forms its own Pruno maximowiczii-Quercion crispulae community. Rhododendro quinquefolii-Betuletum globispicae occurs at higher elevations than do *B. schmidtii* communities.

B. davurica is also found in Korea, northeast China and Russia (OKITSU 2006). Corylo heterophyllae-Betuletum davuricae is distributed throughout central Honshu and includes many continental species. A Russian *B. davurica* community, Ulmo japonicae-Pinetum koraiensis, is similar to the Japanese Corylo heterophyllae-Betuletum davuricae community (KRESTOV et al. 2006), with the two communities having been separated since at least the most recent glacial period. Corylo heterophyllae-Betuletum davuricae is restricted to the Central Honshu region, under similar climatic conditions as its Russian counterpart (Fig.13). Higher Continentality index 26.1 to 28 is the site for concentration of *B. davurica* has a relatively high Continentality index (26.1–28) (Fig. 14) and grows in areas of low annual precipitation (500–1500 mm) (Fig. 15).

Geography of *Betula* species common with the continent

Japan was connected to mainland Asia several times during the last glacial period, allowing for the establishment of several species of *Betula* in both Japan and on the continent. Global temperatures were 7 degrees Celsius lower during the Last Glacial Maximum than at present; during this time, the forefront of the boreal zone was composed of evergreen conifer forest and located at 35 degrees north, while the *Larix daurica* boreal forest extended to

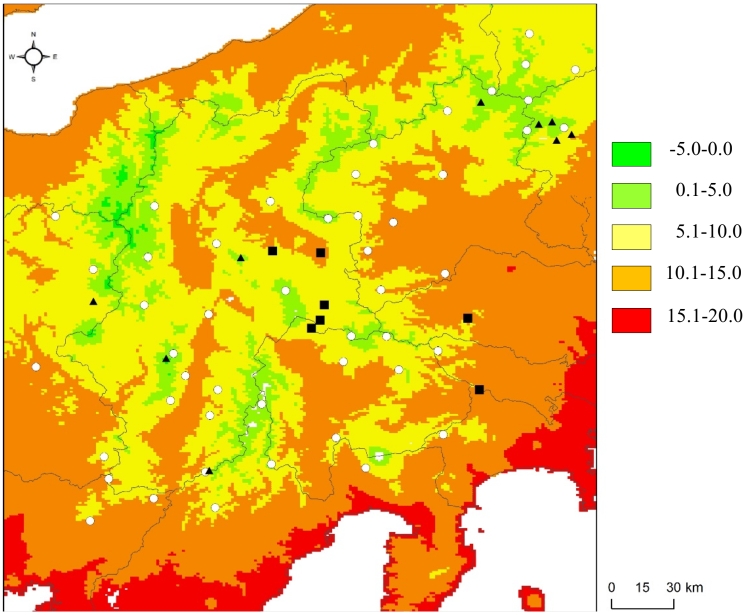

Fig.13. Annual mean temperature (˚C). *B. davurica* (■); *B. costata* (▲); *B. schmidtii* (○).

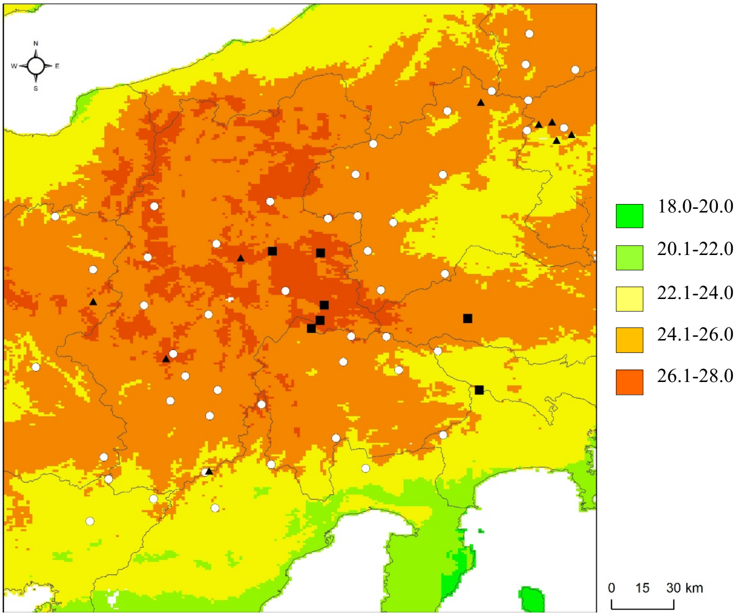

Fig. 14. Continentality index (Tmax-Tmin). *B. davurica* (■); *B. costata* (▲); *B. schmidtii* (○).

Tohoku in the south (NASU 1980; TSUKADA 1983, 1984). Boreal species could migrate from mainland Asia into Hokkaido and northern Honshu via the northbound route (Fig. 7). Palynological studies show that 10,000 yr B.P., *Betula* occupied Hokkaido and northern Tohoku instead of beech (TSUKADA & NAKAMURA 1988), and suggest that *B. ermanii*, *B. platyphylla*, and *B. ovalifolia* replacing via the land bridge. Temperate species, including *B. costa-*

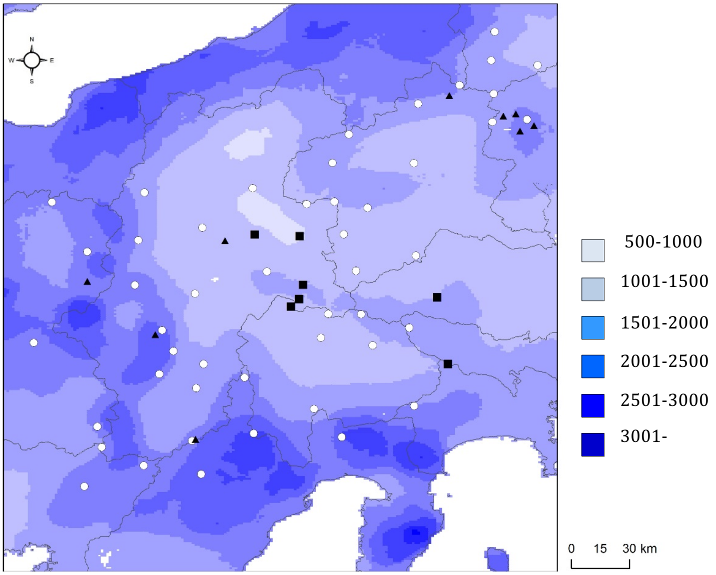

Fig. 15. Precipitation (mm). *B. davurica* (■); *B. costata* (▲); *B. schmidtii* (○).

ta, *B. schmidtii* and *B. davurica*, however, must have entered Japan via the southbound land-bridge that connected Japan to the Korean Peninsula. Three latter species are restricted to the inland climatic conditions that prevail in Central Honshu, but are not considered to be climax species. *B. schmidtii* occurs on rocky convex sites as the topographic climax species, whereas *B. davurica* occurs on landslide or coppice sites as the pioneer species (OGAWA & OKITSU 2011; OKITSU 2006). In Japan, they are found in central Honshu, a region where beech does not grow (WADA 1982), as well as in *B. schmidtii* forests in Korea and the southern part of Russia. The climatic conditions of inland Honshu are shown in Figs. 13–15. Fig.13 displays annual mean temperature; the three *Betula* species occur in areas of the cool temperate zone

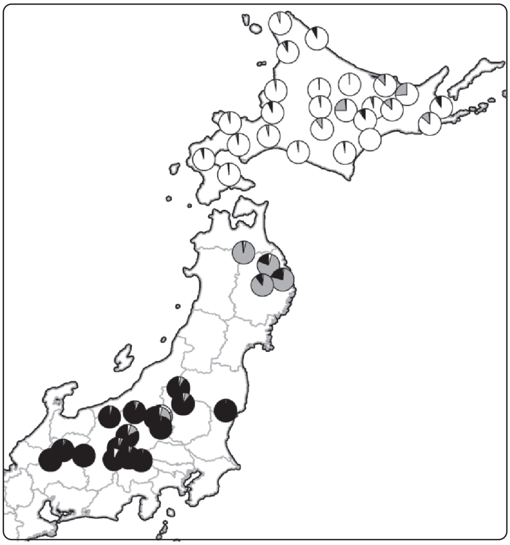

Fig. 16. Genetic composition of *Betula platyphylla* by nuclear DNA (HIRAOKA et al. 2013).

where average temperatures are lower than 5 degrees Celsius; Fig. 14 shows the Continentality index, for which three *Betula* species score less than 24, and *B. davurica* lower than 26. Although this index score is lower than the continent (>40), in oceanic conditions *B. davurica* is restricted to the most inland climate, where rates of precipitation are lower (Fig. 15). Tab. 3 shows the similarity of isolated Japanese *B. globispica*, *B. davurica,* and *B. schmidtii* forests in comparison with continental vegetation such as Kitagewio terebintaceae-Betulion davuricae and Corylo heterophyllae-Quercion mongolicae that feature large densities of *B. davurica*. Japanese Corylo heterophyllae-Betuletum davuricae forests are similar to continental vegetation communities, and there are many common species, including *Corylus heterophylla*, *Syringa reticulata*, *Dioscorea nipponica, Viburnum sargentii, Maackia amurensis, Moehringia lateriflora, Convallaria keiskei,* and *B. platyphylla.*

B. ovalifolia, *B. ermanii*, *B. platyphylla,* and *B. davurica* are species that reached the boreal zone and thus had opportunity to migrate into Japan via the northbound land-bridge route, and, with the exception of *B. ovalifolia*, possibly through the southbound route as well; MIYASHITA (2003) demonstrated that the populations of *B. ermanii* in Hokkaido and Honshu differ genetically, as it was found by HIRAOKA et al. (2013) for *B. platyphylla*. Three genetic groups are generally recognized (Fig. 16). *B. schmidtii*, *B. costata*, *B. ermanii*, *B. platyphylla,* and *B. davurica* could all have entered via the southbound route.

For the reasons mentioned above, *B. ermanii*, *B. platyphylla*, *B. davurica* most likely became established in Hokkaido through the northbound route, whereas *B. schmidtii*, *B. costata*, *B. davurica*, *B. ermanii* and *B. platyphylla* became established in central Honshu via the southbound route. The Tohoku region of northern Honshu is where northern and southern elements appear to converge.

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