

SPECIAL FEATURE REVIEW

Listen to the voices of local beech forests: An ecological and evolutionary conception of beech under phylogenetic and environmental constraints

A comprehensive overview of studies related to the ecology and genetics of *Fagus crenata* Blume (Siebold's beech, Japanese beech) at the species' northernmost range limit

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Abstract

Temperate forest species, including *Fagus crenata* Blume, have been experiencing distributional shifts during the climate oscillation throughout the Holocene epoch. This review describes the distinctive context of *F. crenata* populations at the northern range from the perspective of past distribution shifts, future expansion predictions, biotic and abiotic interactions in population establishment, forest vegetation characteristics, and genetic diversity during the expansion process. The current northern distribution limit of *F. crenata* is in southern Hokkaido and Okushiri Islands. Since 1900, a dozen of northern limit hypotheses has advocated the presence of restriction factors; however, the species shows signs of expanding its habitat northward at present. The current northern limit is not determined by physiological limitations because of the fact that artificial plantations of *F. crenata* grow well beyond its range. Several studies regarding climate scenarios have predicted species persistence in the future. Sociological studies revealed that a decline in vegetation units is observed from the southern to the northern populations on the Oshima Peninsula, Hokkaido. Also, vegetation on Okushiri Island includes remnants of warm temperate flora indicating a physiographic constraint of the *F. crenata* forest on the island, reflecting a past distributional shift. Most of the current northern marginal populations were revealed to be established at the time of large forest disturbance. The genetic diversity of local populations has been lost during the northward distribution shift due to the founder effect in the colonizing process. Then, the gene flow from rearward populations has dwindled by the completion of the population establishment.

KEYWORDS

deciduous broad-leaf species, distributional expansion, Fagaceae, founder population, marginal population

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1 | INTRODUCTION

The current distribution of woody plant populations is a consequence of long-term dynamics associated with past distributional shifts. Most of the temperate forest tree species in the Northern Hemisphere have expanded their distribution northward during periods of climate warming during the Holocene epoch (Davis & Shaw, 2001; Delcourt & Delcourt, 1987). Moreover, the northern distribution limit of temperate forests on the Eurasian and North American continents have moved northwards with the glacial retreat between 25,000 and 15,000 years BP (Davis, 1983; Huntley, 1988). In addition, northward distribution shifts of temperate forest species during the Holocene have also occurred in East Asia, where no ice sheets prevailed at the last glacial maximum (LGM) (Qian & Ricklefs, 2000; Tsukada, 1988; Yu et al., 2000).

Fagus crenata Blume (Siebold's beech; Japanese beech) forest is a representative landscape of temperate forests in the Japanese Archipelago. It covers the montane regions from Kyushu, Shikoku, Honshu, to Hokkaido (31°–43°N and 130°–141°E) and is regarded as a flagship species of forest ecosystems. Currently, the geographic distribution of *F. crenata* has reached the montane zones northeast of the Kuromatsunai Depression in southern Hokkaido (Kito, 2003; N. Tanaka et al., 2016; Tatewaki, 1948, 1958). *F. crenata* at the northern distribution limit shows good growth and regenerates well (Matsui, Kitamura, et al., 2012; Matsui, Namikawa, et al., 2012; Namikawa et al., 2010), and as it does not seem to suffer from any physiological restriction on individual persistence (J. Tanaka, 1900), the factors determining the northern distribution limit of this species have claimed the interest of scientists. Hence, a wide variety of hypotheses about the northern limit of *F. crenata* has been proposed.

Historically, inductive reasoning for the present northern limit of *F. crenata* has focused on many aspects (Table 1) such as limiting factors attributed to frequent wildfires (Honda, 1900), seed dispersal rate (Nanbu, 1927), andesite from volcanic activity (Furuhata, 1932), insufficient precipitation (Takeda, 2004; Tsukada, 1982b), characteristic vegetation arrangement due to the oceanic climate and continental chilling (Aoyama, 1987; Kira et al., 1976), the existence of niche interactions at the ecotone (Watanabe, 1987), summer temperature in the Kuromatsunai Depression (Ohmori & Yanagimachi, 1988), late frost damage (Hayashi, 1996; Kaji & Takahashi, 1999), small rodent predation (Kitabatake & Kaji, 2000), and a combination of various climatic determinants (Yagihashi et al., 2007). The supporting evidence for some of these claims is contradictory, but recent studies have advocated that the species is

currently expanding northward (Igarashi, 1994; Kito, 2003), taking advantage of phenological gaps (Kobayashi, 2009). Moreover, a new founder population was identified 12 km north of the previously known northernmost population, which provides circumstantial evidence of a current northward expansion of distribution (Kitamura & Nakanishi, 2021; N. Tanaka et al., 2016).

In addition to the historically presented factors regarding the northern distribution limit, recent investigations have revealed a number of ecological and genetic characteristics unique to *F. crenata* at the northern range. This review provides an overview of these ecological and genetic studies on the northernmost natural *F. crenata* forests and the unique characteristics of the species at the northern range margin. Nomenclature for vascular plants in this paper follows the YList (Yonekura & Kajita, 2007) unless otherwise stated.

2 | CURRENT NORTHERN DISTRIBUTION LIMIT

The existence of the northern distribution limit of *F. crenata* on the Oshima Peninsula in southern Hokkaido was first published in 1900 (Honda, 1900; J. Tanaka, 1900). Accordingly, the distribution of *F. crenata* populations across the northern range confirmed that the species later expanded slightly to the northeast of the Kuromatsunai Depression, which was a transitional zone between the temperate forest zone and the Pan-mixed forest zone (Tatewaki, 1948, 1958). Thereafter, the precise locations of the northern limit line were determined to be approximately 7 km east of the Kuromatsunai Depression (Figure 1) (Kito, 2003).

The current distribution pattern of the northern range populations changes noticeably from large, continuous populations to the southwest of the leading edge to small, isolated populations to the northeast (Kito, 2003). At present, the leading-edge populations are observed in the mountain regions of Horonai, Horobetsu, and Niseko (Kito, 2003; Matsui, Kitamura, et al., 2012; N. Tanaka et al., 2016). In these mountain regions, *F. crenata* populations are small and isolated, located more than 1 km apart from each other, while continuous populations are distributed in the Kuromatsunai Depression and regions to its southwest. In the past 200 years, the Kuromatsunai Depression has been inhabited and cultivated for agricultural land use (Kuromatsunai Town, 1987). Therefore, most of the *F. crenata* populations in the Kuromatsunai Depression have been lost to farmland, which has led to forest fragmentation or the creation of partial secondary forests. However, these anthropogenic disturbances did not have deleterious effects on indigenous *F. crenata* ecosystems in this area.

TABLE 1 Northern limit hypotheses of *Fagus crenata*

Hypothesis	Detail	Reference	Contradictory argument (if any)
Frequent wildfires	Beeches were so susceptible to wildfires that frequent wildfires due to strong wind prevent establishment of this species. Therefore, beeches were restricted to montane zones where wildfires rarely occur.	Honda (1900)	Wildfires do not completely extinguish beech trees, but some escape and survive (Tatewaki, 1948). Also, the assumption that the beech growth limit is an average temperature of 6°C is not correct (Watanabe, 1988).
Seed dispersal rate	Because seed dispersal, namely the expansion rate of beech, is slow, the species distribution is limited within current distribution range.	Nanbu (1927)	
Mt. Yotei volcanic activity	Volcanic activity of Mt. Yotei, and its resulting andesite base rocks, prevents further northward expansion of beech species.	Takeda (2004), Tsukada (1982b)	Active volcanoes did not transverse the peninsula. Beech grows on volcanic soils derived from more recent volcanic eruptions than Mt. Yotei (Watanabe, 1988).
Insufficient precipitation	Precipitation during the growing season in the Kuromatsunai Depression might be insufficient for beech growth.	Takeda (2004), Tsukada (1982b)	Beech grows in dry climate in the area south of the Kuromatsunai Depression (Watanabe, 1988).
Ocean climate influence	Vegetation along the Japan Sea coast is influenced by the strong winter cold air mass. This causes a lack of beech in northern temperate vegetation.	Kira et al. (1976)	Coldness and dryness cannot explain the vegetation shift in Hokkaido. Also, the vegetation change is not attributable to the East Asian oceanic climate (Watanabe, 1988).
Cold or dry climate	Cold climate on the Pacific Ocean coast and high inland mountains as well as dry conditions on the Japan Sea coast prevent beech expansion.	Aoyama (1987)	Coldness and dryness cannot explain the vegetation shift in Hokkaido (Ohmori & Yanagimachi, 1988).
Niche interaction	Niche segregation occurred among co-occurring species with similar ecological status, such as beech, oak, and fir.	Watanabe (1987)	
Phenological gap	Bud burst of beech is earlier than other co-existing broadleaf tree species. This phenological advantage enables the species to become established under the canopy of the different species.	Kobayashi (2009)	
Summer temperature in Kuromatsunai Depression	The summer temperature of Kuromatsunai Depression is too high for beech to grow well and expand across this lowland.	Ohmori & Yanagimachi (1988)	Beech is distributed beyond the Kuromatsunai Depression (Watanabe, 1988).
Last frost damage	To the east of the Kuromatsunai Depression, there is a region where beech suffered from late frost damage, thus, the species is not able to expand.	Hayashi (1996), Kaji & Takahashi (1999)	

TABLE 1 (Continued)

Hypothesis	Detail	Reference	Contradictory argument (if any)
Small rodents' predation	High predation pressure by <i>Myodes rufocan</i> in the Kuromatsunai Depression retards the expansion rate.	Kitabatake & Kaji (2000)	
Interactive climate factors	Interactive climate factors such as temperature at germination and precipitation of growing season are not suitable for beech to obtain sufficient population size for successful expansion.	Ito (1982)	
Combination of three climatic determinants	The species distribution can be explained by three climatic factors, that is, low precipitation during the growing season, winter cold, and low snowfall.	Yagihashi et al. (2007)	
Northward expansion continues	The northward expansion is an ongoing phenomenon. We are just witnessing one section of the species expansion process.	Igarashi (1994), Kito (2003), Nanbu (1927)	

Furthermore, *F. crenata* is distributed on two oceanic islands in the Japan Sea; namely, Sado Island, Niigata and Okushiri Island, Hokkaido. Thus, the northern distribution limit of *F. crenata* on islands exists on Okushiri Island (Tatewaki, 1948), where it grows well and forms one of the dominant tree species on the island (Namikawa et al., 2021; Tatewaki, 1940b). The species is distributed across a wide altitudinal range from 24 m to 500 m, which is close to the peak of the top of the highest mountain on Okushiri Island, Mt. Kamuiyama at 584.5 m (Namikawa et al., 2021). *F. crenata* trees on Okushiri Island underwent selective cutting for commercial use after World War II. However, the National Forest Agency brought about a cessation of logging of *F. crenata* trees on Okushiri Island in 1996 for conservation purposes.

3 | RANGE SHIFTS IN THE RECENT PAST

Macro fossils of *F. crenata* cupules were excavated from the Kuromatsunai Depression as well as Churui, in the southern part of the Tokachi Plain, and Kitahiroshima and Atsuma in the Ishikari Plain, Hokkaido, which are northeast of the current northern distribution limit (Yano, 1983). Precise dating of the strata was not conducted, but these macro fossils might indicate that *F. crenata* was distributed in these areas during the Riss-Würm interglacial period (Yano, 1983).

Palynological studies in relation to southern Hokkaido have revealed the recent northward expansion of *F. crenata* after the LGM (Bradshaw et al., 2010; Igarashi, 1994; Kito & Ohkuro, 2012; Kito & Takimoto, 1999; Nakamura & Tsukada, 1960; Takiya & Hagiwara, 1997; Tsukada, 1982a, 1982b). As the continental ice sheets did not exert any significant influence on vegetation history in East Asia (Ehlers & Gibbard, 2007), the cryptic refugia (Stewart & Lister, 2001; Tzedakis et al., 2013) of *F. crenata* in Hokkaido likely existed in the southern part of the Oshima Peninsula 11,000 years BP, from where the recent northward expansion started (Takiya & Hagiwara, 1997; Uemura & Takeda, 1987). The species reached the current northern limit approximately 1000 years BP (Igarashi, 1994; Sakaguchi, 1989; Takiya & Hagiwara, 1997). The most recently established leading edge population of the northernmost range populations was found 12 km to the north of the previously known edge (N. Tanaka et al., 2016). The distance from the known populations is within the range of possible seed dispersal agents such as jays (Johnson & Adkisson, 1985; N. Tanaka et al., 2016) and spotted nutcrackers (Kobayashi & Watanabe, 2003; Nishi & Bekku, 2015; Vander Wall & Balda, 1977). Moreover, Kitamura and Nakanishi (2021) indicated that this population was a newly founded population by the reason of non-significant spatial genetic structure of the mature trees. This is one piece of circumstantial evidence in support of the continuing northward shift of the species' distribution range.

4 | BIOTIC FACTORS FOR SUSTAINABLE POPULATIONS IN THE NORTHERN RANGE

There are several characteristic traits observed in relation to *F. crenata* in the northern range. For example, northern populations show a larger leaf size (Hagiwara, 1977), thicker branches (Osada et al., 2015), faster growth in diameter (Hagiwara, 1988), earlier leaf flush (Hashizume et al., 1996; Osada et al., 2018), and higher whole tree transpiration (Tateishi et al., 2010) than do the southern populations. A recent study has revealed that the *F. crenata* in the northern range exhibits higher plasticity in terms of leaf morphology, which might be due to the adaptations to the changing environment at the distribution margin (Ishii et al., 2018).

Also, the successful establishment of *F. crenata* at the northern front can be attributed to the absence of the specialist lepidopterous herbivore, *Sntypistis punctatella* (Kobayashi, 2009). In general, this insect exerts the highest predation pressure on *F. crenata* by outbreaking every 8–11 years (Kamata, 2006). Foliage consumption by herbivores and defense chemicals in *F. crenata* leaves have decreased drastically across the northern distribution front of *F. crenata*, which would indicate that the geographic restrictions on herbivores prevented them from keeping pace with the expansion of tree species (Kobayashi, 2009). Thus, the northward expansion of *F. crenata* can be supported by the “enemy release hypothesis” (Moorcroft et al., 2006), that is, the escape from natural enemies, such as animals and insects, in a native habitat enables invaders to successfully establish in a non-native habitat (Figure 2).

The predator satiation hypothesis has been widely accepted as an evolutionary benefit for mast seeding in *F. crenata* (Igarashi & Kamata, 1997; Silvertown, 1980). This hypothesis has also shown relevance in terms of pre-dispersal seed predation in the northern distribution range of *F. crenata* where seed production was more than 20 times higher than the previous year (Yasaka et al., 2003). On the one hand, seed predation has increased toward the northern edge of the northern range (Kobayashi, 2018). This is attributable to the predation pressure exerted by the most effective invertebrate, *Pseudopammene fagivora* (Terazawa, 1997; Terazawa et al., 1995), whose distribution has caught up with the northern expansion, and even spread further to the north of the natural distribution of *F. crenata*. However, *F. crenata* forests without this insect species in the northern margin and further north do not suffer from seed predation, so successful population growth appears possible (Figure 2).

Also in the northern distribution range, successful regeneration can be achieved by current-year seedlings

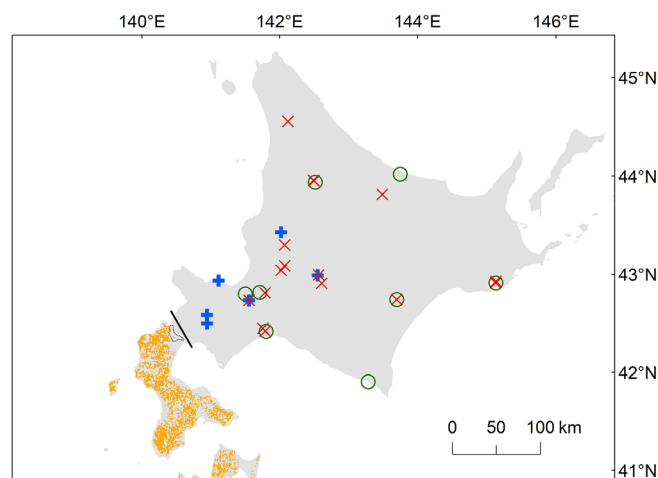


FIGURE 1 Geographic location of planted *Fagus crenata* trees beyond the natural range limit in Hokkaido (T. Matsui & N. Tanaka, unpublished data). Yellow dots, natural *F. crenata* forest distribution; black line, the northern range limit of natural *F. crenata*; area surrounded by the dotted line near the northern range limit, Kuromatsunai depression; red crosses, neither seedlings nor saplings were found; green circles, seedlings were found, but no saplings; blue crosses, both seedlings and saplings were found. [Color figure can be viewed at wileyonlinelibrary.com]

evading infectious fungi (Sahashi et al., 1994) due to the absence of a dark rainy season in early summer (Namikawa et al., 2011).

5 | VEGETATION

F. crenata forests in northern Japan, including southern Hokkaido, are dominated by *F. crenata* but also include associated trees such as *Viburnum furcatum*, *Quercus crispula* var. *crispula*, *Acer japonicum*, *A. palmatum*, and *Lindera umbellata* var. *membranacea*. Among those beech forests, two distinct subtypes are observed: one on the Japan Sea side and one on the Pacific side. The forest on the Japan Sea side is characterized by the exclusive dominance of *F. crenata*, making a monotonous physiognomy, and dense growth of *Sasa kurilensis* and/or *S. paniculata*. This subtype is restricted to the Japan Sea side, including southern Hokkaido, where the snow cover in winter is very thick.

Vegetational studies on the *F. crenata* forest in the area including the northern limit of the species, the Kuromatsunai Depression and its vicinity, are few in number and are fragmental rather than inclusive (Hukusima et al., 1984; Kim & Nakamura, 1987; Takeda & Nakanishi, 1984; Tatewaki, 1948). Tatewaki (1948) is a representative study on Japanese beech forests that focuses on the Utsai beech forest, which has been listed as a Natural Monument. Such forests are characterized by the

dominance of *F. crenata* alone in the tree layer and the dense growth of *S. paniculata* in the shrub layer, which are common features of the Japan Sea side beech forests. In addition, at the northernmost margin, *F. crenata* forests become discontinuous with outlying isolated stands (Kito, 2003; Matsui, Namikawa, et al., 2012; N. Tanaka et al., 2016; Tatewaki, 1948). However, there have not been any precise studies regarding the species composition of these outlying isolated stands.

5.1 | Oshima Peninsula

In the southwestern part of Hokkaido, *F. crenata* forests are well developed from sea level to the limit of the timber line, and three associations comprised of seven sociations have been described (Tatewaki, 1958). Associations and sociations were primarily divided by the combination of physiognomic dominants in each layer (i.e., synusie, with the former termed “consociation” to distinguish it from phytosociological “association”). The climax of the beech forest was the *Fagus crenata*—*Sasa* association with monotonous aspect. It is also sometimes associated with *A. japonicum* or *A. tschonoskii* in the shrub layer (*F. crenata*—*Acer* association). On the slightly wetter lower slopes, a *F. crenata*—*Viburnum wrightii* var. *wrightii* association is found, while on the upper slopes of the rather dry ridge of Mt. Ohira (Tatewaki et al., 1958), *F. crenata*—ericaceous shrubs associations are developed. In this association in dry habitats, *Vaccinium smallii* and *V. japonicum* occasionally co-dominate, *Rhododendron kaempferi* is dominant, and *Eubotryoides grayana* is abundant at times. Therefore, there might be a close relation between dominant species in the shrub and/or herb layer and site conditions despite beech dominance in the tree layer.

Hukusima et al. (1984) carried out a phytosociological study on species composition of *F. crenata* forests in the Oshima Peninsula and the Japan Sea side region of Honshu. In respect to the floristic composition, the beech forests in Hokkaido were distinguished markedly from the beech forests in the Japan Sea side region of Honshu for the following two reasons: (1) the following species common to beech forests in the Japan Sea side region of Honshu were either not present or rare on the Oshima Peninsula: *A. distylum*, *Heloniopsis orientalis*, *Magnolia salicifolia*, *Padus grayana*, *Shortia uniflora*, *Carex multifolia* var. *multifolia*, *Arachniodes mutica*, *Corylus sieboldiana* var. *sieboldiana*, *Hamamelis japonica* var. *discolor* f. *obtusata*, and *Dryopteris sabaiei* (first three species were not distributed in Hokkaido); and (2) *Abies sachalinensis* var. *mayriana* and *Ilex rugosa* occurred exclusively in the northern region of the Oshima Peninsula. Moreover, they

identified *F. crenata* forests in Hokkaido by their floristic composition: a *Saso kurilensis*—*Fagetum crenatae* association (Suzuki, 1949). This association was further subdivided into the following six subassociations and six variants (i.e., nine vegetation units), which showed distinctive floristic compositions and habitat conditions (Table 2).

Hukusima et al. (1984) pointed out that the number of vegetation units decreased from south to north along the Oshima Peninsula. Therefore, there were only four vegetation units, that is, A-b, C, D, and E-a, in the northernmost range of the Kuromatsunai Depression (Table 2). However, this is not a feature of beech forest at its northernmost range. The decreases in the number of vegetation units toward the northern limit of beech results from the following two facts: (1) the geographical range limits of some differential species, such as *Pinus parviflora* var. *pentaphylla* (differential species of F), and *S. soldanelloides* var. *magna*, *H. japonica* var. *discolor* f. *obtusata* and *Clethra varvinervis* (E-b and F-b), were at the southern region of the Oshima Peninsula; and (2) subassociation B with an altitudinal range higher than 500 m a.s.l. could not be established in the Kuromatsunai Depression due to the low altitudinal range of the topography (below 200 m a.s.l.). Thus, the decrease in vegetation units in the northernmost range might be caused by constraints associated with the flora and physiographic conditions.

5.2 | Okushiri Island

Namikawa et al. (2021) compared the species composition of *F. crenata* forests between Okushiri Island and surrounding areas, that is, the Oshima Peninsula and the northern Tohoku region of Honshu. Type A1 (refer to Namikawa et al., 2021), the representative vegetation on Okushiri Island and the northern region of the Oshima Peninsula, was characterized by the occurrence of *I. rugosa* var. *rugosa*. Furthermore, elements of boreal forests, such as *Betula ermanii* var. *ermanii*, *Clintonia uden-sis* and *D. expansa*, were partly present in type A1, which is a floristic feature of beech forests in the northern region of the Oshima Peninsula. On the other hand, species with a high rate of occurrence on the Japan Sea side of Honshu, including the northern Tohoku region, but with a low rate of occurrence on the Oshima Peninsula, such as *D. sabaiei*, *A. mutica*, *P. grayana*, and *Mitchella undulata* (Hukusima et al., 1984; Takeda & Nakanishi, 1984), were frequently found among type A1 vegetation. This is a floristic feature of beech forests on Okushiri Island as distinguished from those on the Oshima Peninsula. Furthermore, several stands at lower

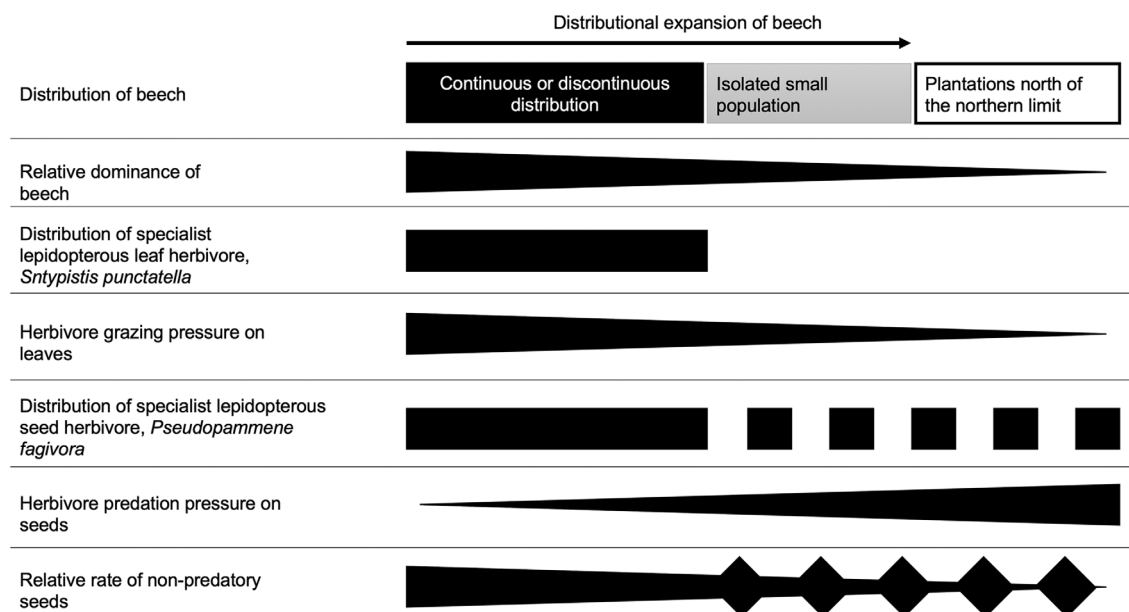


FIGURE 2 Distribution and predatory damage schema of specialist lepidopterous leaf and seed herbivory over the northern expansion front of *Fagus crenata*. Diamonds in “Relative rate on non-predatory seeds” indicate the occurrence of mast seeding in populations without *Pseudopammene fagivora* at the northernmost isolated populations and *F. crenata* plantations beyond the geographic distribution front.

altitudes on Okushiri Island included the representative warm-temperate element of *Ardisia japonica* var. *japonica*. In addition, Tatewaki (1940a, 1940b) listed the warm temperate elements of *D. dickinsii*, *D. lacera*, and *Cymbidium goeringii* on Okushiri Island, but these were absent from the Oshima Peninsula. These warm temperate elements were probably a remnant of the Quaternary vegetational shift.

6 | POPULATION ESTABLISHMENT IN THE NORTHERN RANGE

One of the characteristics of *F. crenata* populations in the northern range is that the species is established in the early phases of the ecological succession of the habitat. In the northern range of *F. crenata*, transition from *Q. crispula* to *F. crenata* forest has often been observed (Kobayashi, 2009; Suzuki, 1949). This might be due to the phenological advantage of young *F. crenata* trees in the early spring. *F. crenata* juveniles can flush leaves and start photosynthesis earlier than *Q. crispula* canopy trees, thus, *F. crenata* can invade and become established under the *Q. crispula* canopy (Kobayashi, 2009).

From an ecological point of view, the dominance of dwarf bamboo in the forest understory prevents successful regeneration of cool temperate deciduous forests dominated by *F. crenata* (Nakashizuka, 1988), therefore, the species generally depends on a disturbance regime of small-scale tree fall gaps to regenerate (Nakashizuka &

Iida, 1995). Moreover, one characteristic regeneration regime in the northern range was reported by a dendro-chronological study of an outlying isolated *F. crenata* population at the expansion front (Namikawa et al., 2010). The study revealed that the different age groups of *F. crenata* aggregated at different locations of a forest that was mixed with *Q. crispula*, *Tilia japonica*, *A. mono*, and *A. sachalinensis*. The established site for each age group corresponded to the ecological emptiness left by landslides and typhoon windthrow. Large-scale blowdowns are one of the disturbance regimes associated with cool temperate mixed broadleaf/conifer forests (Nakashizuka & Iida, 1995). It seems that the establishment of *F. crenata* forest in the northern range depended on the occurrence of episodic natural disturbances at intervals of several decades that retarded the migration rate at the expansion front (Namikawa et al., 2010).

Another characteristic behavior of *F. crenata* at the expansion front is that the trees grow faster than those in the rearward populations. We collected increment cores from 10 trees from the leading-edge Niseko population, determined the age, and compared them with previous results from the rearward northern range population at Karibayama (Kitamura et al., 2007). The relationship between tree age and diameter at breast height (DBH) revealed that the slope of the age versus DBH regression line of *F. crenata* in the Niseko population was almost twice as steep as that in trees in Karibayama (Figure 3). In 2021, we observed that the trunk of the largest tree (aged 130 years) in the Niseko population cracked and split, indicating a short species longevity at the northern

TABLE 2 Differential species of six subassociations and six variants, and habitat conditions of *Fagus crenata* forests in Hokkaido (after Hukusima et al., 1984)

Association	Subassociation	Differential species of subassociation	Variant	Differential species of variant	Geographical distribution	Altitudinal distribution	Existence in Kuromatsunai
Saso <i>kurilensis</i> – <i>Fagetum</i> <i>crenatae</i>	A <i>Dryopteris crassirhizoma</i> subassociation	<i>Hydrangea serrata</i> var. <i>yesoensis</i>	A-a	<i>Carex dolichostachya</i>	Shiriuichi	Below 205 m a.s.l.	×
		<i>Dryopteris crassirhizoma</i>		var. <i>glaberrima</i> variant			
		<i>Thelypteris pozoi</i> subsp. <i>mollissima</i>					
		<i>Panax japonicus</i>					
		<i>Peracarpa carnososa</i> var. <i>circaeoides</i> ^a	A-b	Typical variant	All areas	—	○
		<i>Pachysandra terminalis</i>					
		<i>Dryopteris austriaca</i> subassociation			All areas beyond Kuromatsunai	Above 500 m a.s.l.	×
		<i>Maianthemum japonicum</i> ^b					
		<i>Streptopus streptopoides</i> subsp. <i>japonicus</i>					
C	Typical subassociation	—			All areas	—	○
		<i>Vaccinium smilii</i> ^a					
		<i>Vaccinium japonicum</i>			All areas	—	○
		<i>Ilex crenata</i> var. <i>paludosa</i> ^a					
		<i>Toxicodendron trichocarpum</i>					
		<i>Eubotryoides grayana</i> var. <i>grayana</i>					
		<i>Rhododendron albrechtii</i>					
		<i>Ilex rugosa</i>					
		<i>Rhododendron pentandrum</i>					
E	<i>Tripetaleia paniculata</i> subassociation	<i>Tripetaleia paniculata</i> ^a	E-a	Typical variant	All areas	—	○
		<i>Ilex sugerokii</i> var. <i>brevipedunculata</i>	E-b	<i>Shortia soldanelloides</i> var. <i>magna</i> ^{a,c}	Shiriuichi	—	×
				<i>Hamamelis japonica</i> var. <i>discolor</i> f. <i>obtusata</i> ^{b,c}			
				<i>Clethra barbinervis</i> ^c			

(Continues)

TABLE 2 (Continued)

Association	Subassociation	Differential species of subassociation	Variant	Differential species of variant	Geographical distribution	Altitudinal distribution	Existence in Kuromatsunai
F	<i>Pinus parviflora</i> var. <i>pentaphylla</i> subassociation	<i>Pinus parviflora</i> var. <i>pentaphylla</i> ^c <i>Rhododendron brachycarpum</i>	F-a	<i>Ilex rugosa</i> variant <i>Vaccinium hirtum</i> var. <i>hirtum</i> <i>Euonymus oxyphyllus</i> ^a <i>Carex conica</i> var. <i>conica</i> <i>Thujopsis dolabrata</i> var. <i>honda</i> ^c	Shiriuichi & Hiyama	—	×
			F-b	<i>Clethra barbinervis</i> variant <i>Shortia soldanelloides</i> var. <i>magna</i> ^{a,c} <i>Hamamelis japonica</i> var. <i>discolor</i> f. <i>obtusata</i> ^{b,c} <i>Clethra barbinervis</i> ^c <i>Mitchella undulata</i> ^b	Shiriuichi	—	×

Note: ○, present. ×, not present.

^aScientific name adopted in original articles.

^bSpecies common to beech forests from low altitudes to mountainous regions along the Japan Sea but rare in the Oshima Peninsula.

^cSpecies distributed in the southern region of the Oshima Peninsula.

distribution front (Figure 3). Fast diameter growth was also suggested at Rebunge Pass, where the northernmost marginal population on the Pacific Ocean coast is located (Matsui, Kitamura, et al., 2012); namely, the maximum annual ring width was 7.5 mm. Also, Matsui, Namikawa, et al. (2012) discussed the general trend for the increase in growth of *F. crenata* after large-scale disturbances at the northern range limit. The turnover rate of *F. crenata* in Honshu was calculated to be 100–200 years (Nakashizuka, 1984, 1987). However, the current results suggest that *F. crenata* reaches maturity earlier and the population turnover rate is shorter at the northern margin of the expansion front.

7 | PREDICTION OF FURTHER NORTHWARD DISTRIBUTION EXPANSION

The current geographic distribution of plant species is a reflection of the spatiotemporal interactions of a variety of biotic and abiotic factors. One of the major factors determining the current distribution of temperate forests in the Northern Hemisphere is climate conditions. The

climatic factors determining the northern limit of *F. crenata* have been revealed to be Kira's Warmth Index, the minimum temperature of the coldest month, summer precipitation, and winter precipitation (Yagihashi et al., 2007). It is interesting to note that winter precipitation and the warmth index can satisfactorily explain the whole distribution of this species (Matsui et al., 2004), but distribution models were not able to reconstruct the current northern margin without summer precipitation suggesting that summer precipitation is more important than the other climatic factors in determining the northern distribution limit of this species (Yagihashi et al., 2007). The abundance of *F. crenata* forests in Hokkaido and Honshu is ensured by the amount of precipitation in the growing season (Peters, 1997; Tsukada, 1982a; Yagihashi et al., 2007). At the northern range margin, physiological characteristics might be an important limiting factor because *F. crenata* is less competitive against its temperate deciduous counterpart *Q. crispula* in the xeric growing season (Maruyama & Toyama, 1987).

That the northward expansion of *F. crenata* is an ongoing process affords a feasible explanation of the present northern range (Igarashi, 1994; Kito, 2003; Nanbu, 1927). A general increase in global temperature has been predicted (Parmesan & Yohe, 2003) and the velocity of climate change (VoCC) (Loarie et al., 2009) in Hokkaido was estimated to be 68–378 m year⁻¹ (Takano et al., 2019). This is faster than the expansion rate of *F. crenata* in Hokkaido, which is 11–40 m year⁻¹ (Igarashi, 1994; Kito, 2003; Takiya & Hagiwara, 1997; Yagihashi et al., 2007). Therefore, the species was predicted to be unable to keep up with the VoCC but to persist in its northern ranges (Matsui, Takahashi, et al., 2009).

One of the pieces of evidence supporting this notion is that the current northern range does not appear to correspond to any physiological limitation as artificial plantations of *F. crenata* can grow well on the northeastern ranges beyond the natural northern limit (Figure 1). Matsui and Tanaka (unpublished data; Botanic Garden, Hokkaido University, unpublished data) investigated *F. crenata* trees planted in Hokkaido as arboreta, botanical gardens, and ornamental plantations. A total of 153 trees at 16 sites (Figure 4) were found growing well at latitudes ranging from 42.1°N to 43.5°N and longitudes from 140.7°E to 144.8°E.

On the other hand, two climate scenarios predicted the potential habitat of *F. crenata* forests to expand to the northeast in Hokkaido over the next 80 years (Matsui, Tanaka, et al., 2009). In addition, distribution model approaches have predicted a further upward/northward shift of this species (Matsui et al., 2004; Nakao et al., 2013). Although the species is highly susceptible to extinction, which has raised conservation issues in

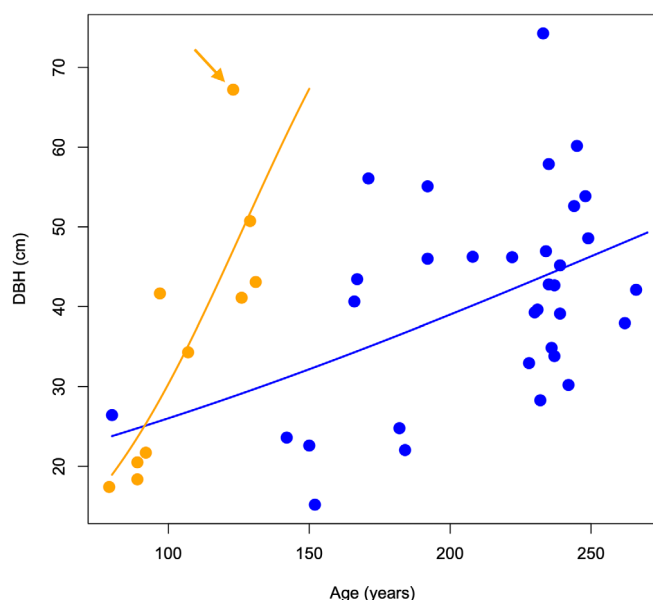


FIGURE 3 Relationships between age and diameter at breast height (DBH) of *Fagus crenata* at the leading-edge Niseko and the rearward Karibayama populations. Orange and blue circles represent individuals in Niseko and Karibayama populations, respectively. The orange arrow indicates the largest individual in Niseko population which cracked and split in 2021. Lines indicate regression curves obtained by the logistic function, $DBH/100 = \exp(a + b * \text{age}) / (1 + \exp(a + b * \text{age}))$; $a = -3.938$ and $b = 0.031$ for Niseko, $a = -1.642$ and $b = 0.006$ for Karibayama. [Color figure can be viewed at wileyonlinelibrary.com]

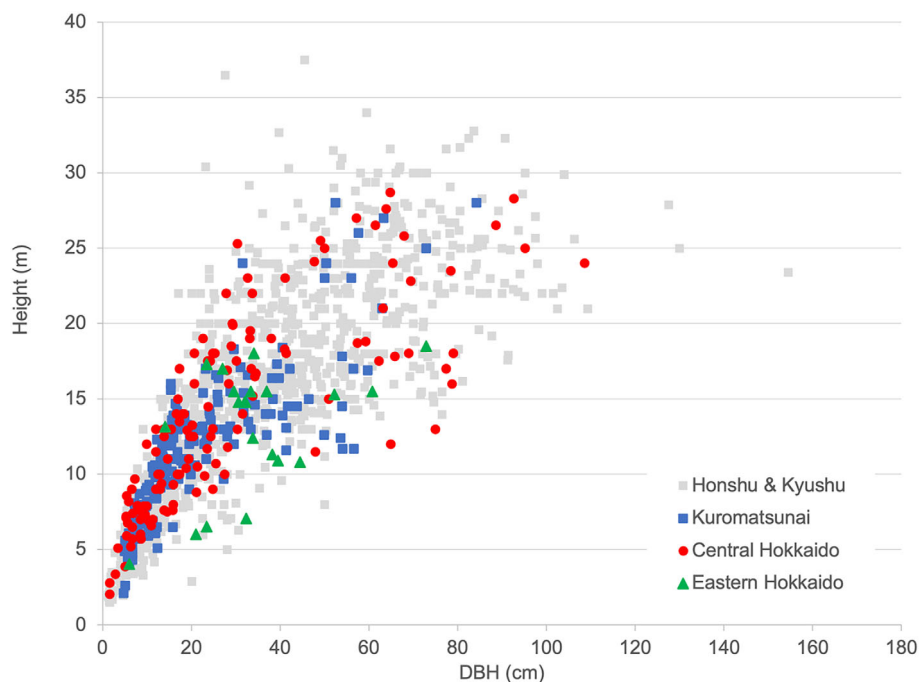


FIGURE 4 Relationships between diameter at breast height (DBH) and tree height of 137 trees of *Fagus crenata* planted beyond the natural range limit in Hokkaido along with 192 trees in Kuromatsunai and 939 from Honshu and Kyushu (T. Matsui & N. Tanaka, unpublished data; Botanic Garden, Hokkaido University, unpublished data) (Kinkityugoku Shinrin Kanrikyoku Forestry Agency, 2009a, 2009b, 2009c, 2011; Kyusyu Shinrin Kanrikyoku Forestry Agency, 2010; Masaki et al., 2017; Ministry of the Environment Government of Japan, 2016; Murakami et al., 2003; Shizuokashi, 2018; Tyubu Shinrin Kanrikyoku Forestry Agency, 2008). Central Hokkaido includes Uryu, Ebetsu, Sapporo, Otaru, Samani, Shibetsu, Takikawa, Nanporo, Nakagawa, Tomakomai, Furano, and Bibai. Eastern Hokkaido includes Akkeshi, Maruseppu, Rubeshibe, and Ikeda. [Color figure can be viewed at wileyonlinelibrary.com]

relation to its southwestern distribution, the distribution model suggested that the habitat of *F. crenata* in Hokkaido would remain sustainable for the next 80 years (Nakao et al., 2013).

8 | ECOLOGICAL GENETICS IN THE NORTHERN MARGINAL POPULATIONS

The leading-edge population of plant species undergo multiple colonizing events, which inevitably affect genetic changes in the local populations (Antonovics et al., 2001; Barrett & Husband, 1990; Currat et al., 2008; Cwynar & MacDonald, 1987; Eckert et al., 2008; Keller et al., 2009; Petit et al., 2004; Tollefsrud et al., 2016). This is also true for the northern distribution range of *F. crenata* (Kitamura et al., 2015; Kitamura & Nakanishi, 2021; Takahashi et al., 1994). The first genecological study, which assessed allozyme polymorphism in 14 populations from Honshu to Hokkaido, revealed the loss of rare alleles in the northern range due to a bottleneck event across the Tsugaru Strait (Takahashi et al., 1994). Another study, which

employed 12 nuclear microsatellite loci in 1693 trees from 33 populations across the species' northern distribution range, demonstrated that the genetic diversity gradually decreased toward the northernmost distribution edge (Kitamura et al., 2015). This study also suggested a strong founder effect prevailed among the small, isolated front-line populations.

The genetic consequences for populations during the expansion front colonization have been quantified by gene flow at the most recently colonized small patch of *F. crenata* (Kitamura & Nakanishi, 2021). The study showed strong genetic differentiation between the leading-edge population and the posterior distribution, which may be attributed to founder events in the early phase of establishment and the present fragmentation. The study revealed a significant spatial genetic structure among juveniles due to the short-distance barochorous seed dispersal. However, the mature trees of this population did not show a significant spatial genetic structure, which is thought to be due to long-distance seed dispersal. Thus, this population is a newly founded young population and represents one piece of evidence for the northward expansion of this species.

Genetic deterioration through inbreeding can generally be expected in fragmented populations (Ellstrand & Elam, 1993); however, it was not the case for this species at the northern front. The selfing rate at the earliest phase of colonization was estimated to be high, but it became negligible soon after establishment. Successful seed production by outcrossing can be achieved by 20 mature trees per hectare (Terazawa, 1997). Practically speaking, 25 mature trees were established in ca. 0.4 ha in this leading-edge population; therefore, the density of mature trees is high enough to enhance outbreeding in seed production. On the other hand, the recovery of genetic diversity was restrained as numbers of individual trees reached maturity and the population size grew. This may diminish the potential for population adaptiveness to the new environment and retard further expansion (Kitamura & Nakanishi, 2021).

9 | KNOWLEDGE GAPS AND FUTURE ISSUES

The northward distribution expansion of *F. crenata* in Hokkaido has occurred over the last 11,000 years (Takiya & Hagiwara, 1997; Uemura & Takeda, 1987) or 6000 years (Bradshaw et al., 2010), with further expansion to the northeast likely to continue (Kitamura & Nakanishi, 2021; Matsui et al., 2004; N. Tanaka et al., 2016). However, the detailed colonizing processes, such as the source of distribution expansion, seed dispersal agents, such as birds and the existence of cryptic refugia, and the probability of further expansion have not yet been clarified.

At the northernmost distribution front of *F. crenata*, evolutionary responses at the range margin have yet to be studied. For example, fecundity decline and dormancy breaking prevention were observed in the trailing rear edge for *F. sylvatica* (Saltr  et al., 2015). It is important to study adaptive traits at the leading edge as neutral molecular markers and quantitative traits respond differently during habitat fragmentation (Young et al., 1996). Local adaptation during expansion, such as evolutionary changes to increase dispersal at the expansion front, may be another topic of interest for study (Hill et al., 2011).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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