論　文（Original article）

Current distribution and climatic range of the Japanese endemic conifer *Thuja standishii* (Cupressaceae)

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Abstract

Thuja standishii (Gordon) Carr. (Cupressaceae) is an important endemic conifer of Japan but unlike other endemic Cupressaceae species there is a general lack of information about the species including its current distribution, ecology and conservation status. This study investigated the geographic range of the species and evaluated the number of recent population extinctions using available published and online resources along with field based investigations. Additionally, the species potential range was investigated using species distribution modelling. *Thuja standishii* was found to have a wide range in Japan from 40.67° N in northern Honshu to 33.49° N in Shikoku occurring across a variety of habitats from warm temperate evergreen forest to near the alpine zone. The core of its range is in central Japan including in both high and low snow-fall mountain regions. On the other hand, the species is extremely rare in western Japan being confirmed at only eight locations including five sites in Chugoku and three in Shikoku. These include the most extreme warm-edge populations known in the species that were poorly predicted by the whole range species distribution model. These populations are of great conservation significance and either represent long term persistence in refugia isolated from the species core range in central Honshu or remnants of a formerly more widespread occurrence in the warm temperate zone of western Japan lost over millennia to human activity. Overall, the species population trajectory appears to be stable with evidence for three population losses only that occurred in the mid-20th century.

Key words: climate relicts, conservation, Japanese endemic conifer, range-losses, rear-edge population, species distribution model, *Thuja standishii*

1. Introduction

The genus *Thuja* L. (Cupressaceae) contains five extant species including three in East Asia and two in North America (LePage 2003). The genus likely evolved around 60 million years ago at high latitudes in North America with the oldest unambiguous *Thuja* fossil from the Paleocene (66 to 55 million years ago) of the Canadian Arctic (Cui et al. 2015). From its Arctic origin, *Thuja* is thought to have expanded its geographic range southwards reaching East Asia in the Miocene (Peng and Wang 2008). The three extant species of *Thuja* in East Asia are geographically restricted with *Thuja koraiensis* Nakai found in mountainous areas of the Korean Peninsula and Changbai Mountain, China, *Thuja sutchuenensis* Franchet is confined to the Daba Mountains of southwest China and *Thuja standishii* (Gordon) Carr. is endemic to Japan. All three Asian species are of conservation concern due to past logging with *Thuja sutchuenensis* classified as Endangered, *Thuja koraiensis* as Vulnerable and *Thuja standishii* as Near Threatened (IUCN Red List of Threatened Species; www.iucnredlist.org). The distribution, ecology and genetic diversity of both *Thuja sutchuenensis* and *Thuja koraiensis* have been relatively well studied (Yang et al. 2009, Liu et al. 2013, Tang et al. 2015, Hou et al. 2018). By contrast, *Thuja standishii* has received little research attention with basic information on the limits of its geographical range, reproductive biology, impact of past logging and phylogeography lacking. This general paucity of knowledge of the species is exemplified by the fact unlike the other two Asian species the overall population trend is classified as unknown (Carter and Farjon 2013).

Thuja standishii (kurobe or nezuko in Japanese and Japanese arbor-vitae in English) is distributed on the islands of Honshu and Shikoku and across its range can grow as a multi-stemmed shrub under 1m tall to a tree 35 m in height (Eckenwalder 2009) (Fig. 1). The species can purportedly reach a great age with trunks reaching up to 3 m in diameter (http://www.rinya.maff.go.jp/tohoku/introduction/gaiyou_kyoku/annai/midokoro/midokoro_sennenkurobe.html). It is most closely related to the Chinese endemic *Thuja sutchuenensis* while the geographically closest member of the genus, *Thuja koraiensis*, is phylogenetically closer to the North American *Thuja plicata* (Li and Xiang 2005). Macrofossil evidence shows that *Thuja standishii* has occurred continuously in Japan for at least the past four million years

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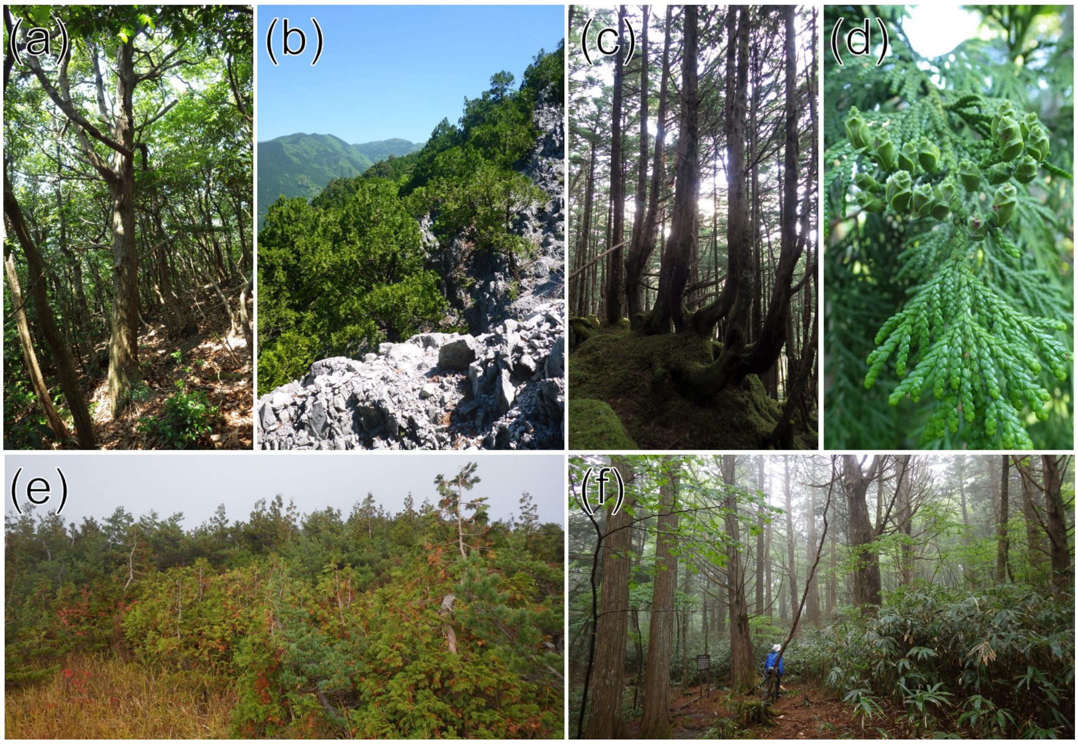

Fig. 1. *Thuja standishii* in its natural habitat.
(a) Single stemmed individual (centre) in warm temperate evegreen forest at Mt. Hanataka at 515 m a.s.l., Shimane Prefecture; (b) *T. standishii* dominated forest on limestone at Monobe Valley (590 m a.s.l.), Kouchi Prefecture; (c) A large multi-stemmed individual in rocky *Tsuga diversifolia* dominated subalpine forest at 2050 m a.s.l. in the Yatsugatake Mountain Range; (d) Close up of the foliage and immature female cones of *T. standishii* at 520 m a.s.l. on Washigamine Peak, Dogo Island, Shimane Prefecture; (e) Short multi-stemmed thicket of *T. standishii* with *Pinus parviflora* at Sanpouiwa Peak (1700 m a.s.l.), Gifu/ Ishikawa Prefecture border; (f) Tall single stemmed mixed forest of *T. standishii* (centre and right) and *Chamaecyparis pisifera* (left) at Atebi Daira (1200 m a.s.l.), Nagano Prefecture.

(Momohara 2016) and that it occurred near sea level during the colder and drier Last Glacial Maximum in Tohoku (Suzuki 1991) and the Japan Sea side of Honshu (Kamoi et al. 1988) as part of the subalpine conifer forests that dominated Honshu in lowland areas at this time (Takahara et al. 2000).

In Japan, *Thuja standishii* is rarely used in cultivation and has undergone little selection of cultivars (Eckenwalder 2009) unlike the two North American species. The species is also not used in plantations probably because of its slow growth (Debreczy et al. 2011) and its wood quality does not surpass that of the widely planted Japanese cypress (*Chamaecyparis obtusa*) (Nakagawa 1994). However, the wood is resistant to decay (Hirose et al. 1968) and in the past has been prized for use in ceilings, fanlights and furniture (Kurata 1971). Wood artefacts from the Edo Period of Tokyo show that it was used for coffins (Suzuki and Noshiro 2006), stakes, furniture (Matsuba 1999) and sewer construction (Suzuki and Noshiro 2008) but was always a very minor species compared to other conifers (Matsuba 1999, Suzuki and Noshiro 2008). Overall, the rarity of forest dominated by *Thuja standishii* and its insignificant role in forestry probably underlies the lack of research into the species compared to other endemic Cupressaceae conifers of Japan, especially the widely planted plantation conifers *Cryptomeria japonica* and *Ch. obtusa*.

In central Honshu and Tohoku, *Thuja standishii* is known to occur in mountainous areas where it grows in coniferous forest with almost all conifer species that are found within its range (Debreczy et al. 2011) including *Ch. obtusa*, *Ch. pisifera*, *Cr. japonica*, *Pinus parviflora*, *Sciadopitys verticillata*, *Tsuga diversifolia* and *Thujopsis dolabrata*. At higher altitudes the species forms part of the subalpine vegetation to 2400 m in elevation around the edges of rocky summits, near lakes and on highland moors (Kurata 1971) (Fig. 1e). The species is resilient to snow and is common in the snowy mountains on the Japan Sea side of Honshu forming an important part of upper subalpine forests (Gansert 2004). However, the species is extremely rare in western Japan with records from the Kii Peninsula, Chugoku and Shikoku only (Hayashi 1960) but its distribution in these areas is poorly understood. For example, in Shikoku, Hayashi (1960) mapped the species as occurring in five areas but only two of these (Mt. Higashiakaishi and Monobe Valley) are confirmed by vegetation mapping (Biodiversity Center of Japan, http://www.biodic.go.jp). Also, unlike Honshu, few herbarium records of *Thuja standishii* from Shikoku are available.

Understanding past range contractions of the species is difficult because the species' pollen is very difficult to distinguish from other genera of the Cupressoideae subfamily which in Japan also includes *Chamaecyparis, Juniperus* and *Thujopsis* (Takahara and Kitagawa 2000). Also, macrofossils of *Thuja standishii* are extremely rare, with the youngest known from the Last Glacial Maximum of lowland eastern Honshu at only two sites (Kamoi et al. 1988, Suzuki 1991). Nevertheless, there is evidence of some range loss in the 20th century with the species considered to have become extinct in at least two prefectures (Japanese Red Data Database; http://jpnrdb.com/).

This paper aims to provide some fundamental information about the present distribution and climatic range of *Thuja standishii* which is vital for the future study of the ecology, reproductive biology and genetic diversity of this important Japanese endemic conifer. Specifically, this study aims to (1) investigate the current distribution of the species, with a particular focus on the limits of its range, especially in western Japan; (2) examine the species' climatic range in terms of temperature (3) understand its potential climatic range using species distribution modelling; and (4) summarise available evidence for 20th century range losses due to logging or other human disturbance.

2. Materials and Methods

2.1 Present range of Thuja standishii

The present range of *Thuja standishii* was investigated by searching online resources, published literature, using personal records and records obtained upon request from other researchers. Online resources consisted of records from a database of herbarium specimens from across Japan called Science Museum Net (Snet) (http://science-net.kahaku.go.jp) and records from flora descriptions of national forest reserves, scientific papers and hiking blogs where the species location could be accurately determined using mapped locations and/or georeferenced photos. For records from hiking blogs, records were checked by comparing to vegetation maps provided by the Biodiversity Center of Japan (http://www.biodic.go.jp). Snet records were deleted if they had two or less decimal places for either latitude or longitude, sample location names did not match their actual geographic position or the record was located within a water body. In addition, the distribution of vegetation dominated or co-dominated by *Thuja standishii* was examined by extracting polygons of all vegetation types whose names included the Japanese name of *Thuja standishii* from 1 to 50,000 vegetation maps provided in shapefile format by the Biodiversity Center of Japan using a script in R (R Core Team 2014).

2.2 Species distribution modelling

The spatial distribution model of *Thuja standishii* under current climate was modelled using Maxent version 3.4.1 (Phillips et al. 2006). This program produces a continuous output of habitat suitability values ranging from 0 to 1 where 0 is least suitable and 1 is most suitable (Gogol-Prokurat 2011). Default settings were used except for using a random seed and implementing 10 replicates. In order to investigate the most informative climatic variables for *Thuja standishii* to use in model testing, the permutation importance and percent contribution of all 19 bioclim variables (Hijmans et al. 2005) at a spatial resolution of approximately 30 seconds (0.93 x 0.93 km at the equator) were evaluated in preliminary Maxent runs using 618 distribution data points (162 when duplicates within each climate layer pixel were removed) using two approaches. The first approach identified the most important bioclim variables by retaining those variables that had both permutation importance and percent contribution scores of 3% or above (from the average of 10 replicates) (following the approach of Radinger and Wolter 2015) which resulted in four best variables (bioclim 4 models) (isothermality (bio 3), maximum temperature of the warmest month (bio 5), mean temperature of the warmest quarter (bio 10) and annual precipitation (bio 12)). The second approach comprised ranking the importance of each bioclim variable separately for both permutation importance and percent contribution (with a higher score meaning greater importance) and then a sum of these values for each bioclim variable was calculated (based on the approach by Acosta and Vergara 2013). The best eight variables (bioclim 8 models) which had a sum of 23 or more were retained (mean diurnal range (bio 2), bio 3, bio 5, minimum temperature of the coldest month (bio 6), bio 10, bio 12, precipitation of the driest month (bio 14) and precipitation seasonality (bio 15)). To address potential issues of sampling intensity bias which could impact the accuracy of modelling results (Boria et al. 2014), the 618 distribution records were thinned using SpThin (Aiello-Lammens et al. 2015) implemented in R (R Core Team 2014) with 10 repetitions and spatial thinning (i.e. the distance by which samples are separated by) of 2, 5 and 10 km, respectively. Modelling runs to determine the best overall model were then undertaken in Maxent using all 19 bioclim variables (bioclim 19 models), the bioclim 8 models and the bioclim 4 models, and species records with and without spatial thinning. The best models of the 12 tested were assessed using the Akaike information criteria (AIC), sample size corrected Akaike information criteria (AICc) and the Bayesian information criteria (BIC) approach implemented in ENM Tools 1.3 (Warren et al. 2010) of which the AICc criteria has been shown to have the best average performance in model selection (Warren and Seifert 2011).

In order to examine the habitat suitability modelled for *Thuja standishii* by geographic region, habitat suitability values for each of the four best models were extracted in QGIS 3.02 using the distribution records spatially thinned in SpThin (Aiello-Lammens et al. 2015) to exclude records closer than 1 km apart (resulting in 141 records). The 10th percentile of training presence threshold was used as a threshold for predictions of presence or absence of suitable habitat. This threshold sets as a threshold the value that excludes 10 percent of localities that have the lowest predicted values and should not be as sensitive to particular extreme localities as using the lowest presence threshold (Radosavljevic and Anderson 2014).

2.3 Analysis of the temperature range of Thuja standishii

In order to examine the temperature range of *Thuja standishii* across its whole distribution, mean temperature of the warmest quarter (bio 10) and mean temperature of the coldest quarter (bio 11) values were extracted in QGIS 3.02 using the 141 spatially thinned records. The temperature range of *Thuja standishii* was compared to the temperature range of alpine (represented by *Pinus pumila* and high mountain short shrubland vegetation types), subalpine forest (*Abies vietchii*, *A. mariesii*, *Betula ermanii* and *Tsuga diversifolia*), cool temperate broadleaf forest (*Fagus crenata* and *Quercus crispula*) and warm temperate evergreen forest (*Castanopsis sieboldii* and *Quercus salicina*) vegetation types extracted from the 1 to 50,000 vegetation maps provided by the Biodiversity Center of Japan.

2.4 Documenting past distribution losses

In addition to present records, places where the species formerly occurred but have likely now become locally extinct or are unconfirmed were investigated by examining the published literature, herbarium records and the Japanese Red Data database (http://jpnrdb.com/) with the latter source recording where species have become either extinct or data deficient for each prefecture. The most important sources of past distribution information were the classic reference of tree distribution in Japan by Hayashi (1960) and Kurata (1971). In addition to literature searches, field work was undertaken to check all records of the species in western Japan recorded by Hayashi (1960) except for those in the Kii Peninsula. For all unconfirmed or potentially extinct records their present habitat suitability was estimated using the four best Maxent models (see Results below) with habitat suitability values extracted in QGIS 3.02 using a random point layer made within a 4 km diameter buffer around each point record.

3. Results

3.1 Present range

In central Honshu, *Thuja standishii* was most common in the northern Alps, Mt. Ontake area and mountain ranges of northern Yamanashi, western Saitama, Nagano, Gunma and Tochigi Prefectures (Fig. 2). The species was found to have a scattered distribution in Tohoku with a northern limit in the Hakkoda (40.67° N) and Shirakami (40.51° N) mountain ranges. The southwestern limit of the species range in central Honshu is in northern Fukui (35.86° N) and far northern Aichi Prefectures

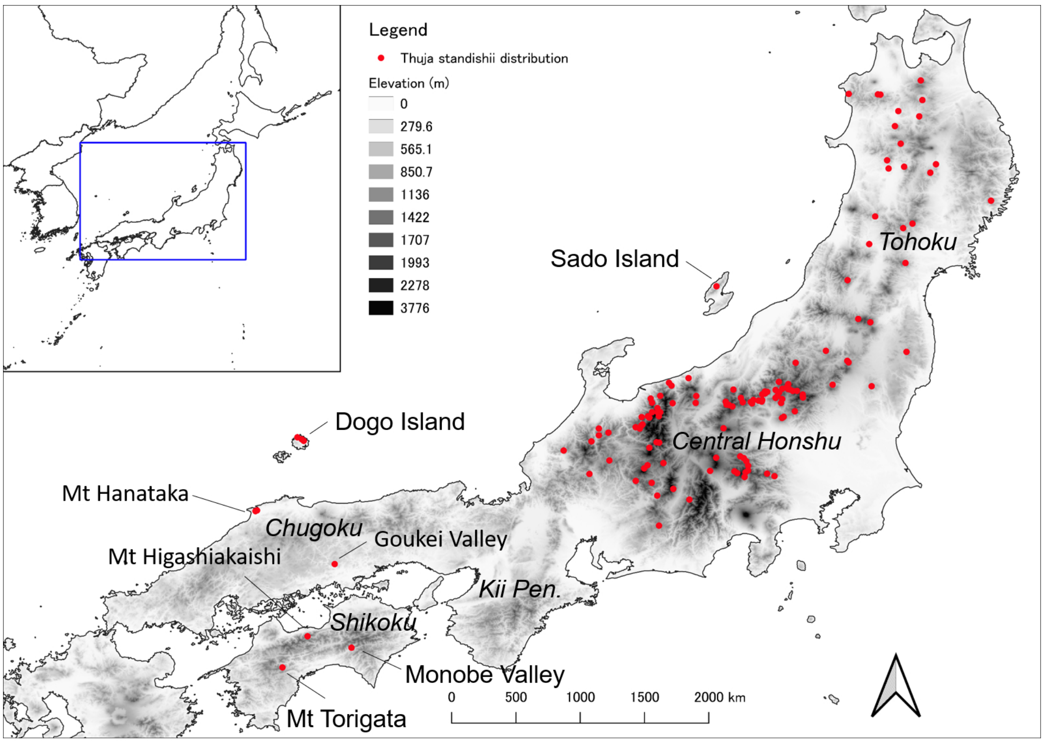

Fig. 2. The known modern range of *Thuja standishii* indicated by the red points.
A digital elevation model is also shown.

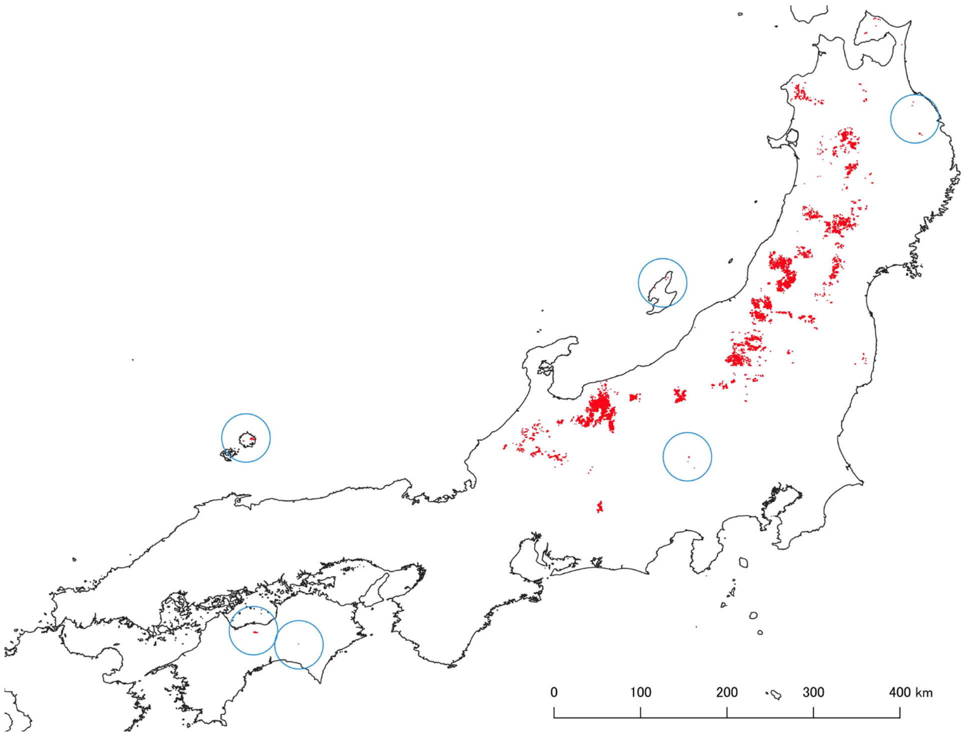

Fig. 3. Distribution of all vegetation types with a name that includes *Thuja standishii.*
Vegetation data was sourced from the Biodiversity Center of Japan (http://www.biodic.go.jp). The blue circles encircle small and disjunct mapped patches.

(35.22° N). The lowest elevation site in Honshu was at 270 m along the Nyuugawa River in a disjunct population on Sado Island, Niigata Prefecture. The map of vegetation types dominated or co-dominated by *Thuja standishii* (Fig. 3) is fairly consistent with distribution records for the Japan Sea side of Honshu but it under represents the species actual presence on the Pacific side and over represents the species actual range in Tohoku. In western Japan, the species presence was confirmed by on the ground field work at eight locations including four sites in Shimane Prefecture (three on Dogo Island in the Oki Island group and one around 100 km to the southwest at Mt. Hanataka, mainland Shimane Prefecture), Gokei Valley in Okayama Prefecture and at three locations in Shikoku (Mt. Higashiakaishi, Monobe Valley and Mt. Torigata). The latter site is the most southerly population known at a latitude of 33.49° N.

3.2 Species distribution modelling

The best model as determined using the AICc criterion was the bioclim 8 model using spatial thinning of 2 km (bioclim 8-2km) followed by all three other bioclim 8 models (Table 1). All these four models had area under the curve (AUC) values over 0.9 (Table 2) which is considered to represent 'outstanding' predictive ability (Hosmer et al. 2013). The four models had similar predictions except for the bioclim 8-10 km model which had stronger predictions for western Japan and Tohoku regions (Fig. 4). Habitat suitability was highest for Kanto, Hokuriku and Chubu regions with average values above 0.72 and moderately high values for Tohoku (above 0.48) but still well above the 10th percentile presence/ absence threshold (Fig. 4 and 5). In contrast, average habitat suitability values were low in Shikoku being between 0.12 for the best model (bioclim 8-2 km) model and 0.31 for the fourth most accurate model (bioclim 8-10km). Bioclim 8-2 km and bioclim 8-5 km model predictions were below the 10th percentile presence/ absence threshold while bioclim 8-no thinning and bioclim 8-10 km were marginally above the threshold (Fig. 5). Chugoku had average suitability values below the 10th percentile habitat suitability threshold for all four best models even when excluding the confirmed presence record at Gokei Valley (result no shown). This population had the lowest habitat suitability value of any presence record for all models (average across all four models equals 0.0014). The species is absent, or is represented by only one record, from some areas of predicted suitable habitat including the Mt. Fuji area, northwest Iwate Prefecture and the Southern Alps (Fig. 4).

3.3 Temperature range of Thuja standishii

The current distribution of *Thuja standishii* extends across a wide range of temperature with an overall range of 13.5° C for mean temperature of the warmest quarter and 14.3° C for the mean temperature of the coldest quarter (Fig. 6). When compared to the temperature range of major vegetation types of Japan (excluding Hokkaido and the Ryukyu Islands) the species range

Table 1. The results of model selection implemented in ENM tools ordered by the AICc score.

No.	Model	Log Likelihood	Parameters	AIC score	AICc score	BIC score
1	**Bioclim 8-2 km**	**-1588.74**	**24**	**3225.49**	**3235.83**	**3296.26**
2	**Bioclim 8-5 km**	**-1592.75**	**28**	**3241.50**	**3256.00**	**3324.06**
3	**Bioclim 8-no thinning**	**-1586.56**	**35**	**3243.12**	**3267.12**	**3346.32**
4	**Bioclim 8-10 km**	**-1611.60**	**21**	**3265.21**	**3272.97**	**3327.13**
5	Bioclim 4-2 km	-1621.51	15	3273.01	3276.85	3317.24
6	Bioclim 4-5 km	-1622.16	16	3276.32	3280.71	3323.50
7	Bioclim 19-10 km	-1612.19	25	3274.38	3285.68	3348.10
8	Bioclim 4-10 km	-1637.69	14	3303.38	3306.71	3344.66
9	Bioclim 4-no thinning	-1625.99	26	3303.98	3316.29	3380.65
10	Bioclim 19-no thinning	-1582.88	58	3281.75	3365.22	3452.78
11	Bioclim 19-5 km	-1587.62	61	3297.24	3392.98	3477.11
12	Bioclim 19-2 km	-1584.24	65	3298.49	3412.89	3490.16

The four best models as evaluated by AICc values are shown in bold.

Table 2. Information on the four best models including the number of records used for modelling after spatial thinning, the area under the curve (AUC) with standard deviation and the 10th percentile presence threshold under each model.

Model	No. of samples	AUC	10th percentile presence threshold
Bioclim 8-2 km	117	0.919 (0.026)	0.156
Bioclim 8-5 km	93	0.908 (0.04)	0.185
Bioclim 8-no thinning	162	0.927 (0.034)	0.169
Bioclim 8-10 km	74	0.906 (0.044)	0.206

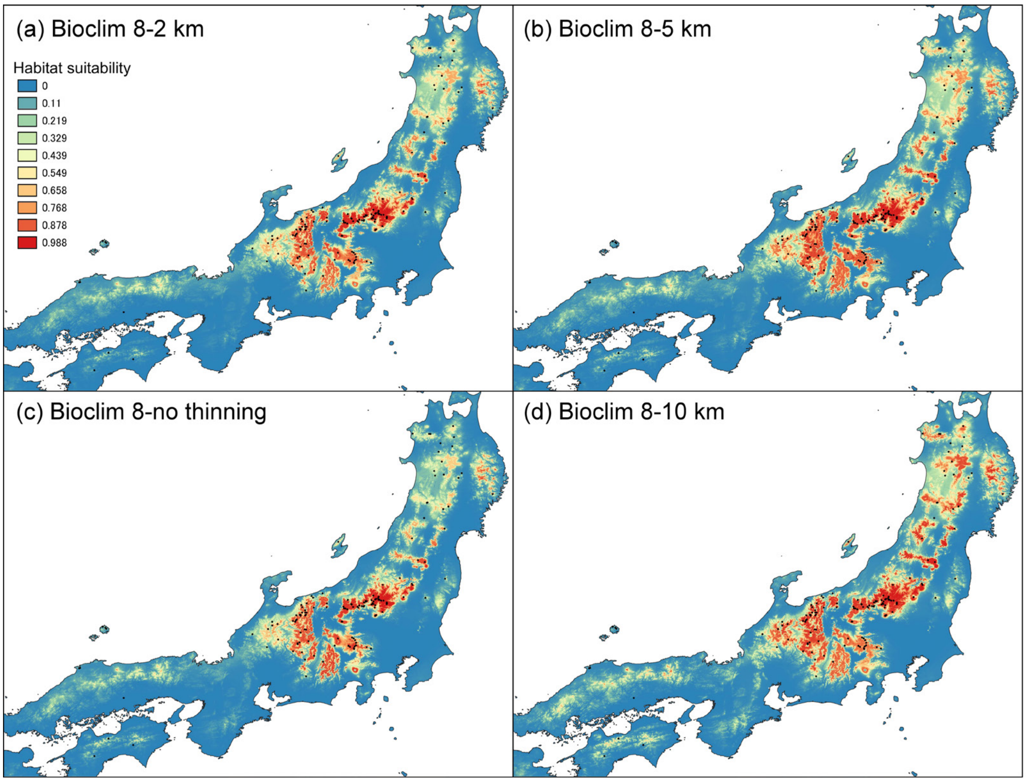

Fig. 4. The modelled present habitat suitability of *Thuja standishii* within its range under the best four models. Black dots indicate actual distribution records.

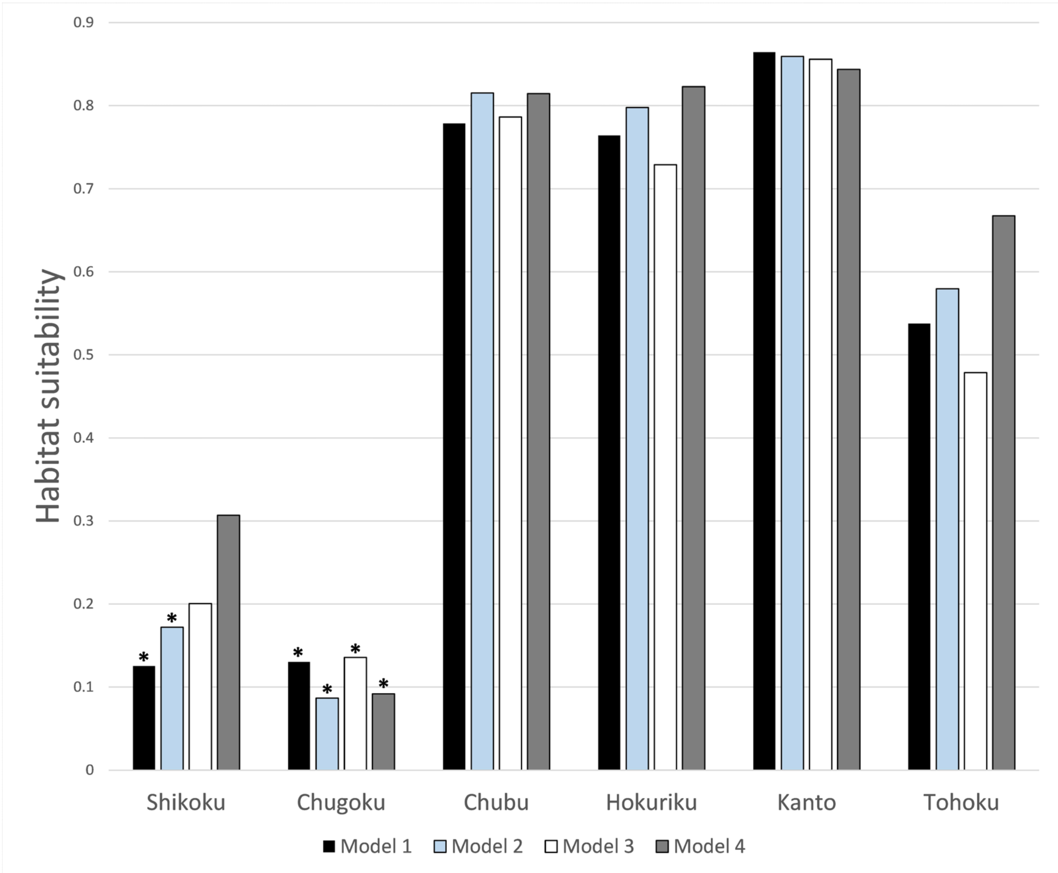

Fig. 5. The average habitat suitability predicted for *Thuja standishii* for each of the best four models displayed by geographic region.
Predictions below the average 10th percentile training presence/absence threshold value are indicated by asterix. Threshold values are as follows: Model 1 (the best 8-2 km model) = 0.156; Model 2 (the best 8-5 km model) = 0.185; Model 3 (the best 8-no thinning model) = 0.169; and Model 4 (the best 8-10 km model) = 0.206.

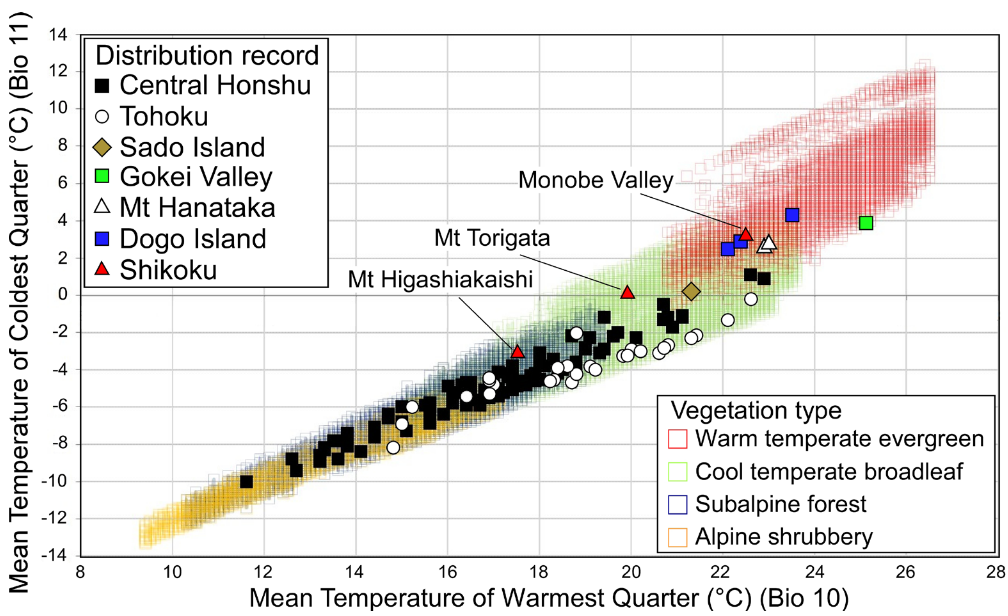

Fig. 6. The present climatic range of *Thuja standishii* shown in relation to the climatic range of the major vegetation types in Japan (excluding Hokkaido and the Ryukyu Islands).
The climatic range is depicted in terms of mean temperature of the warmest quarter (bio 10) and the mean temperature of the coldest quarter (bio 11) which clearly differentiates the major vegetation types. Each distribution record is shown with differing symbols according to their geographical origin.

occurs from near the alpine to the warm evergreen temperate zones. All but two records from central Honshu and Tohoku overlap the temperature range of cool temperate, subalpine or alpine vegetation types while all records in Chugoku occur in the warm temperate zone and the three Shikoku sites occur in subalpine (Mt. Higashiakaishi), cool temperate (Mt. Torigata) and warm temperate zones (Monobe Valley), respectively (Fig. 6).

3.4 Potential range losses and range uncertainty

Three locations where the species is no longer recorded were evidenced by herbarium specimens collected in the 1950's from Mt. Ishizuchi (Ehime Prefecture), Tawara (Tottori Prefecture) and the Tanzawa Mountains in Kanagawa Prefecture (Table 3 and Fig. 7). In addition, 10 records outside the species known range were found based on published records and the Japan Red Data online database (Table 3 and Fig. 7). Field searches in western Japan at Tawara, Mt. Shiraga (Kouchi Prefecture) and Mt. Ishizuchi were unsuccessful in relocating the species. Based on the species distribution modelling, the most suitable unconfirmed sites are in the high mountains of inland Shizuoka Prefecture recorded by Hayashi (1960) while other unconfirmed sites are lower in habitat suitability but all exceed the value of the Gokei Valley population (Table 3 and Fig. 4).

4. Discussion

Thuja standishii is widespread across 7.2 degrees of latitude with its core distribution area in the central Honshu mountain ranges while it is rarer and has a scattered geographic range in Tohoku and western Japan (Fig. 2). The species has a broad climatic range occurring from the warm temperate to near the alpine zone, forming an emergent tree above warm temperate evergreen broad-leaved forest to a krummholtz shrub co-dominant with subalpine conifers such as *Tsuga diversifolia* and *P. parviflora*. This wide ecological range is similar to other Japanese Cupressaceae species that also have wide elevational ranges (and therefore tolerances to temperature) including *Ch. obtusa*, *Ch. pisifera*, *Cr. japonica* and *Thujopsis dolabrata* (Hayashi 1960). The species occupies a diverse range of habitats that are mostly characterized by harsh environments including dry ridges or rocky mountain peaks, areas with heavy snow or exposed highland moors. *Thuja standishii* also shows resilience to waterlogging being found growing along the edge of lakes with trunks almost completely submerged in water (e.g. at Shirakoma Pond, Yatsugatake Mountain Range, Nagano Prefecture (personal observation)) and can be favoured by low nutrient geological substrates like limestone (e.g. Mt. Kurohime, Niigata Prefecture) (Shimizu 1962). Species distribution modelling of *Thuja standishii* indicates the species occupies

Table 3. Habitat suitability values from each of the four best models estimated for all 13 possibly extinct or unconfirmed distribution records of *Thuja standishii.*

				Bioclim 8-2 km		Bioclim 8-5 km		Bioclim 8-no thinning		Bioclim 8-10 km	
No.	Site	Prefecture	Record type	Average (StDev)	Max.	Average (StDev)	Max.	Average (StDev)	Max.	Average (StDev)	Max.
1	Mt. Ishizuchi[a]	Ehime	Herbarium specimen	0.26 (0.13)	0.54	0.38 (0.18)	0.71	0.39 (0.17)	0.73	0.55 (0.13)	0.73
2	Mt. Kanpu[b]	Ehime/Kouchi	Other	0.16 (0.1)	0.44	0.22 (0.15)	0.62	0.24 (0.14)	0.62	0.4 (0.17)	0.73
3	Mt. Shiraga[c]	Kouchi	Other	0.07 (0.04)	0.18	0.09 (0.06)	0.25	0.11 (0.07)	0.3	0.22 (0.12)	0.48
4	Odaigahara[c]	Nara/Mie	Other	0.07 (0.05)	0.17	0.13 (0.08)	0.29	0.13 (0.07)	0.28	0.25 (0.12)	0.43
5	Tawara[d]	Tottori	Herbarium specimen	0.27 (0.06)	0.42	0.24 (0.07)	0.42	0.24 (0.07)	0.41	0.26 (0.09)	0.51
6	Southern Fukui[c]	Fukui	Other	0.08 (0.03)	0.12	0.1 (0.04)	0.16	0.08 (0.03)	0.12	0.13 (0.07)	0.25
7	Mt. Kurohoshi[c]	Shizuoka	Other	0.67 (0.19)	0.87	0.76 (0.19)	0.91	0.79 (0.2)	0.96	0.81 (0.13)	0.92
8	Mt. Narayoyama[c]	Shizuoka	Other	0.3 (0.26)	0.86	0.36 (0.29)	0.91	0.35 (0.31)	0.95	0.45 (0.28)	0.91
9	Mt. Senzusan[c]	Shizuoka	Other	0.74 (0.17)	0.89	0.8 (0.15)	0.9	0.83 (0.18)	0.96	0.82 (0.1)	0.91
10	Mt. Tenguishi[c]	Shizuoka	Other	0.13 (0.08)	0.31	0.15 (0.1)	0.39	0.15 (0.11)	0.42	0.25 (0.15)	0.56
11	Mt. Daimugen[c]	Shizuoka	Other	0.8 (0.11)	0.91	0.85 (0.1)	0.9	0.9 (0.11)	0.98	0.85 (0.06)	0.9
12	Tanzawa Mt.s.[e]	Kanagawa	Herbarium specimen	0.29 (0.14)	0.63	0.34 (0.16)	0.73	0.28 (0.17)	0.73	0.44 (0.19)	0.82
13	Mt. Tsukuba[f]	Ibaraki	Other	0.08 (0.09)	0.27	0.1 (0.11)	0.37	0.12 (0.12)	0.39	0.1 (0.12)	0.42

For each record the average value habitat suitability value is given with the standard deviation in brackets plus the maximum value. The source of each record are provided below the table.

[a] AO-01193, Mt. Ishizuchi, Ehime Prefecture, O. Tokui 1952/07; [b] Yamazaki, S. Catalogue of tree herbarium records of Shikoku. Forestry and Forest Products Research Institute, Shikoku Branch report, pg. 53 (in Japanese); [c] Hayashi, Y. (1960) Taxonomical and phytogeographical study of Japanese conifers. Norin-Shuppan, Tokyo, Japan (In Japanese); [d] AO-01191 and AO-01192 Tawara, Mihashi-son, Tohaku- Gun, Tottori Prefecture, Y. Hayashi 1954/11/1; [e] AO-01195 North face of Mt. Komotsuri, Tanzawa, Kanagawa Prefecture, Y. Hayashi 1955/08; [f] Ibaraki Prefecture Red Data Book (Plants) (2012) pg 239 (in Japanese).

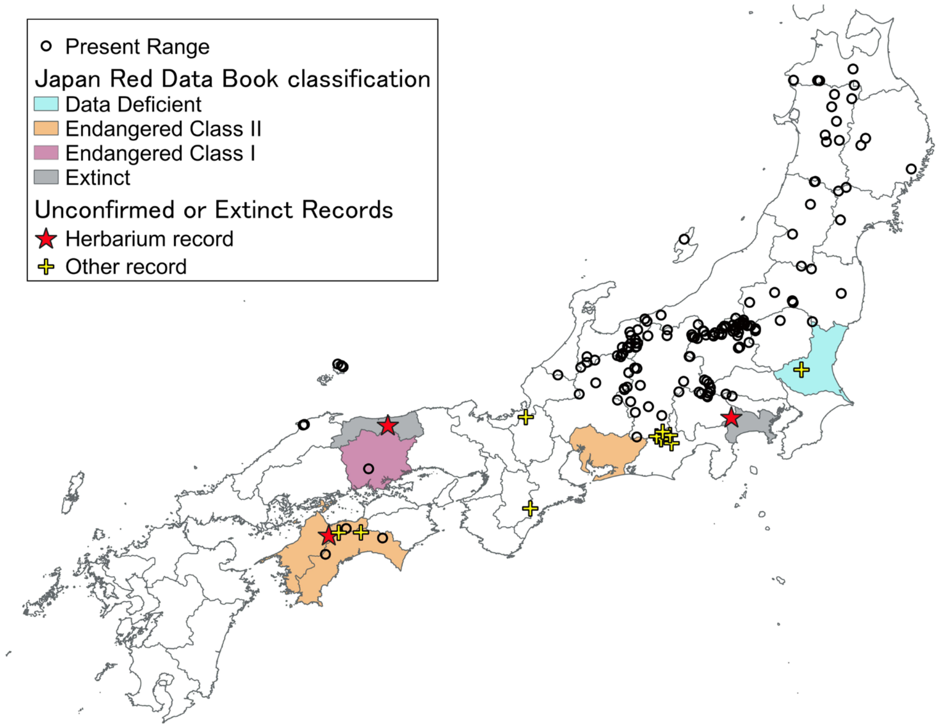

Fig. 7. The distribution of unconfirmed or extinct distribution records of *Thuja standishii* based on herbarium records or other data (for data sources see Table 3).
In the background is shown the species current conservation within each prefecture status based on the Japan Red Data book (http://jpnrdb.com/). No colour indicates that the species is not listed on the Red Data list in the prefecture.

most of its potential distribution but is over predicted in Tohoku and parts of the Pacific side of Honshu and under-predicted in western Japan (Fig. 4).

4.1 Thuja standishii in eastern Japan

Thuja standishii is common in the high snow-fall mountains on the Japan Sea side of central Honshu. The species is resilient to snow as is well demonstrated by its occurrence in high moorland such as near the Tateyama Kurobe Alpine Route (personal observation) where snow depth attains up to 3 m in winter (Nakamura and Abe 1993). In such locations the species forms large multi-stemmed patches that are possibly clonal. In Tohoku, *Thuja standishii* was confirmed to have be relatively rare and have a scattered distribution despite continuous areas of modelled suitable habitat along the regions mountain ranges. This is especially the case for the Pacific side of Tohoku with the only confirmed record at Mt. Goyo (Okuda 1968) in the Kitakami Mountain Range of northwest Iwate Prefecture. A similar finding of 'empty habitat' in Tohoku has been found for other subalpine conifers such as *Tsuga diversifolia* (Tsuyama et al. 2014) and *Abies mariesii* (Daimaru and Taoda 2004). In fact, Tohoku is recognised for the rarity of subalpine coniferous forests in the subalpine climatic zone which is instead often vegetated by dwarf bamboo, meadows or deciduous broad-leaved stunted scrub with subalpine conifers absent small patches or confined to rocky ridges (Kikuchi 1981). The factors underlying the rarity of coniferous trees in the subalpine zone of Tohoku remains unresolved but is likely to be a combination of seed dispersal limitations, heavy snow and frequent avalanches (at least on the Japan Sea side) and exposure to strong winds (Kikuchi 1981, Makita and Ogawa 1978).

On the Pacific side of Honshu the species is common in the Chichibu Mountains in Sataima and Yamanashi Prefectures. However, it is otherwise rare on the Pacific side of Honshu forming isolated populations (e.g. Mt. Yamizo and Mt. Otakine in Fukushima Prefecture). In these locations snow depth is markedly lower than the Japan Sea side at 0.1-0.5 m (Nakamura and Abe 1993) that, along with other occurrences in low snowfall areas of western Japan, demonstrates that *Thuja standishii* can by no means be considered a 'specialist' of heavy snow fall areas. Rather the species can be considered to display a high level of plasticity of habit with, for example, some populations in high snowfall areas comprised of-tall single-stemmed trees on ridges and multi-stemmed twisted shrubs on slopes with high snow accumulation (personal observation). On the Pacific side large geographic areas with no confirmed records (e.g. Mt. Fuji) or only one record (e.g. the entire Southern Alps including the mountains of inland Shizuoka Prefecture) were observed despite predicted suitable habitat. A similar absence of the dwarf conifer *P. pumila* from Mt. Fuji despite suitable modelled climate has been noted by Horikawa et al. (2009) who considered that volcanic eruptions or lack of time for dispersal from glacial populations may explain its absence. However, this explanation is hard to reconcile for *Thuja standishii* because most other subalpine and temperate conifers of central Honshu are present (Miyawaki et al. 1971). In the case of inland Shizuoka Prefecture, the absence of *Thuja standishii* is likely to be a result of insufficient sampling due to difficulty of access. Unconfirmed records from this area by Hayashi (1960) require targeted searches for confirmation (Fig. 7).

4.2 Thuja standishii in western Japan

Thuja standishii was confirmed to occur in Chugoku and Shikoku in western Japan with the most southern population at Mt. Torigata (Yamanaka 1964) rather than Monobe Valley (Hayashi 1960). The most likely area where the species occurs but was not confirmed in this study is the Mt. Ishizuchi area. Some of the records of *Thuja standishii* in western Japan are at the edge of the species climatic range (Fig. 6) and were poorly predicted by the whole range species distribution models. These include all three of the known populations of *Thuja standishii* growing within warm temperate evergreen forest at 500 m a.s.l. at Mt. Hanataka (Shimane Prefecture), Gokei Valley, at 180 m a.s.l. (Okayama Prefecture) and Monobe Valley, at 590 m a.s.l. (Kouchi Prefecture). These stands were multi-aged and had banks of juveniles in the understorey indicating continuous regeneration. These rear-edge populations may be classic examples of climate relict populations, that is, populations that have occurred *in situ* over multiple glacial cycles accumulating genetic variants adapted to the warmer climate (Woolbright et al. 2014). Their persistence is unlikely to be explained by buffering from the regional climate in cool microclimates because individual trees are not restricted to specific topographic positions or aspects. Even in the lowest altitude populations at Gokei Valley (180 m) and the Kumi Valley (45 m) on Dogo Island, where the species is mostly restricted to shaded, northern facing steep slopes, a few individuals grow exposed on ridge tops. Another hypothesis is that these populations may represent remnants of a formerly wider distribution of the species in western Japan. Agricultural history extends back at least 6,600 years (Tsukada et al. 1986) in western Japan and past logging and conversion to agriculture over millennia has resulted in a drastic reduction in the area of primary forests of this region (Biodiversity Center of Japan 2010). Around 1500 years ago, there was widespread human disturbance of natural forests across Japan as evidenced by an increase of secondary forest trees such as *Pinus* subgenus *Diploxyon* and *Quercus* in the fossil pollen record (Kitagawa et al. 2014). Conifers such as *Cr. japonica* decreased in abundance at this time due to human exploitation (Tsukada 1982) while human disturbance resulted in population extinctions shrinking the overall geographic range of some conifers such as *Sciadopitys verticillata* (Tsukada 1963). Declines in Cupressaceae pollen concomitant with increases of secondary forest trees are recorded from multiple sites in western Japan (Miyake et al. 2000, Sasaki et al. 2011) suggesting declines in Cupressaceae dominated primary forests which could have included *Thuja standishii*. It is notable that some of the *Thuja standishii* populations in western Japan are found only on nutrient poor geological substrates that would have been less attractive for clearing. For example, all three known population in Shikoku occur on serpentine geology (Mt. Higashiakaishi) or limestone (Mt. Torigata and Monobe Valley). The latter location consists of an unstable limestone rocky slope with almost no soil on which *Thuja standishii* is almost the sole tree species (Fig. 1b). Examination of fossils, if they can be found, and genetic studies (including potentially using species specific markers to distinguish *Thuja standishii* pollen using ancient DNA techniques) are required to better understand the past distribution of *Thuja standishii* in western Japan. Specifically, such studies are needed to determine whether rare populations at the warm-edge of the species range are climate relicts persisting since at least the Last Glacial Maximum or, rather, are survivors of the widespread human impacts on forests of western Japan over the last few millennia.

4.3 Possible extinctions

This study was unable to be confirm the species presence on the Kii Peninsula which is recorded by Hayashi (1960) and Kurata (1971) from the Odaigahara highland area. It is possible that the species never occurred on the Kii Peninsula as it was not described in Yatoh's (1962) description of the Cupressaceae conifers of the Kii Peninsula. Its absence is somewhat surprising given suitable modelled habitat, albeit marginal, and the fact that the Kii Peninsula's isolated high mountain ranges share almost the same suite of cool temperate and subalpine conifers as the central Honshu mountain ranges (Yatoh 1955, 1956a, 1956b, 1957, 1962) where *Thuja standishii* is common. Alternatively, the species may have become extinct due to destruction of forests from bark stripping of deer which has been severe in the Odaigahara area (Shibata 1984). The thin bark of *Thuja standishii* makes it particularly vulnerable to bark stripping (personal observation). If the species has gone extinct from the Kii Peninsula it would entail a range-loss of 180 km from the nearest populations in central Honshu.

Despite searches in this study and by others (Flora Kanagawa 2003, Tottori Prefecture 2012) it was not possible to relocate the species at Mt. Ishizuchi in Ehime Prefecture, Tawara in Tottori Prefecture and in the Tanzawa Mountains in Kanagawa

Prefecture. Particularly in the case of Tawara and Tanzawa Mountains, it is most likely that these past records represent true losses. While the Tawara population is thought to have been logged for house construction (Tottori Prefecture 2012) the cause of the Tanzawa Mountains extinction is unknown. However the potential for rediscovery cannot be discounted given that new additions are still being made to the flora of places like the Tanzawa Mountains (e.g. Tamura and Irino 2003) despite the long history of botanical study in the area.

4.4 Conclusions

Overall, this study has found that *Thuja standishii* has a wide geographic and climatic range distributed from northern Tohoku to Shikoku and occurring in warm temperate forest to the edge of the alpine zone. The species was found to occupy most of its modelled range except for parts of Tohoku, Mt. Fuji and the Southern Alps while isolated small populations in western Japan were poorly predicted. Although the current population trend is likely to be stable, ecological and genetic research is needed to ascertain why *Thuja standishii* has been vulnerable to local extinction after disturbances such as logging. The populations in Chugoku and Shikoku at the species rear- edge are of particular conservation importance as they may harbour unique genetic diversity related to their warm climate habitats. Overall, this study provides a basis for future research on the conservation and genetic diversity for *Thuja standishii*, one of Japan's most important but least understood endemic conifers.

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References

Acosta, L. E., and Vergara, J. (2013) New records and distribution modeling of *Gryne orensis* (Sørensen) (Opiliones: Cosmetidae) support the Mesopotamian–Yungas disjunction in subtropical Argentina. Zootaxa, 3736, 143-158.

Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B. and Anderson, R. P. (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography, 38, 541-545.

Biodiversity Center of Japan (2010) Biodiversity of Japan: a harmonious coexistence between nature and humankind. Nature Conservation Bureau, Ministry of the Environment. Heibonsha, Tokyo.

Boria, R. A., Olson, L. E., Goodman, S. M. and Anderson, R. P. (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecological Modelling, 275, 73-77.

Carter, G. and Farjon, A. (2013) *Thuja standishii*. *The IUCN Red List of Threatened Species* 2013:e.T42264A2968225. http://dx.doi.org/10.2305/IUCN.UK.2013-.RLTS.T42264A2968225.en. Downloaded on 09 November 2018.

Cui, Y. M., Sun, B., Wang, H. F., Ferguson, D. K., Wang, Y. F., Li, C. S., Yang, J. and Ma, Q- W. (2015) Exploring the formation of a disjunctive pattern between eastern Asia and North America based on fossil evidence from *Thuja* (Cupressaceae). PloS One, 10, e0138544.

Daimaru, H. and Taoda, H. (2004) Effect of snow pressure on the distribution of subalpine Abies mariesii forests in northern Honshu Island, Japan. Journal of Agricultural Meteorology, 60, 53-261.

Debreczy, Z., Rácz, I. and Musial, K. (2011) Conifers around the world: Conifers of the temperate zones and adjacent regions. DendroPress Budapest, Hungary

Eckenwalder, J. E. (2009) Conifers of the world: the complete reference. Timber Press.

Flora Kanagawa (2003) Kanagawa Prefecture Plant Record Investigation Society News, 55, 663-694.

Gansert, D. (2004) Treelines of the Japanese Alps-altitudinal distribution and species composition under contrasting winter climates. Flora, 199, 143-156.

Gogol-Prokurat, M. (2011) Predicting habitat suitability for rare plants at local spatial scales using a species distribution model. Ecological Applications, 21, 33-47.

Hayashi, Y. (1960) Taxonomical and phytogeographical study of Japanese conifers. Norin-Shuppan, Tokyo, Japan (In Japanese)

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology, 25, 1965-1978.

Hirose, Y., Tomita, B. and Nakatsuka, T. (1968) The isolation and structure of Nezukone. Agricultural and Biological Chemistry, 32, 249-251.

Hosmer Jr, D. W., Lemeshow, S. and Sturdivant, R. X. (2013) Applied logistic regression (Vol. 398). John Wiley and Sons.

Horikawa, M., Tsuyama, I., Matsui, T., Kominami, Y. and Tanaka, N. (2009) Assessing the potential impacts of climate change on the alpine habitat suitability of Japanese stone pine (*Pinus pumila*). Landscape Ecology, 24, 115-128.

Hou, L., Cui, Y., Li, X., Chen, W., Zhang, Z., Pang, X. and Li,

Y. (2018) Genetic evaluation of natural populations of the endangered conifer *Thuja koraiensis* using microsatellite markers by restriction-associated DNA sequencing. Genes, 9, 218.

Kamoi, Y., Saito, M., Fujita, H. and Kobayashi, I. (1988) Plant fossil assemblage of the last glacial age in the northern part of Niigata Prefecture, central Japan. The Quaternary Research, 27, 21-29. (In Japanese)

Kikuchi, T. (1981) The vegetation of Mount Iide, as representative of mountains with heavy snowfall in Japan. Mountain Research and Development, 261-265.

Kitagawa, J., Fujiki, T., Yamada, K., Hoshino, Y., Yonenobu, H. and Yasuda, Y. (2014) Human impact on the Kiso-hinoki cypress woodland in Japan: a history of exploitation and regeneration. Vegetation History and Archaeobotany, 23, 649-664.

Kurata, S (1971) Illustrated important forest trees of Japan. Chikyu-Shuppan-Sha, Tokyo, Japan

LePage, B. A. (2003) A new species of *Thuja* (Cupressaceae) from the Late Cretaceous of Alaska: implications of being evergreen in a polar environment. American Journal of Botany, 90, 167-174.

Li, J. H. and Xiang, Q. P. (2005) Phylogeny and biogeography of *Thuja* L.(Cupressaceae), an eastern Asian and North American disjunct genus. Journal of Integrative Plant Biology, 47, 651-659.

Liu, J., Shi, S., Chang, E., Yang, W. and Jiang, Z. (2013) Genetic diversity of the critically endangered *Thuja sutchuenensis* revealed by ISSR markers and the implications for conservation. International Journal of Molecular Sciences, 14, 14860-14871.

Makita, H. and Ogawa, S. (1978) On the tree line composed of beech (*Fagus crenata*) on Funakata Mountains, Miyagi Prefecture. Annals of the Tohoku Geographycal Association, 30, 182-188 (in Japanese).

Matsuba, R. (1999) Timber consumption around the Early Modern Edo Castle deduced from wooden artefacts recovered at the Tameike Site, Shiodome Site, and three Sumida-ku sites, Tokyo. Japanese Journal of Historical Botany, 7, 59-70.

Miyake, N., Nehira, K., Nakagoshi, N. and Hirayama, T. (2000) An investigation of vegetation changes by pollen analysis of forest soils. The Quaternary Research, 39, 139-150.

Miyawaki, A., Sugawara, H. and Hamada, T. (1971) Vegetation of Mt. Fuji. Fuji Kyuko Company Limited (In Japanese).

Momohara, A. (2016) Stages of major floral change in Japan based on macrofossil evidence and their connection to climate and geomorphological changes since the Pliocene. Quaternary International, 397, 93-105.

Nakagawa, S. (1994) Conifers. Hoikusha. Higashiosaka. 188pp.

Nakamura, T. and Abe, O. (1993) Estimated seasonal snow cover and snowfall in Japan. Annals of Glaciology, 18, 179-184.

Okuda, S (1968) The alpine and subalpine vegetation of Mt. Goyo, Iwate Prefecture. Memoirs of the National Science Museum, 1, 77-83 (in Japanese)

Peng, D. and Wang, X. Q. (2008) Reticulate evolution in *Thuja* inferred from multiple gene sequences: implications for the study of biogeographical disjunction between eastern Asia and North America. Molecular Phylogenetics and Evolution, 47, 1190-1202.

Phillips, S. J., Anderson, R. P. and Schapire, R. E. (2006) Maximum entropy modeling of species geographic distributions. Ecological modelling, 190, 231-259.

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2013.

Radinger, J., and Wolter, C. (2015) Disentangling the effects of habitat suitability, dispersal, and fragmentation on the distribution of river fishes. Ecological Applications, 25, 914-927.

Radosavljevic, A., and Anderson, R. P. (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. Journal of biogeography, 41, 629-643.

Sasaki, N., Takahara, H. and Yumoto T. (2011) Vegetation history of Satoyama woodlands based on pollen records from Kyoto Basin, Japan, Chikyū kankyō, 16, 115-127 (In Japanese)

Shibata, E. (1984) Damage to conifers by the sika deer (*Cervus nippon*) on Mt. Ohdaigahara. Nara Botany, 7, 1-6. (In Japanese)

Shimizu, T. (1962) Studies on the limestone flora of Japan and Taiwan (Part I). Journal of the Faculty of Textile Science and Technology, Shinshu University, 30, 1-105.

Suzuki, K. (1991) *Picea* cone-fossils from Pleistocene strata of northeast Japan. Saito-Ho-on Kai Museum of Natural History Research Bulletin, 59, 1-41.

Suzuki, S. and Noshiro, S. (2006) Materials and forms of wooden coffins of the Edo period excavated from the Sugen-ji and Shoken-ji sites, Shinjuku, Tokyo. Japanese Journal of Historical Botany, 14, 61-72. (In Japanese)

Suzuki, S. and Noshiro, S. (2008) Transition in construction timber usage and its social background in the early modern Edo period deduced from wooden remains excavated from the Nihonbashi 1-chome site, Chuo-ku, Tokyo. Japanese Journal of Historical Botany, 16, 57-72. (In Japanese)

Takahara, H., Sugita, S., Harrison, S. P., Miyoshi, N., Morita, Y. and Uchiyama, T. (2000) Pollen-based reconstructions of Japanese biomes at 0, 6000 and 18,000 14C yr bp. Journal of Biogeography, 27, 665-683.

Takahara, H. and Kitagawa, H. (2000) Vegetation and climate history since the last interglacial in Kurota Lowland, western Japan. Palaeogeography, Palaeoclimatology, Palaeoecology, 155, 123-134.

Tamura, A. and Irino, A. (2003) Newly distributed *Acer nipponicum* H. Hara in Kanagawa Prefecture. Journal of Phytogeography and Taxonomy, 51, 75-76. (In Japanese)

Tang, C. Q., Yang, Y., Ohsawa, M., Momohara, A., Yi, S-R., Robertson, K., Song K., Zhang S-Q. and He, L. Y. (2015) Community structure and survival of tertiary relict *Thuja sutchuenensis* (Cupressaceae) in the subtropical Daba Mountains, southwestern China. PloS One, 10, e0125307.

Tottori Prefecture (2012) Threatened Wildlife of Tottori Prefecture: Animals, fungi and plants. Red Data Book Tottori 2nd Edition (https://www.pref.tottori.lg.jp/192848.htm) (in Japanese)

Tsukada, M. (1963) Umbrella pine, *Sciadopitys verticillata*: past and present distribution in Japan. Science, 142, 1680-1681.

Tsukada, M. (1982) *Cryptomeria japonica*: glacial refugia and late-glacial and postglacial migration. Ecology, 63, 1091-1105.

Tsukada, M., Sugita, S. and Tsukada, Y. (1986) Oldest primitive agriculture and vegetational environments in Japan. Nature, 322, 632.

Tsuyama, I., Nakao, K., Higa, M., Matsui, T., Shichi, K. and Tanaka, N. (2014) What controls the distribution of the Japanese endemic hemlock, *Tsuga diversifolia*? Footprint of climate in the glacial period on current habitat occupancy. Journal of Forest Research, 19, 154-165.

Warren, D. L. and Seifert, S. N. (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecological Applications, 21, 335-342.

Warren, D. L., Glor, R. E. and Turelli, M. (2010) ENMT.ools: a toolbox for comparative studies of environmental niche models. Ecography, 33, 607-611.

Woolbright, S. A., Whitham, T. G., Gehring, C. A., Allan, G. J. and Bailey, J. K. (2014) Climate relicts and their associated communities as natural ecology and evolution laboratories. Trends in Ecology and Evolution, 29, 406-416.

Yamanaka, T. (1964) Limestone vegetation in Shikoku, Japan. Acta Phytotaxonomica et Geobotanica, 21, 29-33. (In Japanese)

Yang, B. H., Song, J. H., Lee, J. J., Hur, S. D. and Hong, Y. P. (2009) Genetic variation and structure of the relict populations of Korean Arborvitae (*Thuja koraiensis* Nakai) in South Korea, employing ISSR markers. Journal of Korean Forestry Society. 98, 1-7 (In Korean)

Yatoh, K. (1955) Conifers of the Kii Peninsula (I). Bulletin of the Faculty of Agriculture, Mie University, 11, 73-94

Yatoh, K. (1956a) Conifers of the Kii Peninsula (II). Bulletin of the Faculty of Agriculture, Mie University, 12, 57-76

Yatoh, K. (1956b) Conifers of the Kii Peninsula (III). Bulletin of the Faculty of Agriculture, Mie University, 13, 123-132

Yatoh, K. (1957) Conifers of the Kii Peninsula (IV). Bulletin of the Faculty of Agriculture, Mie University, 14, 111-120.

Yatoh, K. I. (1962) Dendrological notes on Cupressaceae of the Kii Peninsula. Research Bulletins of the College Experiment Forests Hokkaido University, 21, 415-423.

日本の固有の針葉樹クロベの現在の分布及び気候範囲。

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要旨

クロベは日本固有の重要な針葉樹だが、他のヒノキ科の種と異なり現在の種の分布の情報が不足している。本報告ではクロベの現在の分布を調査し、近年絶滅した集団の数を、公開されている利用可能なオンラインリソースと野外調査の結果を併せて評価した。さらに、Maxent による種分布モデルを用い、クロベの生息可能域を予測した。クロベは本州北部（北緯 40.67°）から四国（北緯 33.49°）の温暖な照葉樹林から山岳地域の近くまで日本に広く分布していた。その分布域の中心は日本の中央部で、多雪・少雪の両方の山岳地域を含んでいた。一方、西日本ではクロベは非常に稀で、中国地方に 5 箇所、四国地方に 3 箇所の合計 8 集団しか確認されなかった。これらの中には、種分布モデルでは推測されなかった非常に温暖な地域に存在する集団もあった。こうした集団は、本州中央部の分布の中心から隔離されたレフュージアが長期間持続していたか、もともと西日本の温暖な地域により広く分布していたクロベが数千年に渡る人間活動で消失して残存したものであり、保全上非常に意義のある集団である。20 世紀半ばの人為的撹乱により 3 集団の絶滅が認められるが、全体としてはクロベの集団の推移は安定していた。

キーワード：遺存集団、保全、日本の固有針葉樹、分布域縮小、南限集団、分布モデル、クロベ

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