

Evaluation of habitat sustainability and vulnerability for beech (*Fagus crenata*) forests under 110 hypothetical climatic change scenarios in Japan

Matsui, Tetsuya^{1*}; Takahashi, Kiyoshi²; Tanaka, Nobuyuki³; Hijioka, Yasuaki⁴; Horikawa, Masahiro^{3,5}; Yagihashi, Tsutomu⁶ & Harasawa, Hideo^{4,7}

¹Hokkaido Research Centre, Forestry and Forest Products Research Institute, 7 Hitsujigaoka, Sapporo, Hokkaido 062-8516, Japan;

²Centre for Global Environmental Studies, National Institute for Environmental Studies, Tsukuba, Ibaraki, Japan; E-mail ktakaha@nies.go.jp;

³Department of Plant Ecology, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki, Japan; E-mail ntanaka@ffpri.affrc.go.jp;

⁴Social and Environmental Systems Division, National Institute for Environmental Studies, Tsukuba, Ibaraki, Japan; E-mail hijioka@nies.go.jp;

⁵E-mail maho@ffpri.affrc.go.jp;

⁶Tohoku Research Centre, Forestry and Forest Products Research Institute, Morioka, Iwate, Japan; Email yagihashi@affrc.go.jp;

⁷Email harasawa@nies.go.jp;

*Corresponding author; Fax+81 11851 4167; E-mail tematsui@ffpri.affrc.go.jp

Abstract

Questions: Are there any sustainable or vulnerable habitats in which beech (*Fagus crenata*) forests could survive in Japan under 110 hypothetical climate change scenarios?

Location: Six islands of Japan on which beech grows naturally.

Methods: An ecological habitat model was used to simulate the potential habitat shifts of beech forests under 110 climate change scenarios. The amount of suitable habitat loss and gain was calculated with three migration options and risk surfaces. Vulnerable and sustainable habitats were identified to evaluate the potential risks and survival of beech forests.

Results: The total areas of potential suitable habitats differed considerably depending on the future temperature and precipitation changes. Some areas on the Sea of Japan (SOJ) side showed higher probability of maintaining suitable habitats, whereas there were wider areas in which suitable habitats could not persist under any of the 110 climate change scenarios.

Conclusions: The risk surfaces of the suitable habitats showed that decreases in precipitation along with increases in temperature reduced the total areas of suitable habitats. Increases in precipitation with increases in temperature of more than or equal to 2°C always reduce the areas of suitable habitats. Under increased precipitation

with a temperature increase of <2°C, the areas of suitable habitats showed an increase, maintenance of the status quo or a decrease, depending on the size of the increase in precipitation. Beech forests in western Japan are predicted to be vulnerable to climate change, whereas some mountains on the SOJ side are predicted to be possible future refugia.

Keywords: Ecological habitat models; Habitat shift; Migration; Potential refugia; Risk surfaces.

Nomenclature: Yonekura & Kajita (2003).

Introduction

All parts of the world may have unprecedented climate change, which will affect ecosystems, plant species and herbivores, resulting in novel species assemblages and interactions (Thomas et al. 2004). In the Swiss Alps, the upward shift of plant species has led to homogenization of alpine summit regions, (i.e. increasing alpha-diversity with decreasing beta-diversity; Jurasinski & Kreyling 2007). In western Europe, climate warming has resulted in a significant upward shift in forest plant species (Lenoir et al. 2008). In Spain, at the low *Fagus altitudinal* limit, *Fagus sylvatica* is being progressively replaced

by the Mediterranean holm oak forest (Penuelas et al. 2007). In Vermont, USA, in the northern hardwood-boreal forest ecotone, northern hardwoods have increased in dominance from 70% in 1964 to 89% in 2004 in the lower half of the ecotone (Beckage et al. 2008). In studies of potential habitat shifts, 80 tree species in the eastern US (Iverson & Prasad 1998), 32 plant species in the UK (Pearson et al. 2002) and 1350 plant species on a European continental scale (Thuiller et al. 2005) were modelled and simulated with climate change scenarios predicting that many plant species would be affected by climate change.

Some studies have presented a novel approach. For example, Fitzpatrick et al. (2008) studied hotspot and climate change for *Banksia* in western Australia. Trivedi et al. (2008) compared macro (European) and local models for vascular plants at a mountain range in Scotland under low and high climate change scenarios. Ohlemuller et al. (2006) used a bioclimatic modelling approach for the risk assessment of 17 European woody species, with additional measures based on the distance between presently occupied areas and areas predicted to be climatically suitable in the future, and the degree of change in climatic suitability in presently occupied and unoccupied locations.

However, those habitat-modelling approaches have been applied to only a limited number of climate change scenarios. This means that the model predictions have not encompassed the range of all possible shifts in suitable plant habitats. It would be useful to show all the possible shifts in habitat under all climate change scenarios. One possibility is to simulate the distribution models under combinations of different hypothetical climatic values (Box et al. 1999). For example, the temperature can be changed from -5°C to $+5^{\circ}\text{C}$ at 1°C intervals, and precipitation can be changed from -50% to $+50\%$ at 10% intervals. In this manner, the impact of climate change on suitable habitats for target taxa under a wide range of hypothetical climatic scenarios could be evaluated. By doing this, it would also be possible to identify either sustainable suitable habitats (i.e. potential refugia) or vulnerable suitable habitats for target taxa in the future. Moreover, if a set of results from detailed model simulations for various subjects, such as in agriculture, forestry, hydrology, or epidemiology, were stored in a single database for every possible combination of expected climatic change, conservation managers or policy makers could simultaneously see the consequences of multiple model runs from different subjects under a given climatic condition (the Climate Change Policy

Support Models; Hijioaka et al. 2006). Therefore, such an approach should be useful for integrating and evaluating the impact of climate change on ecosystems. The proposed approach was applied to the study of a Japanese endemic dominant tree species *Fagus crenata* (Buna or Siebold's beech), in order to contribute to the Climate Change Policy Support Models (Takahashi et al. 2008). However, Takahashi et al. (2008) did not present the ecological habitat sustainability and vulnerability or the ecological interpretations of their findings, and they failed to take migration limitations of the forests into account.

Therefore, the objectives of the present study were: to adopt such a prediction approach and apply it to the study of *F. crenata* as a model case; to evaluate the risk surfaces of the suitable habitats along the gradient of temperature and precipitation change; to identify both stable and vulnerable *F. crenata* forests; to provide ecological interpretations and conservation implications relative to the forests; and to show the effectiveness of this approach. For the entire analysis, three different migration options were also taken into consideration.

Material and Methods

Fagus crenata forest

Fagus crenata is one of the major forest types in the Japanese cool-temperate deciduous forests; *F. crenata* forests make up ca. 17% of Japanese natural forests (Fig. 1). Southern Hokkaido, Tohoku, and the Sea of Japan coast of Honshu contain the majority of *F. crenata* forests, and Shikoku and Kyushu support the forest at higher altitudes (Yamanaka 1979). These forests are known for their importance as habitats for wildlife (Yui et al. 1991; Hara 1996). The Shirakami Mountains were designated as a World Natural Heritage site because they contain one of the largest pristine *Fagus* forests in the world. Therefore, assessment of the impact of climate change and conservation planning for the forests are of international interest.

Predictive distribution models

It was assumed that the distributions of *F. crenata* in Japan were in equilibrium with the climate and classification tree analysis was used for the construction of the predictive distribution model for the forests. The ENVI model (Matsui et al. 2004b), a classification tree model (Breiman et al. 1984), was

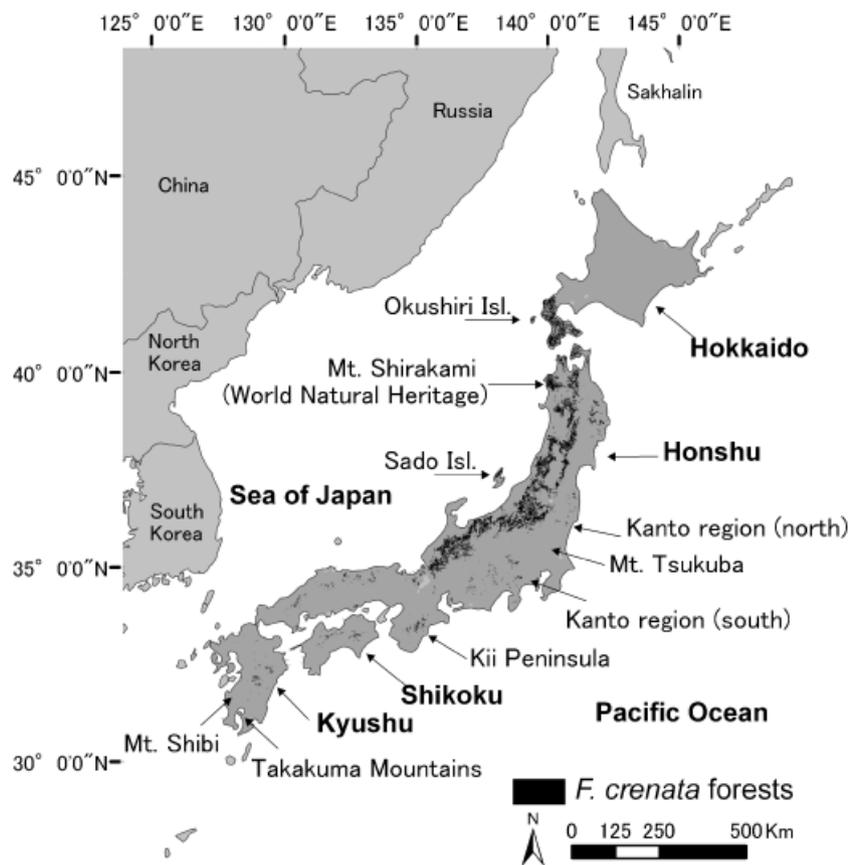


Fig. 1. Study sites and distributions of *Fagus crenata* forests (black dots). The study sites are confined to six islands of Japan, where *F. crenata* naturally grow (Hokkaido, Honshu, Shikoku, Kyushu, Sado Island and Okushiri Island). Other important geographical names and their approximate locations are also shown. The map projection is Lambert Conformal Conic.

constructed with the presence/absence of *F. crenata* forests as a response variable and four climatic parameters (warmth index, mean minimum daily temperature for the coldest month, and summer and winter precipitation) and five environmental parameters (surface geology, topography, slope aspect and inclination, and soil type) as predictor variables. To find the optimal tree size, we applied cross validation (Matsui et al. 2004a), which can eliminate over-fitting and under-fitting problems (Clark & Pregibon 1992; Venables & Ripley 1999). The model can estimate the probability of occurrence of *F. crenata* forests with ca. 1-km² spatial resolution. The spatial resolution of the study was 30''N×45''E (ca. 1 km×1 km at 40°N). This was called the Standard Area Grid (Anon. 1992) in Japan. This type of model represents the conditions of the realized niche under which populations of a species currently persist in the face of competitors and natural enemies (Thomas et al. 2004).

The predictive distribution models dealt with in this study do not encompass the mechanisms of an

ecosystem. However, this approach can provide a useful approximation as to the potentially dramatic impact of climate change on biodiversity (Pearson & Dawson 2003). In agreement with Pearson & Dawson (2003), our data show the potential risks of ongoing climate change on *F. crenata* forests.

In this study, we subjectively called a group of grid squares "suitable habitats" if the probability of occurrence of *F. crenata* forests in it was larger than 0.5. A value of 0.5 was chosen after examining the Kappa statistics (Cohen 1960). Suitable habitats were defined as areas with a certain environmental condition under which the chance of occurrence or dominance of a target species was higher than that in other areas (Matsui et al. 2007).

Computation of suitable habitats under hypothetical climate change scenarios

The prediction of suitable habitats for *F. crenata* forests under hypothetical climate change scenarios was computed as follows. Temperature was either

decreased by as much as 2°C or increased by as much as 7°C, and precipitation was either decreased by up to 50% or increased by up to 50% from a baseline climate (Anon. 1996). The baseline climate was the monthly mean values between 1953 and 1982 for temperature and between 1953 and 1976 for precipitation (Anon. 1996) because this time-frame is consistent with that for the construction of the vegetation data (Anon. 1999). The baseline monthly temperature was then varied between -2°C and +7°C with an interval of 1°C, and monthly precipitation was varied between -50% and +50% with an interval of 10%. This resulted in 10×11 combinations of temperature and precipitation. These 110 combinations of climatic patterns cover 99.86% of the combination of changes in temperature and precipitation from the baseline year of the 1980s to the years between 2001 and 2010 and the years between 2081 and 2090, which were projected by 38 climate model simulations assessed in IPCC-AR4 (18 simulations for the SRES-A2 scenario and 20 simulations for the SRES-B1 scenario) (Fig. 2). We chose SRES-A2 and SRES-B1 scenarios because the amounts of greenhouse gas emissions were hypothesized to be the highest and the lowest, respectively (Takahashi et al. 2008).

Most of the temperature changes were between -1°C and +6°C, and precipitation changes were between -40% and +50%. The cases with temperature changes in excess of +6°C were only 0.05% of the total, and those with precipitation changes in excess of +50% were only 0.15% of the total.

If the ranges of temperature and precipitation used in the simulations are far beyond the permissible range for the ENVI model, the results of the simulation will be less reliable. Our preliminary examination showed that the temperature change range between -2°C and +7°C and precipitation change range between -50% and +10% had been encompassed during the construction of the ENVI model. Moreover, *F. crenata* generally prefers moist conditions (Fang & Lechowicz 2006). Thus, we considered that higher precipitation changes of as much as +50% would be applicable to the model simulations.

These 110 climatic datasets were used with the distribution model, ENVI (Matsui et al. 2004b), to predict the potential probability of occurrence of *F. crenata* forests under each dataset. After the computations, grid squares with the probability of occurrence of *F. crenata* forests larger than or equal to 0.5 were extracted and designated as suitable habitats.

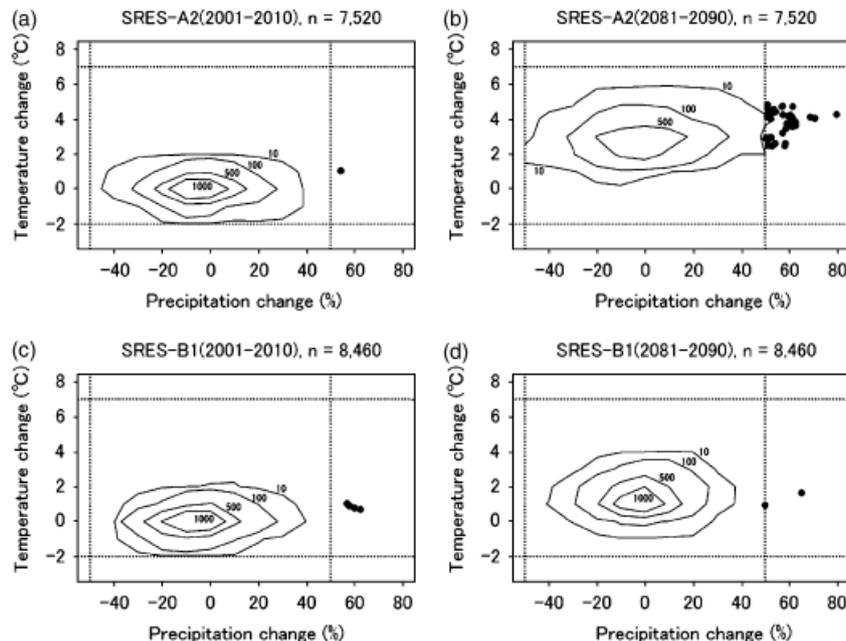


Fig. 2. (a, b) Predicted changes in annual mean temperature (°C) and precipitation (%) under the 18 General Circulation Models (GCMs) for the SRES-A2 emission scenarios in the years between 2001 and 2010 (a), and between 2081 and 2090 (b) for each of Japan's 47 prefectures. (c, d) Twenty GCMs for the SRES-B1 emission scenarios for the years between 2001 and 2010 (c), and between 2081 and 2090 (d) for each of Japan's 47 prefectures. Areas enclosed by dashed lines represent the range of temperature and precipitation changes, which were simulated in this study. Outliers are shown as dots to improve the information content of the figures, otherwise contour lines indicate the density of the dots.

In this study, we assumed that summer and winter precipitation always changed with the same ratio during the simulation timeframe. However, this may reduce the utility of the results, since actual climate changes are likely to violate it with changes in seasonal circulation patterns. Takahashi et al. (2008) examined the sensitivity of the model to the relaxation of this assumption by comparing the areas of suitable habitats between before and after co-varying summer and winter precipitations. They found that co-varying summer and winter precipitation resulted in slight overestimation of the areas of predicted suitable habitats in each prefecture (see Fig. 4a and f of Takahashi et al. 2008). It would be possible to obtain more detailed simulation results if summer and winter precipitation varied independently of each other; however, for this purpose, $10 \times 11 \times 11$ simulations would be required. For the present study, the simplified assumption was preferred in order to keep the dimensionality of the inputs at a low level.

Preparation of migration filters

Studies that predict the potential impact of future climate change on biodiversity usually consider two scenarios regarding the ability of species to track the changing conditions: either unlimited or no dispersal (Pearson 2006). This study assumed three types of conditions in terms of *F. crenata*'s migration: (1) species can migrate into all the predicted suitable habitats in the future (free migration); (2) species can migrate into the neighbouring grid squares only (limited migration); and (3) species can only persist within the currently established grid squares (no migration). According to these three assumptions, spatial filters were built to fulfil the requirement of each condition.

Net species colonization at northern boundary ranges, which are necessary for a northward shift and for range conservation, may be hampered because of habitat fragmentation (Honnay et al. 2002). Thus, for the limited migration option, a spatial filter was built on GIS, which allows range expansions of *F. crenata* only within the eight neighbouring grid squares. Furthermore, if the percentage of land use by any anthropogenic activities, such as vegetable-growing fields, residential areas or forest plantation, exceeded 50% within a single grid square this grid square was assumed to have no chance of *F. crenata* range expansion in the future. For the calculation of the areas occupied by anthropogenic activities, a GIS-based 1/50 000 polygon vegetation map in the Natural Environment Information GIS dataset was

used, which was prepared by the Japan Integrated Biodiversity Information System (Anon 1999).

Fagus crenata forests establish primarily in the mountains and, thus, spatial filters of anthropogenic activities do not always significantly influence the migration of the forest in many parts of the nation. However, in northern Japan, especially in Hokkaido, *F. crenata* forests establish from the lowlands to the middle part of the mountains. Thus, the anthropogenic filter is still appropriate for its use. After application of the three different filters, the number of grid squares considered for the analysis was 345 167 for the free migration option (the same number as the original), 42 947 for the limited migration option, and 23 432 for the no migration option.

After the simulations, predicted distributions of suitable habitats, diagrams of isopleths for the relative areas of suitable habitats and maps showing the number of times each grid square was assigned as a suitable habitat during the 110 simulations were used to help interpret the results.

Results

The 110 simulations showed that both the temperature and precipitation affected the magnitude of changes in the suitable habitats of *F. crenata* forests (Fig. 3). The changes in the numbers of ca. 1-km² grid squares assigned as suitable habitats showed that increased temperature with decreased precipitation decreased the total areas of suitable habitats at a higher rate (Figs 3 and 4). These trends are relatively easy to observe by studying hypothetical simple climate change trajectories shown by arrows in Fig. 4. For example, in the case of the arrows marked A in Fig. 4, a maximum temperature change of 4°C with a precipitation change of -40% resulted in decreases of suitable habitats to <10% under the three migration scenarios. However, even when the temperature increased, reductions in the areas of suitable habitats were slightly less severe if the precipitation increased significantly at the same time. In the case of the arrows marked B in Fig. 4, a temperature change of 4°C with a precipitation change of +40% resulted in decreases of suitable habitats to ca. 30% under the free migration option, to ca. 20% under the limited migration option and to ca. 10% under the no migration option. Moreover, if the temperature increased less and the precipitation slightly more, the areas of suitable habitats did not generally change much. In the case of the arrows marked C in Fig. 4, a temperature change

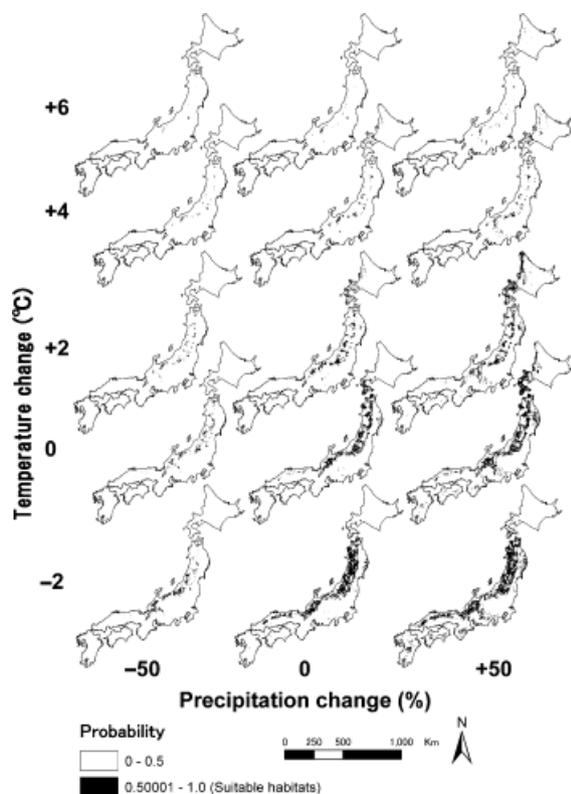


Fig. 3. Examples of predicted probability distributions for *Fagus crenata* forests under the 110 hypothetical climate change simulations. Suitable habitats (probability ≥ 0.5) are represented as red squares. The map projection is Lambert Conformal Conic.

of 2°C with a precipitation change of +50% resulted in decreases in the areas of suitable habitats of <10% under the free migration option, but as much as ca. 30% under the limited migration option and as much as ca. 40% under the no migration option. If the temperature increased in excess of 6°C, suitable habitats were reduced to less than ca. 10% under any precipitation change and any filtering conditions.

If the temperature decreased, the results differed considerably depending on the migration options and precipitation changes. In the case of the arrows marked D in Fig. 4, a temperature change of -2°C with a precipitation change of -20% resulted in decreases of the areas of suitable habitats of >90% under the free migration option, of >70% under the limited migration option and of >60% under the no migration option.

As a result of the 110 climate change simulations, some grid squares were assigned as suitable habitats more frequently than others (Fig. 5). Some grid squares were the most frequently assigned as suitable habitats for 56/110 times in the simulations.

Similarly, the number of grid squares assigned as suitable habitats for more than or equal to 51/110 times was 180/345 167 (0.05%) under the free migration options (Fig. 6), 155/42 947 (0.3%) under the limited migration option and 79/23 432 (0.3%) under the no migration option (Table 1). These grid squares were distributed primarily in the high mountains on the Sea of Japan side of Honshu (Fig. 6). The elevation and standard deviation of the 180 grid squares were 1138 ± 308 m. The distributions were especially distinct in the areas of Gassan, Okutadami, the northern Hida Mountains and Hakusan under the no migration option. For the Shirakami Mountain World Natural Heritage, the number of grid squares in the area assigned as suitable habitats was 30 ± 5.4 (mean \pm SD) out of 110 simulations.

In contrast, there were 1267 *F. crenata* forest squares that none of the simulations assigned as suitable habitats for *F. crenata* forests (Figs 5c and 7). These areas were mainly distributed in the Kanto region, Kii Peninsula, Shikoku, and Kyushu (Fig. 7). Areas on the Sea of Japan side showed a relatively small number of *F. crenata* forest squares regardless of the extent of the forests in the areas.

Discussion

Usefulness and uncertainties of suitable habitat prediction under climate change scenarios

The methods used in this study showed the importance of using the whole range of climate change scenarios for the risk assessment of habitat shifts on plant species. The uncertainties of future habitat predictions for plants were highlighted by the isopleth maps of area changes in suitable habitats (Fig. 4) as well as the predicted suitable habitat distribution maps (Fig. 5). These uncertainties depended on the variability of climate change in the future. For example, even if the temperature rise reduces the areas of suitable habitats, simultaneous increases in precipitation can mitigate the negative impact.

Unlike previous studies, the number of hypothetical climate change scenarios in the present study was sufficiently large to cover the whole range of climate change in the near future. For example, although Thuiller (2004) projected the future potential habitats of 1350 European plant species for the year 2050, the number of climate change scenarios used was five. Box et al. (1999) used 12 climate change scenarios for 124 native woody plant species in Florida. Matsui et al. (2004b) and Tanaka et al.

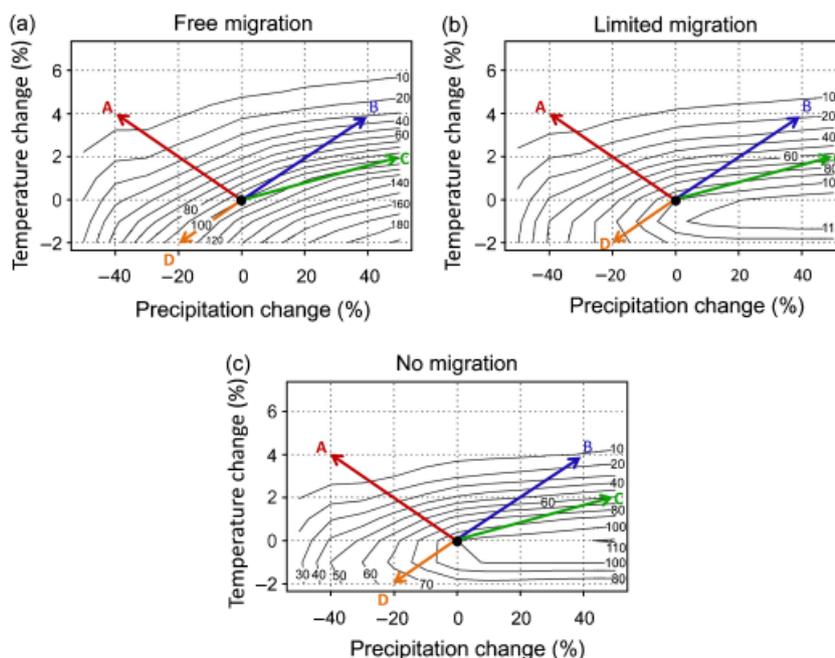


Fig. 4. Climate change impact function for suitable habitats for *Fagus crenata* forests in Japan under the three migration options (a-c). The isolines represent the magnitude of changes (%) in the areas of suitable habitats under different combinations of temperature and precipitation changes. A black closed circle (coordinate: 0, 0) represents the position of the current climatic (neither temperature nor precipitation changes). Arrows A to D show the hypothetical directions of climate changes.

(2006) applied only two climate change scenarios for the habitat shift of *F. crenata* forests in Japan either between 2081 and 2100 (RCM20; Anon. 2004) or between 2091 and 2100 (CCSR/NIES; Yokozawa et al. 2003). Therefore, the method applied in the present study is unique.

Identifying sustainable suitable habitats for F. crenata forests

The importance of the application of the predictive modelling of species distribution to conservation under the threats of climate change has increased (Rodriguez et al. 2007), yet there are not many examples using modelling techniques to identify possible reserves under different climate change scenarios. We here attempted to identify relatively sustainable suitable habitats for the survival of *F. crenata* forests under a wide range of climate change scenarios. We believe that the simulation used in the present study successfully detected such habitats by counting the number of times each one of the 110 simulations assigned each grid square as a suitable habitat or not. Although the maximum number of such habitat sustainability was 56 out of 110, some trends could still be observed. In other

words, these areas mainly distributed on the Sea of Japan side of Honshu (the Gassan region, the Okutadami region, the northern Hida Mountains and the Hakusan region; Fig. 6). We could argue that those areas have a relatively higher probability of remaining potential refugia for *F. crenata* forests under the ongoing climate change systems.

Identifying vulnerable F. crenata forests

Matsui et al. (2004b) detected vulnerable *F. crenata* forests under the CCSR/NIES (IS92a; Yokozawa et al. 2003) climate change scenario in the 2090s by calculating the reciprocal number of distribution probabilities for each grid square. In the present study, however, grid squares that were never assigned as suitable habitats during the 110 simulations were considered vulnerable *F. crenata* forests. We believe this was an alternative approach to identify vulnerable forests to climate change. This approach has the advantage of taking into account a variety of climate change scenarios and encompassing the risks of the uncertain consequences of climate change in the future. The main differences between the two approaches were that the approach used in the present study identified much less

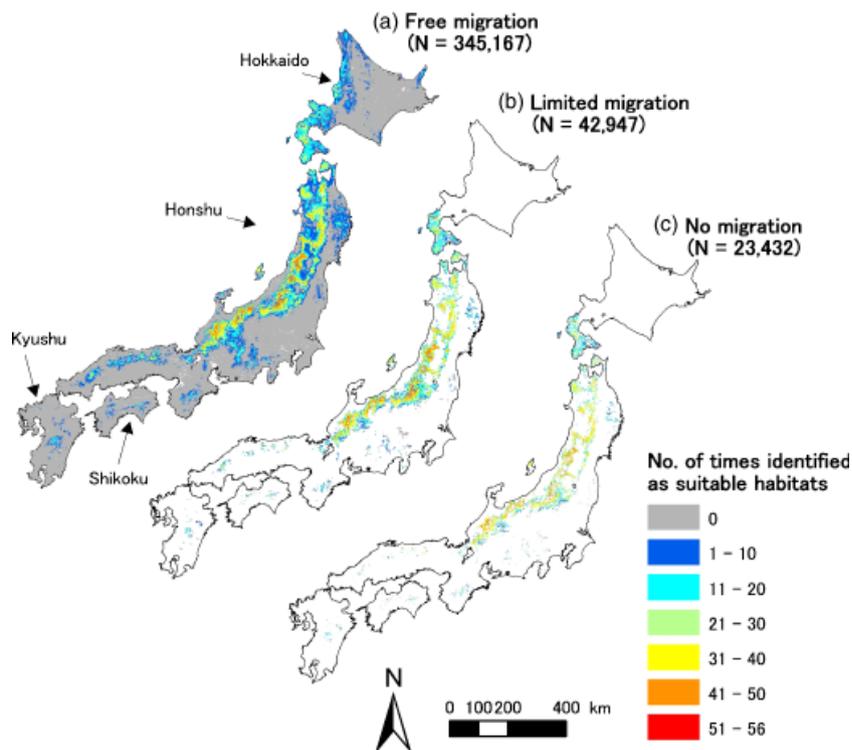


Fig. 5. Number of times for each grid square to be assigned as a suitable habitat for *Fagus crenata* forests under the 110 hypothetical climate change scenarios for each of the three migration options (a-c). The map projection is Lambert Conformal Conic.

vulnerable *F. crenata* forests in southern Hokkaido than that used in the study by Matsui et al. (2004b). A large proportion of vulnerable *F. crenata* forests in the present study were found in Kyushu, Shikoku and the Pacific Ocean side of Honshu (Fig. 7). The *F. crenata* forests in these regions are mainly distributed on the summit part of mountains, and this phenomenon is considered to be the result of the upward/northward shift of the vegetation since the beginning of Holocene ca. 12 000 year ago. *Fagus crenata* in these regions, especially in Kyushu, often co-occurs with evergreen broad-leaved trees, such as *Quercus acuta*, or conifers, such as *Abies firma* (Nishio & Hukusima 1996). For example, on Mount Shibi in south-western Kyushu, in which the westernmost populations of *F. crenata* are distributed, the populations established mainly on the north-western slope of the mountain, and the south-eastern slope supports *Q. acuta* and *Quercus salicina* (Mizunaga 2005). For the southernmost *F. crenata* population in the Takakuma Mountains in southern Kyushu, the tree ring growth was found to be declining, and it was speculated that recent climate warming has hindered the growth of the trees (Mizunaga et al. 2005). On Mount Tsukuba in northern

Kanto, *F. crenata* trees grow only around the summit part of the mountain, and *Q. acuta* grows under the *F. crenata* forest canopy (N. Tanaka, pers. obs.). The lower part of *F. crenata* forest zone in those areas often co-occurs with *F. crenata*, evergreen *Quercus* spp. or conifers, such as *A. firma*, all of which grow in a lower (warmer) forest zone than *F. crenata* forests.

The regeneration of *F. crenata* on the Pacific Ocean side (which is less snowy) is considered sporadic (Shimano 2006), and climate change would delay the timing of snowfall and reduce snow accumulation (Inoue & Yokoyama 2003). This will affect *F. crenata* regeneration (Shimano 2006) and, accordingly, it would be difficult to conceive that *F. crenata* forests on the Pacific Ocean side will be sustainable under climate warming scenarios. In particular, since the genetic diversity of *F. crenata* is greater on the Pacific Ocean side than on the Sea of Japan side (Tomaru et al. 1998; Fujii et al. 2002), the loss of genetic diversity for the species provides reason for concern.

These predicted circumstances are similar to those in the *Fagus hayatae* forests in Taiwan (Hukusima et al. 2005) or in the *Fagus grandifolia*

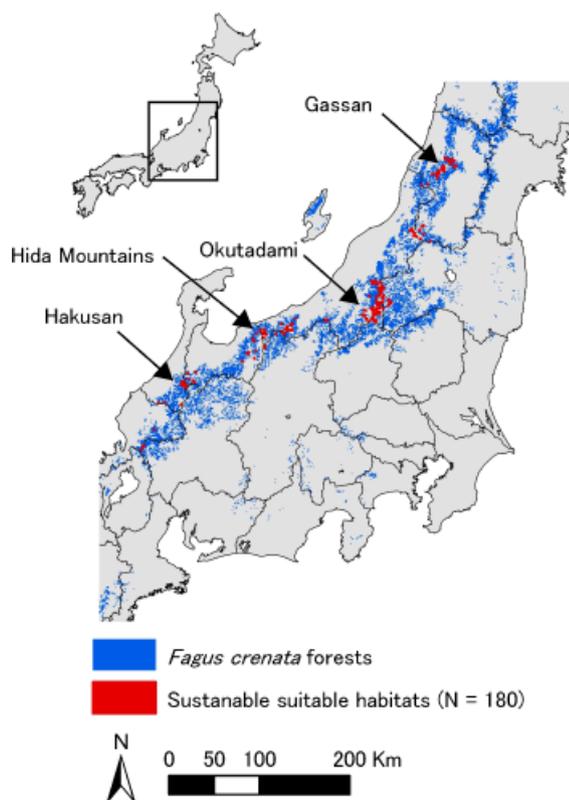


Fig. 6. Locations of sustainable suitable habitats, of which the number of times identified as suitable habitats (probability of occurrence ≥ 0.5) for *Fagus crenata* forests was larger than or equal to 51 under the 110 hypothetical climate change scenarios. As a visual aid, red squares were slightly enlarged, and prefectural borders were drawn. The map is based on Fig. 5a. The map projection is Lambert Conformal Conic.

Table 1. The number of grid squares in each frequency class assigned as suitable habitats for *Fagus crenata* forests under the 110 hypothetical climate change simulations for each of the three migration options.

Frequency class	Free migration	Limited migration	No migration
0	244 070 (70.7%)	4035 (9.4%)	1267 (5.4%)
1-10	48 353 (14.0%)	7327 (17.1%)	2815 (12.0%)
11-20	25 176 (7.3%)	10 391 (24.2%)	5187 (22.1%)
21-30	13 685 (4.0%)	9310 (21.7%)	5956 (25.4%)
31-40	9331 (2.7%)	7806 (18.2%)	5544 (23.7%)
41-50	4372 (1.3%)	3923 (9.1%)	2584 (11.0%)
51-56	180 (0.1%)	155 (0.4%)	79 (0.3%)
Total	345 167 (100%)	42 947 (100%)	23 432 (100%)

var. *mexicana* forests in Mexico (Williams-Linera et al. 2003; Tellez-Valdes et al. 2006). *Fagus hayatae* grows only on mountains at the top of the mountains in north-eastern Taiwan and is on the red list

(Anon. 2007). *Fagus grandifolia* var. *mexicana* is limited to about 10 populations in a cloud forest in north-eastern Mexico (Williams-Linera et al. 2003). Although *F. crenata* forests in Western Japan distribute over much wider areas than those of *F. hayatae* or *F. grandifolia* var. *mexicana*, there is a danger that *F. crenata* in western Japan could become threatened depending on the course of future climate change.

Contributions to conservation planning

Conservation planning of natural vegetation is the process of locating, configuring, implementing and maintaining areas that are managed to promote the persistence of biodiversity and other natural values (Pressey et al. 2007). This study contributes to conservation planning by determining the best locations for *F. crenata* under likely future climatic conditions.

The results of the current study indicate the worst climate change scenarios for *F. crenata* forests; however, they also show the extent to which climate change will affect the loss of suitable habitats and how to minimize such losses. The results show that, if the temperature increases in the future by $<2^{\circ}\text{C}$, suitable habitats for *F. crenata* forests might be sustained under the free migration option. If migration of the population is not possible, then a 1°C temperature increase could be the threshold maximum temperature change value for sustaining the current geographical extent of suitable habitats for *F. crenata* forests. In western Japan in particular, *F. crenata* trees grow at the top of mountains, and so no more upward shifts are expected to take place.

Palynological evidence suggests that the northward speed of migration of *F. crenata* since the beginning of the interglacial period, ca. 12 000 years ago, was ca. 233 m yr^{-1} in northern Honshu (Tsukada 1982) and ca. $11\text{--}40\text{ m yr}^{-1}$ in Hokkaido (Igarashi 1994; Takiya & Hagiwara 1997; Kito 2003; Yagihashi et al. 2007). However, the maximum migration speed of 233 m yr^{-1} has not been confirmed in the field. Recent molecular evidence suggests that the migration rates of *F. grandifolia* in North America after the last glacial period were much slower than has previously been deduced from the fossil pollen record (McLachlan et al. 2005). This suggests a theory for *F. grandifolia* that colonization was driven by local dispersal from disjunct glacial refugia at the end of the last glacial period (Pearson 2006). This molecular evidence in North America also suggests that the migration speed of *F. crenata* was slower than previously deduced from palynolo-

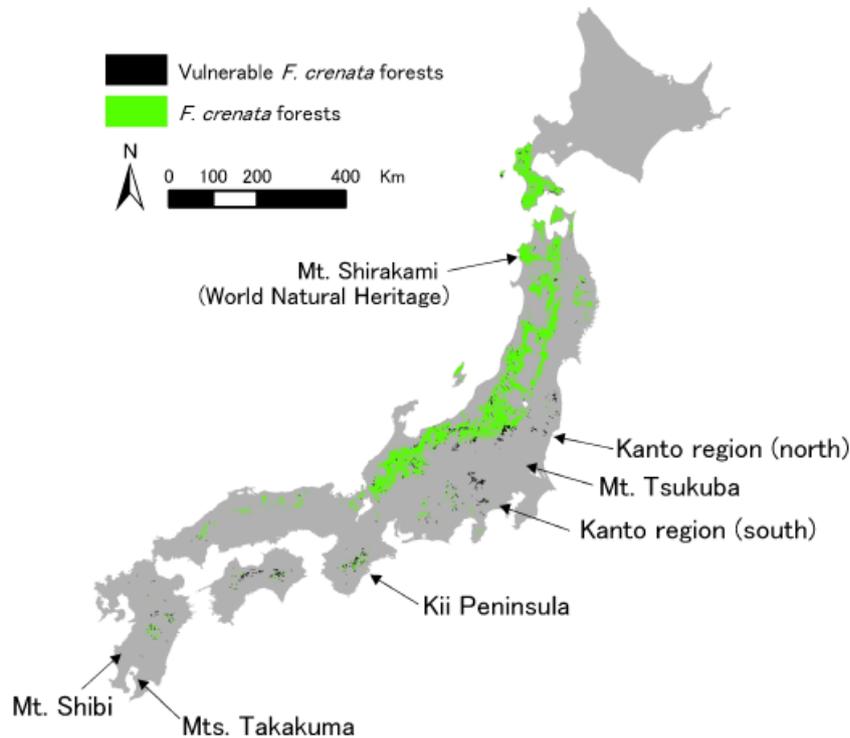


Fig. 7. Locations of 1267 grid squares of vulnerable *Fagus crenata* forests (black squares). The vulnerable grid squares were defined as the present *F. crenata* grid squares never assigned as suitable habitats (probability of occurrence ≥ 0.5) under the 110 hypothetical climate change scenarios. As a visual aid, both black and green squares were slightly enlarged. The map is based on Fig. 5c. The map projection is Lambert Conformal Conic.

gical evidence. Moreover, the number of years taken for *F. crenata* to produce nuts is estimated to be 40–50 years (Hashizume 1987; Hara 1996). Accordingly, it would be prudent to estimate that the average migration speed of ca. $11\text{--}40\text{ m yr}^{-1}$ is more realistic than 233 m yr^{-1} . Moreover, the landscape fragmentations of natural vegetation can be attributed to a multitude of anthropogenic activities. Under such circumstances, the migration speed of *F. crenata* cannot keep up with the pace of climate warming, and geographical gaps between the locations of suitable habitats and actual *F. crenata* forests will be apparent in the future.

Conclusions

The method used in this study shows the importance of using a large number of climate change scenarios for the risk assessment of habitat shifts for plant species. The risk surfaces of the suitable habitats show that precipitation decreases along with temperature increases reduced the total areas of suitable habitats. Decreases in precipitation and temperature reduce the areas of suitable habitats,

except for some cases under the free migration option. An increase in precipitation with a temperature increase of more than or equal to 2°C always reduces the areas of suitable habitats. With an increase in precipitation linked with a temperature increase of $<2^\circ\text{C}$, the areas of suitable habitats show an increase, maintenance of the status quo or a decrease, depending on the size of the increase in precipitation.

Both sustainable and vulnerable habitats for *F. crenata* forests were identified with the proposed method. The forests in western Japan were predicted to be highly vulnerable to climate change, whereas some of the high altitudes on the Sea of Japan side were predicted as possible future refugia.

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