Chapter 1

Influences of Climate Change on the Distribution and Population Dynamics of Subalpine Coniferous Forest in the Hakkoda Mountains, Northern Japan

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Abstract Recent research in the Hakkoda Mountains has shown that climate change during recent decades has caused a shift in the distribution of subalpine coniferous forest, which is dominated by *Abies mariesii*. To examine this shift, we analyzed past and present aerial photographs and found population dynamics evidence that suggests a shift of this species' distribution to higher elevations. A fine-scale habitat suitability model for the species elucidated the environmental conditions that determine its present distribution, and this model can be applied to predict the future distribution under the predicted warming scenarios. The model showed that not only temperature but also topography and snow deposition will regulate the future distribution. One important suggestion is that habitats at the periphery of moorlands will act as refugia for *A. mariesii* during the warming process. The fine-scale habitat model may therefore guide the management by providing a measure of how populations will adapt to environmental change.

Keywords *Abies mariesii* • Altitudinal distribution • Aerial photographs • Distribution shift • Population change • Refugia • Snowfall

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1.1 Introduction

The ongoing climate change caused by global warming is greatly affecting terrestrial ecosystems. Warming has shifted the distributions of many plant and animal species poleward and upward (Parry et al. 2007). An increasing number of studies on the upward shift of the range of plants in alpine ecotones have been conducted in Europe and North America (e.g., Beckage et al. 2008; Lenoir et al. 2008). Climate change is expected to decrease or even eliminate the habitats of some alpine and subalpine plants because these plants are isolated in high-elevation patches near mountain summits (Horikawa et al. 2009), leaving them nowhere to move, and ecosystems at higher latitudes may be similarly vulnerable to climate change.

Many studies have predicted the effects of climate change on the distributions of wild plants and vegetation (Araújo et al. 2005; Huntley et al. 1995; Iverson and Prasad 1998; Thuiller et al. 2005). However, most of these predictions have been based on coarse-grained (e.g., 50-km grid) climate response surfaces or idealized scenarios that assumed uniform warming and which therefore failed to consider spatially heterogeneous warming at local and landscape scales (Ashcroft et al. 2009). Trivedi et al. (2008) also suggested that recent large-scale modeling studies may overestimate the ability of montane plant species to adapt to global warming because the input climate data had coarse resolution and was biased against cold, high-altitude habitats.

Studies at finer resolution in Japan have used a Japanese grid coding system with 1-km^2 cells, referred to as the “Third Mesh,” that can be used to predict potential refugia for some dominant species, such as stone pine (Horikawa et al. 2009), beech forests (Matsui et al. 2009), and dwarf bamboo (Tsuyama et al. 2011). Each of the Third Mesh cells measures 3000 latitude by 4500 longitude (191 km^2), and their positions were defined by the Geospatial Information Authority of Japan (Japan Map Center 1998). However, because the variation in elevation within a 1-km cell can be potentially large in Japan’s many complex and precipitous mountainous areas, the temperature variation in these cells must be large. The influences of geographical factors, such as topography, are also difficult to be incorporated in climate models (Matsui et al. 2004). Therefore, the 1-km resolution (i.e., using one representative value per 1-km cell) is insufficient for practical conservation management, including measures to encourage adaptation of species to climate change at a regional or local scale. Some population parameters may also be able to be detected in fine-scale analyses.

The Hakkoda Mountains are the peaks of volcanoes at the northern end of Japan’s Honshu Island and retain areas of well-preserved natural vegetation that includes ecosystems ranging from cool temperate to alpine zones. They are therefore suitable for investigating the impacts of climate change on ecosystems and specifically on changes in their altitudinal distribution. In this study, we review studies on subalpine forests in these mountains that are dominated by *Abies mariesii* and summarize the present evidence about the impacts of climate change on the forest and its future distribution under predicted climate change scenarios. Our results show the effectiveness of fine-scale analyses using aerial photographs to support planning of adaptation measures in response to climate change.

1.2 Climate and Vegetation in the Hakkoda Mountains

The Hakkoda Mountains are located in Aomori Prefecture, near the northern end of Honshu Island (40°39′N, 140°51′E). The highest point in the mountains is 1585 m a.s.l. Natural forests remain at elevations higher than 400 m a.s.l. in the mountains. Most of the land above 700 m a.s.l. has been designated a part of the Towada-Hachimantai National Park where harvesting and other forms of forest management are prohibited.

One of the original vegetation types, cool-temperate (montane) deciduous forests dominated by beech (*Fagus crenata*), is distributed from lowland areas to an elevation of about 1000 m a.s.l (Fig. 1.1). Few primeval cool deciduous forests remain at elevations below 400 m a.s.l., whereas sites above 700 m a.s.l. form a mosaic pattern created by a mixture between cool deciduous forests, secondary deciduous forests (dominated by *F. crenata*), and coniferous plantations (*Cryptomeria japonica* and *Larix kaempferi*).

Subalpine coniferous forests dominated by *A. mariesii* are distributed above 800 m a.s.l (Fig. 1.1). The forests between 800 and 1000 m a.s.l. form a transitional zone between cool deciduous forests and subalpine coniferous forests. The subalpine coniferous forests in the Hakkoda Mountains are mostly primeval and well preserved, though some at high elevations form a mosaic pattern with the

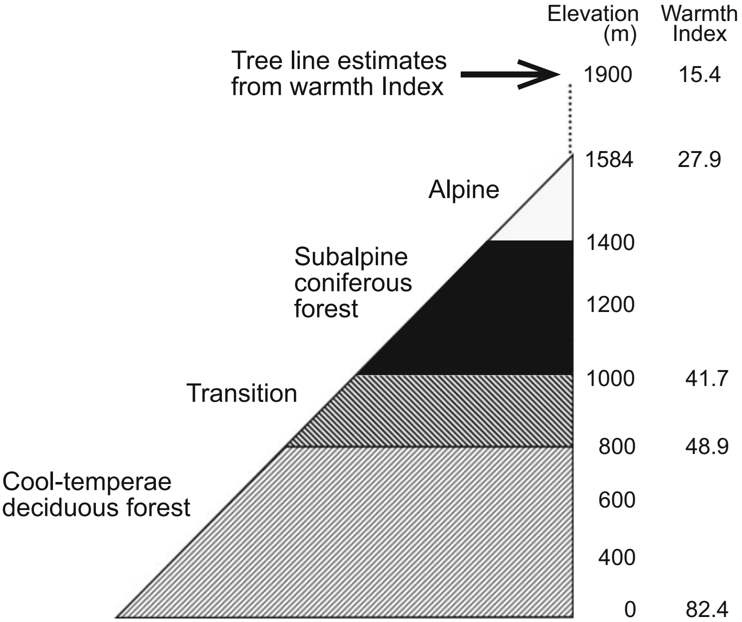

Fig. 1.1 Vertical distribution of vegetation types in the Hakkoda Mountains. The warmth index (see the text for details) is shown for the upper and lower boundaries of the vegetation types

high-altitude vegetation described later in this section. This kind of distribution along a temperature gradient is well explained by the warmth index (WI) that Kira (1977) proposed for the classification of climatic vegetation zones in humid East Asia. WI equals the annual sum of the positive differences between monthly mean temperatures and +5 °C; the index serves as a measure of the effective warmth that sustains plant growth during the growing season.

Several vegetation types other than cool deciduous forests and subalpine coniferous forests are present in the mountains. The types that grow to up to 3-m tall and that are distributed at elevations higher than 1400 m a.s.l. are dwarf forests of Japanese stone pine (*Pinus pumila*), shrubby deciduous vegetation, dwarf bamboo grasslands, and alpine meadows. These form mosaic landscapes with each other and with subalpine coniferous forests and form in response to local environmental conditions such as high elevation, steep topography, and the associated climatic conditions. Alpine meadows grow at the summits in the Hakkoda Mountains. At around 1400 m, *A. mariesii* forms a relatively abrupt tree line (Fig. 1.1).

At elevations of 600–1400 m a.s.l., many patches of moorland are found in depressions filled with volcanic ash created by a massive eruption during the Pleistocene epoch (Muraoka and Takakura 1988; Koike et al. 2005). *Abies mariesii* are distributed at the fringes of the moorland, even when this is lower than the usual lower limit of subalpine coniferous forests (Yamanaka et al. 1988).

The Hakkoda Mountains have among the deepest accumulations of snow in the world, reaching a depth of 3–5 m during the winter. The annual mean temperature and annual precipitation at the Sukayu weather station, in the middle of the mountain range (890 m a.s.l.), are 4–6 °C and 1300–2300 mm (Japan Meteorological Agency 1996).

Abies mariesii is a subalpine conifer that is endemic to Japan and is adapted to habitats with heavy snowfall (Kaji 1982; Sugita 1990). Although *A. mariesii* was not the dominant species during the last glacial period, when snowfall was light, its distribution expanded when snowfall began to increase during the Hypsithermal period (Morita 1985). Since other subalpine coniferous species gradually became locally extinct in many Japanese subalpine forests, particularly those in snowy regions, the snowy subalpine coniferous forests now consist only of *A. mariesii*. However, these forests are sparse or absent in some regions with extreme snowfall (Shidei 1956; Sugita 1992), even when thermal conditions (e.g., WI) are suitable. In the Hakkoda Mountains, *A. mariesii* only grows up to about 1400 m a.s.l (Fig. 1.2), even though its temperature tolerance could allow it to grow at elevations up to about 1900 m (Nogami 1994).

As many reports have suggested, temperatures have been rising in recent decades. At the Aomori weather station (2.8 m a.s.l.), on the northern coast of Honshu, the mean annual temperature has increased by about 0.7 ± 0.5 °C from 1977 to 2003 based on the mean linear trend with 95 % confidence limits (Fig. 1.3a). Annual rainfall at Sukayu (890 m a.s.l.) has increased in recent decades, but at Aomori, there has been no clear trend (Fig. 1.3b). The maximum snow depth showed no clear trend at either station, although the interannual fluctuation at

Fig. 1.2 Forest at the upper limit of *Abies mariesii*. The tree line is fairly sharp at about 1400 m a.s.l.; vegetation communities dominated by shrub species, dwarf bamboo, or alpine plants are distributed above the tree line

Sukayu has tended to increase since 2000 (Fig. 1.3c). However, since the mean temperature has increased, the snowmelt date may have become earlier, and this change would affect tree physiology through its effects on phenological responses.

1.3 Population Dynamics of Subalpine Coniferous Trees in Recent Decades

We investigated differences in the population density and canopy height of *A. mariesii* between 1967 and 2003 by analyzing high-resolution aerial photographs of the Hakkoda Mountains (Shimazaki et al. 2011). We defined 712 plots, each 25 × 25 m, in the photographs and analyzed which environmental variables (elevation, slope aspect, wetness, and distance from the nearest moorland) accounted for the observed changes in the distribution of this species. Since *A. mariesii* is almost the only evergreen tree species in this area, it was easy to identify the species in the photographs.

Our key finding from this analysis is that the population density of *A. mariesii* has decreased significantly in the plots below 1000 m a.s.l. and has increased significantly in the plots above 1300 m a.s.l. since 1967 (Fig. 1.4). The mean elevation, weighted by population density, was 1190 m a.s.l. in 1967 versus 1209 m a.s.l. in 2003; this represents an increase of 0.53 m per year. Of the other

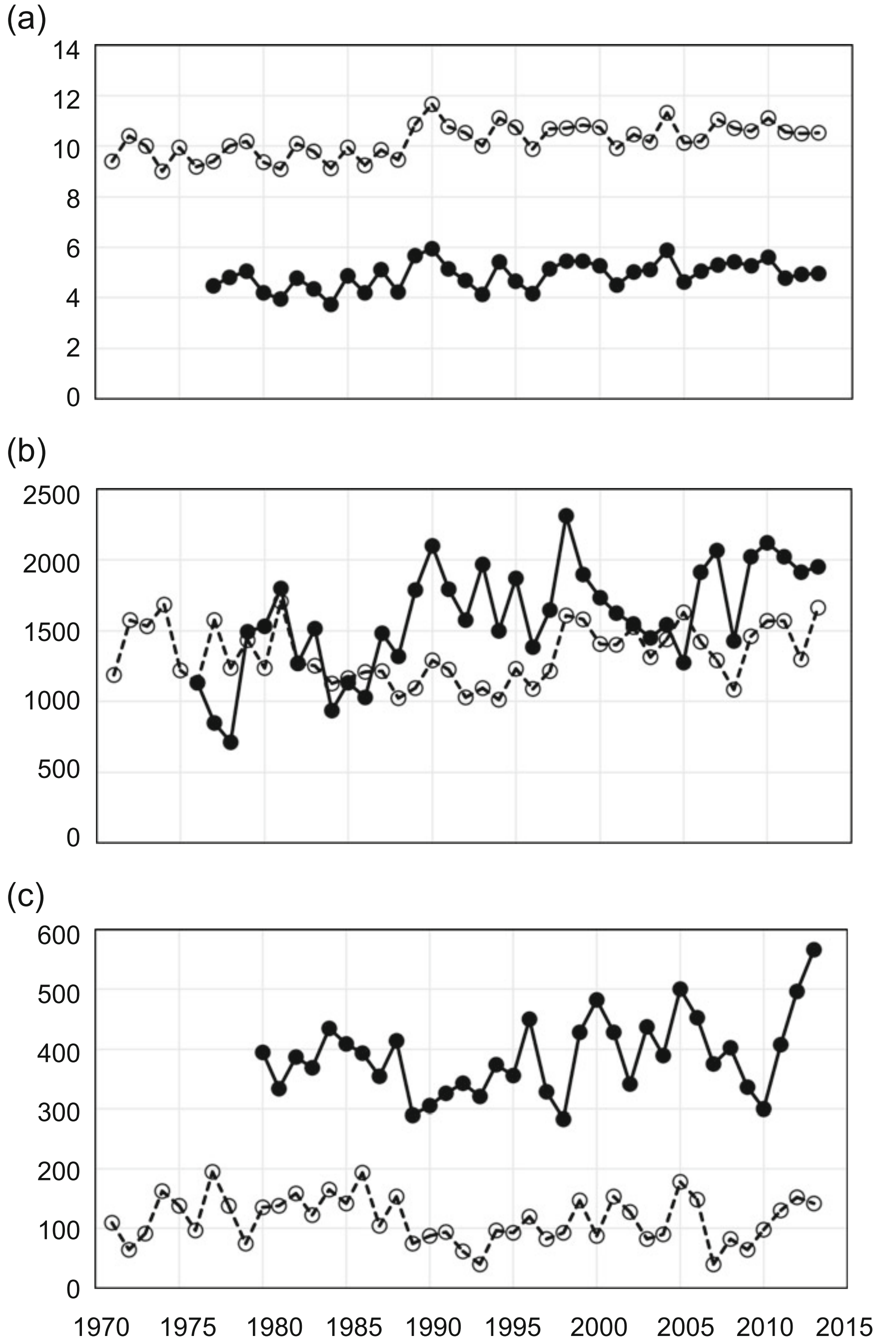

Fig. 1.3 The changes in climatic conditions around the Hakkoda Mountains since 1970. (**a**) Annual mean temperature, (**b**) annual rainfall, and (**c**) maximum snow depth since the 1970s at Aomori (2.8 m a.s.l., *open circles*), a coastal station north of the study area, and at Sukayu (890 m a.s.l., *solid circles*), in the center of the mountainous study area

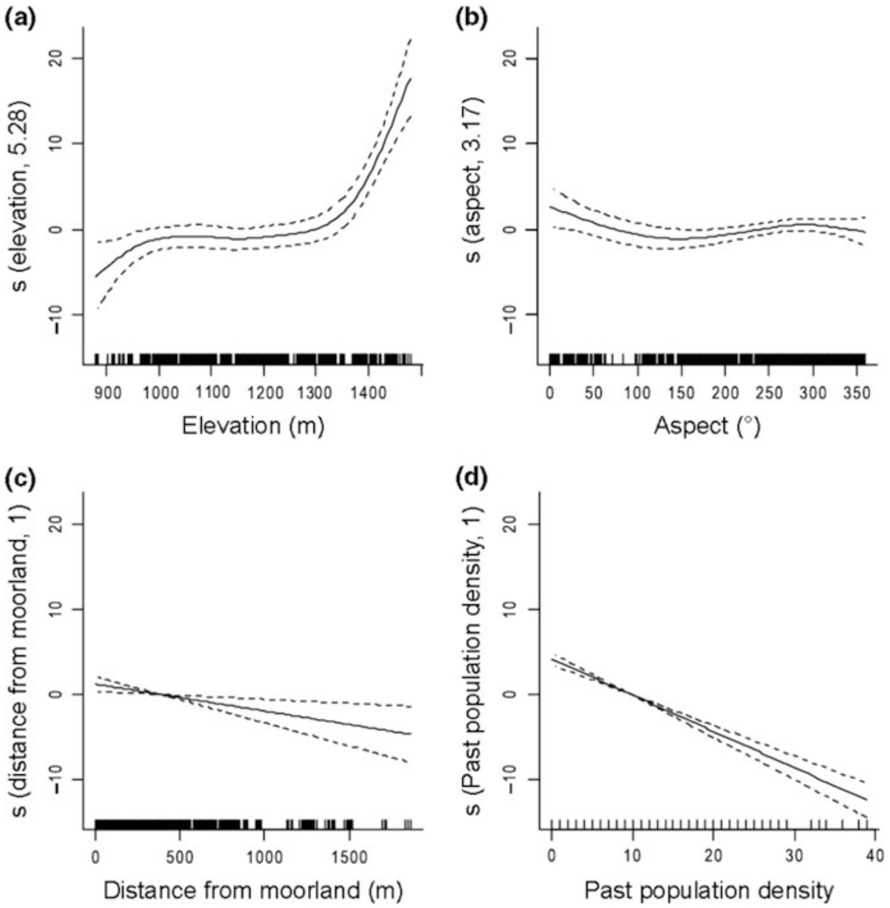

Fig. 1.4 Partial residual plots of the smoothed relationships between changes in the population density of *Abies mariesii* in a generalized additive mixed model as a function of (**a**) elevation, (**b**) slope aspect, (**c**) distance from the nearest moorland, and (**d**) the past population density. *Dashed lines* indicate the 95 % confidence intervals (Modified after Shimazaki et al. 2011)

factors in our analysis, slope aspect did not seem to affect population density, but the population density decreased significantly with increasing distance from moorland and with increasing past population density. Such upward shifts of mountain plants have been commonly reported in Europe and North America (Beckage et al. 2008; Lenoir et al. 2008). Although the cause of the shift in the distribution limits is not clear, Gehrig-Fasel et al. (2007) suggested that a significant increase in forest cover at the upper distribution limit of forests in the Swiss Alps was partly attributable to climate change.

In the Hakkoda Mountains, the decrease in tree density below 1000 m a.s.l. seems to be most strongly associated with climate change, although the factors that contributed to the density increase above 1300 m a.s.l. are debated. Pollen analysis suggests that *A. mariesii* forests in the Hakkoda Mountains became established about 600 years ago (Morita 1985), and the upper limit of the species' distribution predicted based on temperature is expected to be much higher than the current distribution limit (Nogami and Ohba 1991). At high altitudes, an increase in temperature and a decrease in snowfall or in the duration of snow cover have promoted the expansion of *A. mariesii* into areas that were previously unsuitable for the species due to heavy snowfall (Daimaru and Taoda 2004).

The increase in the population density of *A. mariesii* was particularly pronounced at high elevation (Fig. 1.4a) and near moorlands (Fig. 1.4c). The latter finding suggests that the zones around the moorlands represent potential refugia for *A. mariesii* (Fig. 1.5). If *A. mariesii* growing around the moorlands represents remnant populations that have survived since the last glacial period, their population density should not have increased. Since *A. mariesii* has a higher tolerance for the perhumid (and probably more acidic) soil environments of the moorlands than *F. crenata*, which is dominant at warmer, lower elevations (Sugita 1992), *A. mariesii* may thrive better than *F. crenata*, which usually outcompetes *A. mariesii* in low-elevation environments (Yamanaka et al. 1988). Murach and Ulrich (1988) observed a similar relationship between European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*): root growth of *F. sylvatica* was much more sensitive to low pH than that of *P. abies*. These results indicate that acidic mineral soils strongly inhibit the growth of beech trees (Marschner 1991).

Fig. 1.5 An *Abies mariesii* population distributed around a moorland, located at about 800 m a.s.l. The deciduous broadleaf trees (mostly *Fagus crenata*) are distributed farther from the moorland

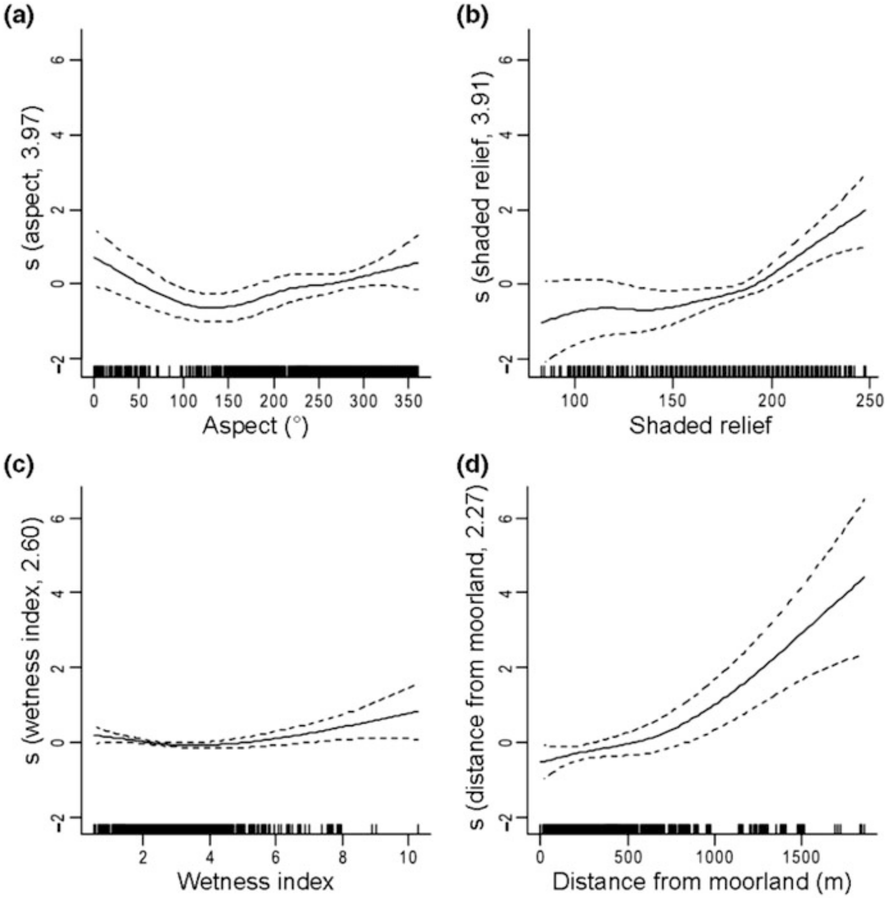

Fig. 1.6 Partial residual plots of the smoothed relationships between changes in the canopy height of *Abies mariesii* in a generalized additive mixed model as a function of (**a**) slope aspect, (**b**) shaded relief, (**c**) the wetness index, and (**d**) distance from the nearest moorland. *Dashed lines* indicate the 95 % confidence intervals (Modified after Shimazaki et al. (2011))

Thus, the growing conditions around moorlands would have prevented the growth of beech trees and provided unoccupied habitats for *A. mariesii*.

We also found that the rate of increase in canopy height was lowest on southeast-facing slopes and close to moorlands (Fig. 1.6a–d). The slow height growth of *A. mariesii* on the southeast-facing slopes (Fig. 1.6a) may be due to the detrimental effect of snowdrifts, which form during winter monsoons that approach from the northwest and that deposit large amounts of snow on the opposite side of the peaks as a result of orographic effects. *Abies mariesii* cannot survive the pressure created by deep snowdrifts as they shift downhill under the influence of gravity because it cannot adopt a creeping (prostrate) growth form (Shidei 1956). In addition, the growing season of *A. mariesii* tends to be shorter in areas with deep snow deposits.

Thus, even if snowfall has decreased since 1967 at a landscape scale, snowdrifts at local scales caused by interactions between the winter monsoon and the mountain topography are likely to limit the height growth of *A. mariesii*.

Interestingly, although the population density of *A. mariesii* increased near moorlands (Fig. 1.4c), the trees grew more slowly there (Fig. 1.6d). Takaoka (1999) investigated the age structure of *A. mariesii* thickets in forest–meadow ecotones in snowy mountains and found that the short canopy height of *A. mariesii* did not suggest an early stage of succession, but instead suggested the effects of adverse environmental conditions, such as heavy snow. As a result, mature *A. mariesii* trees in the forest–meadow ecotones were shorter than those in neighboring forests. We hypothesize that a similar mechanism has probably inhibited the height growth of *A. mariesii* trees near moorlands, where the soil is poorly drained and acidic. These areas do not provide *A. mariesii* with favorable growing conditions. Yet, despite the unfavorable conditions, the much higher sensitivity of *F. crenata* to such conditions probably allowed the moorlands to offer potential refugia for *A. mariesii* populations.

Thus, the populations around the moorlands do not seem to be remnants, but rather increasing populations, which suggest that the areas surrounding the moorlands are potential refugia for *A. mariesii*. However, *A. mariesii* grew more slowly in these areas. On this basis, we suggest that it is not necessary for potential refugia to provide better growing conditions for a species so long as they promote its survival.

1.4 Predicted Distribution Shift of the Subalpine Forest

We constructed a habitat model for *A. mariesii* in the Hakkoda Mountains at a 50-m spatial scale using a decision-tree model with one climate variable (WI), two topographic variables (slope and slope aspect), and two variables (distance and presence/absence) related to moorlands (Shimazaki et al. 2012; Figs. 1.7 and 1.8). In our model (Fig. 1.7), the most important explanatory variable that determined the distribution of *A. mariesii* was WI. The first divergence at WI = 46.5 °C was the dominant factor that defined the boundary between the distributions of *A. mariesii* and *F. crenata*, and this value was in close agreement with the value (WI = 47) estimated by Nogami and Ohba (1991) for this boundary at the scale of Honshu Island.

The second most important explanatory variable was the slope angle. The downhill creep of snow under gravity, which occurs on open slopes steeper than 15° (Leitinger et al. 2008), creates high pressure on tree stems and thus limits the distribution of *A. mariesii*. The third-most-important explanatory variable was the slope aspect. The distribution probability was lower on east-facing slopes, suggesting the detrimental effect of snowdrifts, which form under the influence of winter monsoons that approach from the northwest. *Abies mariesii* cannot survive the high pressures created by snowdrifts (Shidei 1956). In addition, the growing season for *A. mariesii* is shorter in areas with deep snow.

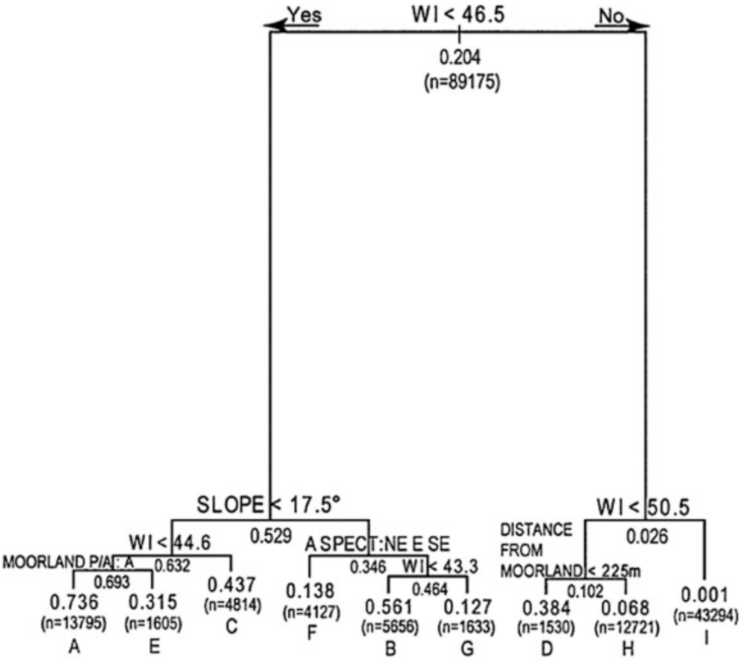

Fig. 1.7 The classification tree model for *Abies mariesii* at a 50-m spatial resolution. The conditions, occurrence probabilities, and number of cells (*n*) are shown at each node. If the condition is met, the left branch is followed; otherwise, the right branch is followed. The length of the *vertical lines* below each true–false split corresponds to the change in the magnitude of the deviance between the parent node (*above*) and the child node (*below*). The warmth index (*WI*), slope, slope aspect, distance from the nearest moorland, and moorland presence/absence (*P*/*A*) data were used as explanatory variables; other environmental variables were not included in this model (Modified after Shimazaki et al. (2012))

Previously, Yamanaka et al. (1988) suggested that *A. mariesii* might have extended its distribution toward lower elevations if there were no competitors. In fact, *A. mariesii* has a higher tolerance for the moist and acidic soil environments around moorlands than beech (Sugita 1992), which would enable it to thrive around moorlands even at WI values higher than 46.5. Shimazaki et al. (2012) applied this classification tree model to several scenarios: warming scenarios (up to +4 °C above present temperatures) and independently for scenarios in which the distribution of moorland decreased or remained stable in response to predicted climate change. The scenario with decreasing moorland was based on a habitat model of moorland as well as on the distribution of *A. mariesii*. Although the suitable areas were notable in the +2 °C scenario, all suitable habitats disappeared in the +4 °C scenario. The distribution of *A. mariesii* will also decrease with a lower temperature increase if the moorland areas simultaneously decrease (Fig. 1.9). Based on the results of this modeling, we conclude that it will be effective to conserve the

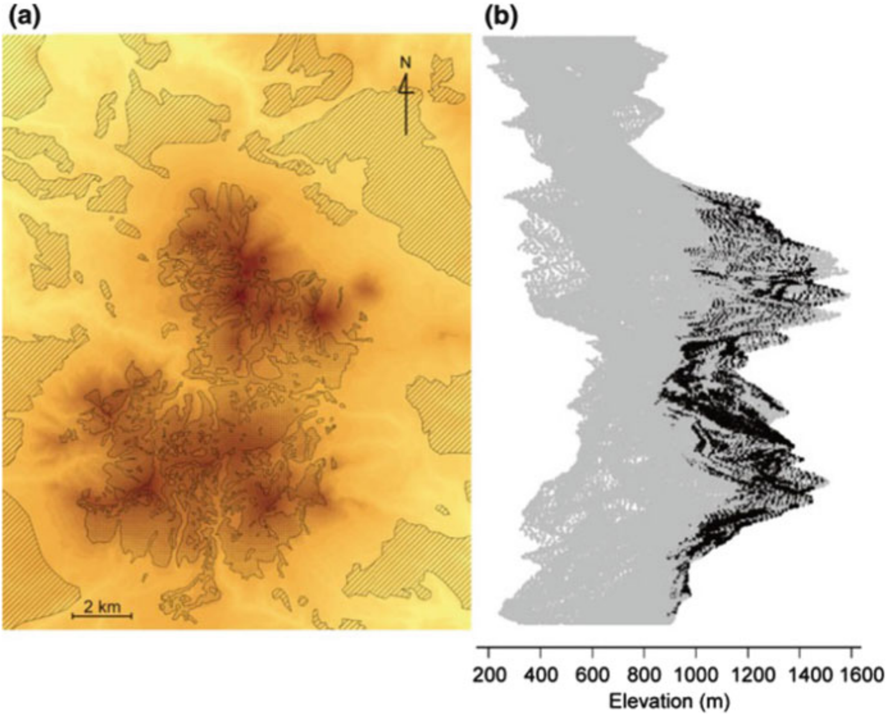

Fig. 1.8 Horizontal and vertical distributions of cells where *Abies mariesii* was present (**a**, *dotted polygons*; **b**, *black dots*) or absent (**a**, outside of the *black dotted polygons*; **b**, *gray dots*) based on aerial photographs. The *background shading* represents the topography of the study area; *darker shades* indicate higher elevations. *Crosshatched areas* depict farms or tree plantations (Modified after Shimazaki et al. (2012))

A. mariesii populations growing around the moorlands that are most likely to persist after global warming, as well as to conserve the moorlands themselves.

1.5 Conclusions

It is clear that the climate change that has occurred since 1967 has already affected the *A. mariesii* populations of subalpine forests in the Hakkoda Mountains. Since 1967, the distribution of *A. mariesii* has shifted about 20 m toward higher elevations. Our high-resolution model revealed the most important factors that are determining the distribution of *A. mariesii* and that can be used to predict its future distribution. Analyses of population and community changes suggested the importance of temperature, mesoscale topography, and fine-scale local environmental gradients associated with snow deposition. Our results also suggest that the

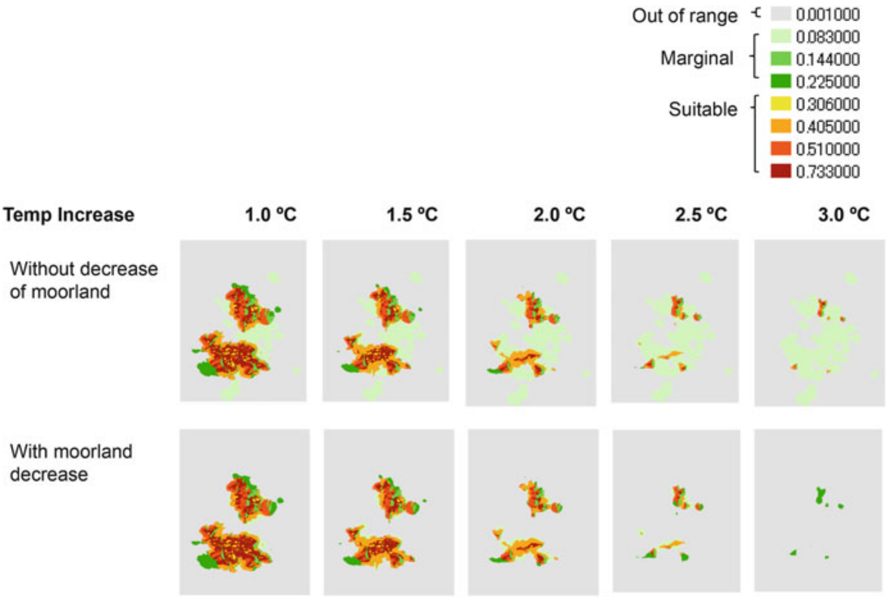

Fig. 1.9 Predicted distributions of potential habitats for *Abies mariesii* under climate change scenarios with temperature increases of 1.0, 1.5, 2.0, 2.5, and 3 °C from present levels and the simultaneous effects of stable (*top*) and decreasing (*bottom*) moorland. The values in the scale represent the probability that a site is suitable for *A. mariesii* (Modified after Shimazaki et al. (2012))

peripheries of moorlands provide effective potential refugia for *A. mariesii* in the Hakkoda Mountains.

Many assessments of the impacts of climate change on vegetation and animals have been made at coarse spatial scales. However, the present results show the importance of accounting for the influence of factors that operate at finer scales and that the assessment and application of adaptation measures will require high-resolution models that incorporate non-climatic variables such as topography and the heterogeneity of landscape units in addition to climatic variables. Although most subalpine areas of Japan have been protected by the government as nature conservation areas, some of these ecosystems will be very sensitive to climate warming (Nogami 1994; Tanaka et al. 2009), and one of the most important adaptation measures for these ecosystems will be the identification of likely population refugia. The present results and other findings from recent studies need to be applied to guide future conservation efforts that account for these and other adaptation measures.

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