Article

Temperature Characteristics of Two *Fomitiporia* Fungi Determine Their Geographical Distributions in Japan

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Abstract: Two morphologically similar fungi, *Fomitiporia torreyae* and *Fomitiporia punctata*, are causal fungi of various tree diseases in Japan and are speculated to be distributed in different climatic zones. Clarifying their distribution ranges and climatic preferences would contribute to the prediction of disease occurrences and consideration of controls. In this study, we predicted the present geographical distributions of *F. torreyae* and *F. punctata* in Japan using a Maxent species distribution model to analyze our data and previously published collection records. In addition, we examined the importance of temperature on these predictions via jackknife analysis and evaluated the effects of temperature on mycelial growth and survival to elucidate determinants of their distribution. The predicted potential distributions showed that *F. torreyae* is mainly distributed in warmer areas compared to *F. punctata*. Jackknife analysis indicated the high importance of temperature variables for each fungal prediction. The two fungi were usually found at locations within upper or lower temperature limits for the growth and survival of each species. These results suggest that temperature is a key determinant of their distributions in Japan. This is the first report to predict fungal distribution based on species distribution modeling and evaluation of fungal physiological characteristics. This study indicates that the projected global warming will influence the future ranges of the two fungal species.

Keywords: *Fomitiporia punctata*; *Fomitiporia torreyae*; Maxent

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1. Introduction

Fomitiporia torreyae Y.C. Dai & B.K. Cui is a wood-decay fungus that belongs to Hymenochaetaceae, Hymenochaetales, Basidiomycota. This species causes various tree diseases in Japan, including stem rot on Japanese cedar (*Cryptomeria japonica*) and Sawara cypress (*Chamaecyparis pisifera*) [1–3], Japanese pear (*Pyrus pyrifolia* var. *culta*) dwarf [4,5], and dieback of Japanese umbrella pine (*Sciadopitys verticillata*) [6]. Since these tree species are economically important for forestry and fruit farming, *F. torreyae* is considered a serious tree pathogen in Japan. Nevertheless, *F. torreyae* had been confused with *Fomitiporia punctata* (Pilát) Murrill until recently [7], and the causative agent of Japanese cedar stem rot was first misidentified as ‘*Fuscoporia punctata* (Fr.) G. Cunn.’ (= *Fomitiporia punctata*) [2]. *Fomitiporia punctata* has also been reported to be associated with some tree diseases, and it also can cause Japanese pear dwarf [8]. In addition, Yamaguchi [9] reported that *F. punctata* caused trunk rot and the death of *Cerasus sargentii* after an inoculation test, though this disease has not yet been recorded in the field.

Since the macro-morphologies of *F. torreyae* and *F. punctata* are very similar, these species are discriminated mainly by their micro-morphological characteristics, including the presence of hymenial setae and the size of basidiospores [7]. However, careful observation is needed because the size ranges of basidiospores are partially overlapped, and the abundance of hymenial setae varies according to the specimen [7]. Host ranges are not well differentiated between these species; *F. torreyae* is found on various conifer and broadleaf

tree species, and *F. punctata* is observed on several broadleaf tree species [7,10,11]. However, their geographical distribution ranges are speculated to differ on the basis of the collection locations of their basidiocarps in eastern Asia; that is, *F. punctata* is widely collected in cool temperate to boreal areas, whereas *F. torreyae* is collected in warm temperate to subtropical areas [7]. Therefore, distribution ranges and climatic preferences—especially temperature preferences—may differ between these fungi, but their geographical distributions and their determinants have not yet been addressed. Terashima [12] reported the effect of temperature on the mycelial growth of *F. torreyae* (as *Fomitiporia* sp.), but the temperature range for survival was not examined. No similar study of *F. punctata*, including the mycelial growth rate in different temperature regimes, has been conducted. Thus, the environmental conditions for the optimal growth and survival of these two fungi, including the temperature characteristics of cultures, have not been fully examined.

Species distribution models are mathematical models to relate species occurrence or abundance with environmental and spatial characteristics of particular sites [13]. These models have been widely used to predict current and future potential distributions of various organisms, including fungi, e.g., [14,15]. Among species distribution models, maximum entropy modeling (Maxent) [16] is one of the commonly used methods with higher-performance approaches [16,17]. Maxent requires only the presence data of particular species [16], and its performance can be higher compared to other methods, even with low numbers of samples [18]. It is difficult to acquire absence data for fungi due to the limited detectability of their basidiocarps; it is also difficult to collect a large quantity of presence data due to the limited number of experts on fungi. Therefore, Maxent is considered one of the best methods for predicting geographical distributions and elucidating determinants for fungal distribution.

Considering that *F. torreyae* and *F. punctata* have been associated with tree diseases, clarifying their ecological and physiological characteristics, such as distribution ranges and climatic preferences, would contribute to the prediction of disease occurrences by these fungi and consideration of their controls. The objectives of this study were to estimate the geographical distributions of *F. torreyae* and *F. punctata* in Japan, and to elucidate the determinants of their distribution. Since these two species are considered to be distributed in different climatic zones [7], this study focused on temperature as a determinant of their distributions. To relate temperature with their geographical distributions, we predicted the potential distribution areas of the two fungi and examined the importance of temperature on these predictions using Maxent. Moreover, we examined the effects of temperature on their mycelial growth to estimate the temperature range for their growth and survival.

2. Materials and Methods

2.1. Species Record

For Maxent analyses, we used datasets on *F. torreyae* and *F. punctata* collections that were previously published with discrimination of these species. These datasets included *F. torreyae* collection records by Kaneko et al. [19] identified by species-selective primers [20], those by Ota et al. [7] identified morphologically and phylogenetically, and those by Nakamura and Hattori [11] identified morphologically. We also added the herbarium records of basidiocarp specimens in the Mycological Herbarium of the Forestry and Forest Products Research Institute (TFM), and culture stock data in the Microbial Genetic Resources of the Forestry and Forest Products Research Institute Genebank (FFPRI) and the Laboratory of Microbial Ecology, Forestry and Forest Products Research Institute (WD). The fungal species of the additional data were identified by the rDNA sequences of the internal transcribed spacer (ITS) region. Newly generated sequences were deposited in GenBank (Table S1).

The published collection data often lacked detailed locality names or latitude and longitude data to indicate the exact point of collection. Of these cases, the specimens deposited in TFM were re-examined by investigating the herbarium records to provide more detailed geographical ranges of the collection sites. The latitude and longitude data

were lacking for most samples, but we successfully restricted most of the collection sites into areas narrower than 1×1 km. The collection data of duplicate localities were removed from the analysis. Later, the latitude and longitude near the center of each collection site were recorded on Google Maps because exact collection points were unknown. For ten sites of *F. torreyae* and seven sites of *F. punctata*, we failed to restrict the collection sites into areas narrower than 1×1 km but succeeded in restricting them to areas narrower than 5×5 km. These collection data were also included in the analysis due to the low number of samples used for the analysis, especially for *F. punctata*. In total, we prepared 73 and 14 presence data of *F. torreyae* and *F. punctata*, respectively (Figure S1 and Table S1).

2.2. Environmental Variables and Maxent Analyses

As environmental variables for Maxent analyses, we prepared 52 climatic variables: monthly and annual average, maximum and minimum temperature, and monthly and annual precipitation. The climatic data were obtained from National Land Numerical Information (average data from 1981 to 2010, 1 km resolution; <https://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html>, accessed on 6 June 2021) provided by the Ministry of Land, Infrastructure, Transport and Tourism, Japan. Shapefiles of each climatic variable were transformed to the ASCII files required by Maxent software using QGIS ver. 3.10.12. [21]. We found high correlations among most environmental variables, with Pearson's correlation coefficients of ≥ 0.8 . Recent studies have shown that Maxent is robust to collinearity among variables [22,23], but its model performance can be affected by increasing model complexity, such as an increasing number of variables [24]. Therefore, we chose monthly and annual average temperatures among the temperature data to reduce the number of variables and used 26 climatic variables for Maxent analyses.

The potential distributions of *F. torreyae* and *F. punctata* in Japan were predicted with Maxent ver. 3.4.4. [25] using the presence data (latitude and longitude) of these fungi and the environmental data mentioned above. We ran Maxent analyses with default settings, except for using 100 bootstrap replicates by sampling replaced with random seeds. In the analysis of *F. torreyae*, 68 presence data were used because the default setting "remove duplicate presence records" excluded five records. The model performances were evaluated based on the area under the receiver operating characteristic curve (AUC). AUC values ranged from 0 to 1, and values > 0.5 indicated that the resulting model was better than random [17]. In addition, variable importance to the model was evaluated by jackknife analysis, which is an optional analysis in Maxent. A jackknife test outputs the gain in models only with or only without each variable. Since we found higher correlations among most environmental variables, the gain in models only with each variable was used for the evaluation of variable importance. To determine how the presence probability was influenced by changes in different variables, Maxent response curves in models using only each variable were generated. To detect temperature ranges at the sampling locations of the two fungi, the temperature data at each location were extracted from the climatic data via Maxent.

2.3. Growth Experiment

We measured the mycelial growth rates of *F. torreyae* and *F. punctata* under various temperatures to estimate the effects of temperature on their growth rates. All isolates used in this experiment were preserved in FFPRI (Table 1). The sampling information of each isolate was included in Maxent analyses. Each isolate was precultured on potato dextrose agar (PDA; Nissui Pharmaceutical, Tokyo, Japan) medium in the dark for 8 days at 25 °C. A disk of mycelia was cut from the edge of the precultured plates using a 6 mm cork borer and transferred to 9 cm plastic culture plates, each containing 15 mL of PDA medium. The inoculated plates were incubated in the dark for up to 7 weeks at eight different temperatures, namely, 5, 10, 15, 20, 25, 30, 35, and 40 °C. Since the colonies reached the edges of the plates, incubation was terminated after approximately 2 to 3 weeks for 20, 25, and 30 °C, and after 6 weeks for 15 and 35 °C. Each isolate had three replicates for

each temperature. Following the incubation period, the radius of each fungal colony was measured in two perpendicular directions. Mycelial growth (mm/day) was calculated as the average radius at specific time intervals.

Table 1. Origins of *Fomitiporia torreyae* and *F. punctata* isolates used in growth experiments.

Species	Isolate No.	Location	Substrate	Year of Isolation	GenBank Accession No. of ITS Region
<i>Fomitiporia torreyae</i>	FFPRI 421023 (WD2641)	Kibune, Kyoto	decayed wood of hardwood	2011	LC651667, LC651668
	FFPRI 421024	Kasumigaura, Ibaraki	decayed wood of <i>Cryptomeria japonica</i>	2019	LC651669
	FFPRI 421026	Sammu, Chiba	decayed wood of <i>Cryptomeria japonica</i>	2019	LC651671
<i>F. punctata</i>	FFPRI 421022 (WD2055)	Chino, Nagano	decayed wood of hardwood	1998	AB777696 *
	FFPRI 421027	Wajima, Ishikawa	decayed wood of conifer	2019	LC651672
	FFPRI 421028	Chihibu, Saitama	decayed wood of <i>Cerasus</i> sp.	2020	LC651673

* A sequence was analyzed by Ota et al. (2014).

To determine the vitality of these fungal colonies incubated at low temperatures, six isolates were precultured on PDA medium in the dark for 1 month at 25 °C. All plates were transferred and incubated at −5 °C or 0 °C. Each isolate had three replicates for each temperature. Vitality tests were conducted after 1, 2, 3, 4, and 8 weeks for 0 °C incubation and weekly for −5 °C incubation throughout the 8-week experiment. To examine the vitality, three ca. 5 × 5 mm pieces of mycelium per plate were randomly excised from the margins of the colonies and transferred to new PDA plates. In the −5 °C incubation, each plate was stored at room temperature, ca. 20 °C, for a few hours before transfer because the colonies were frozen. The transferred plates were incubated for a maximum of 1 month at room temperature. The transferred piece was considered alive when newly grown mycelia were seen on the piece, and then the number of live pieces was recorded. The proportion of live pieces to the total tested pieces was calculated for each isolate.

3. Results

The presence probability of *F. torreyae* by Maxent analysis was higher in coastal areas along the Pacific Ocean from the middle part of the Tohoku region (around Sendai) toward southern Japan than in other areas (Figure 1 and Figure S1). Meanwhile, the probability of *F. punctata* was higher in mountainous areas from the middle parts of the Shikoku and Chugoku regions toward northern Japan (Figure 1 and Figure S1). The AUC values (average ± standard deviation) of *F. torreyae* and *F. punctata* predictions were 0.960 ± 0.006 and 0.889 ± 0.040, respectively.

Among the climatic variables, all temperature variables (each monthly and annual average temperature) examined in the analysis had higher gains in the models based on jackknife analysis in the *F. torreyae* prediction (Figure 2). Meanwhile, monthly average temperatures from December to March had higher gains than other variables in the *F. punctata* prediction (Figure 2). Figure 3 presents representative patterns of the relationships between the presence probability and these temperature variables that had higher gains. The peaks of the presence probability of *F. torreyae* appeared at higher temperatures than those of *F. punctata* (Figure 3). The difference in temperature where the peaks were present between the two species was found in all temperature variables (data not shown). As a general pattern of seasonal climatic changes in Japan, the temperature is highest in August and lowest in January. To detect the limits of temperature ranges at collection locations of the

two fungi, we determined the average maximum temperature recorded in August from 1981 to 2010 and the average minimum temperature recorded in January from 1981 to 2010 at the collection locations of these fungi (Figure 4). *Fomitiporia torreyae* was usually found in areas where the maximum temperature in August was $>29^{\circ}\text{C}$, but *F. punctata* was usually found in areas with maximum temperatures of $\leq 29^{\circ}\text{C}$. Based on January temperatures, *F. torreyae* was always found in areas where the minimum temperature was $>-6^{\circ}\text{C}$, while *F. punctata* was often found at minimum temperatures of $\leq -6^{\circ}\text{C}$. For both the maximum temperature in August and the minimum temperature in January, temperatures at the collection locations of *F. torreyae* tended to be higher than those of *F. punctata*.

Figure 1. Presence probability of *Fomitiporia torreyae* and *Fomitiporia punctata* predicted by Maxent. The vertical scale bar indicates the mean of the probability (100 bootstrap replicates) from 0 (blue, low probability) to 1 (red, high).

Figure 2. Regularized training gain in Maxent models with each environmental variable alone. The gains were calculated by jackknife analysis for variable importance. Values are the mean + standard deviation (100 bootstrap replicates). Monthly and annual average temperature and monthly and annual precipitation were used as variables for the Maxent analyses and are shown on the x-axis.

Figure 3. Relationships between presence probability and average temperature in March. Values were calculated in Maxent models using each variable alone. Red lines and blue shading show the mean of 100 bootstrap replicates and one standard deviation, respectively.

Figure 4. Frequency of collection locations of *Fomitiporia torreyae* and *Fomitiporia punctata* at different levels of maximum temperature in August and minimum temperature in January.

No mycelial growth was observed at 5 °C or 40 °C for either species. The optimal growth temperature was 30 °C for *F. torreyae* and 25 °C for *F. punctata* (Figure 5). *Fomitiporia torreyae* showed distinct mycelial growth at 35 °C, but *F. punctata* did not. No obvious difference was seen between the growth rates of the two species at 10 °C.

Both species survived at 0 °C for at least 2 months, irrespective of the isolate. Some mycelial pieces of *F. torreyae* were dead after 2 weeks of incubation at −5 °C, and the numbers of dead pieces increased with longer incubation (Figure 6). Meanwhile, no mycelial pieces of *F. punctata* died throughout the experiment, and the proportions of live pieces were always higher than those of the *F. torreyae* isolates.

Figure 5. Mycelial growth of *Fomitiporia torreyae* and *Fomitiporia punctata* isolates at different temperatures. Values indicate means ($n = 3$).

Figure 6. Survival of *Fomitiporia torreyae* and *Fomitiporia punctata* isolates at -5°C during 8 weeks of incubation. We used three plates per isolate; three mycelial pieces excised from each plate were tested for survival. Values indicate the proportion of live pieces to total tested pieces ($n = 9$) for each isolate.

4. Discussion

We predicted the potential distributions of *F. torreyae* and *F. punctata* by analyzing the effects of environmental variables on their distributions using Maxent, revealing temperature as an important factor related to their distribution. We also examined the effects of temperature on their mycelial growth and survival to complement their distribution characteristics. The predicted potential distributions showed that *F. torreyae* is mainly distributed in warm temperate areas, whereas *F. punctata* inhabits cool temperate to boreal or mountainous areas. Moreover, jackknife analysis suggested that temperature is a key determinant of their distributions in Japan. This conclusion is also supported by the results of mycelial growth characteristics. All of the collection locations for *F. torreyae* were situated within areas where the minimum temperature in January was above -6°C , and its mycelium died when incubated at -5°C for up to 2 months but survived at 0°C . *Fomitiporia punctata* was not recorded from areas where the maximum temperature in August was higher than 31°C , and its mycelial growth was sparse or not observed above 30°C but was observed below 30°C . Although thresholds of accurate temperatures for growth and survival were not examined in this study, the temperature ranges within the collection locations coincided well with the upper or lower limits of the temperatures for the growth

and survival for both species. Thus, these results strongly support the prediction by Maxent analyses, indicating that their distributions can be explained by the temperatures at each collection site and temperature thresholds for fungal growth and survival.

Fungal species distribution is possibly affected not only by climatic conditions such as temperature, precipitation, and solar radiation but also by the distributions and conditions of host trees, e.g., [26–30]. The collection records of *F. torreyae* and *F. punctata* [7,10,11] suggest that their host and substrate preferences are likely to be broader than those of several wood-decay fungi distributed in temperate areas of Japan [31,32]. Thus, we suggest that their distributions are scarcely affected by host tree distribution. However, other climatic factors including an interaction between temperature and precipitation may affect their distributions as we only included temperature and precipitation variables as environmental variables in the Maxent analyses and, based on a jackknife test, separately evaluated the gain of each variable in the models.

Global warming may affect the phenology and physiology, as well as the geographical distribution, of fungi [33,34]. Generally, the distribution of a species is expected to shift poleward in latitude and upward in elevation with the warming trend. This study suggests that temperature may be a major determinant of the distribution of both species. Thus, global warming could affect their distributions, and *F. torreyae* may spread to northern and mountainous parts of Japan. Since both *F. torreyae* and *F. punctata* are tree pathogens, caution may be required due to shifting diseased areas by global warming. Because these fungi cause similar diseases on Japanese pear [5,8], *F. torreyae* may expand its distribution and perhaps displace *F. punctata* as the cause of Japanese pear dwarf in northern areas through global warming.

In this study, the AUC values of the Maxent predictions for both *F. torreyae* and *F. punctata* were near or above 0.9, suggesting that these predictions are accurate. However, sampling bias could be present in the records, especially those of *F. torreyae*, because most samples of this fungus were collected at relatively accessible locations such as parks, orchards, and urban forests. In Maxent analyses, sampling bias can cause the models to overfit environmental biases, and predicted distributions can be underestimated [35]. In fact, the high-probability areas of *F. torreyae* predicted in this study seemed to be restricted around the collection locations. Nevertheless, further field surveys for explorations of the two fungi may improve predictions and clarify their actual distributions. For further surveys, the maps provided by this study may help to find unreported diseased sites by these fungi. Our Maxent analyses extracted high-probability areas of distributions without collection records nearby, such as coastal areas along the Pacific Ocean in the Chubu region for *F. torreyae* and the northeastern part of the Tohoku region for *F. punctata* (Figure 1 and Figure S1).

This is the first report to predict fungal distribution on the basis of a species distribution model and evaluation of fungal physiological characteristics. The results of both methodologies suggest that temperature is a major determinant of the distributions of *F. torreyae* and *F. punctata* in Japan. Moreover, these results may support previous suggestions that *F. torreyae* is distributed in warm temperate to subtropical areas, while *F. punctata* is widespread in cool temperate to boreal areas [7], and that distribution can be a key characteristic for these fungi. This study provides several ecological and physiological characteristics of the two fungi, and this information shows that a future shift in the diseased areas by global warming can be predicted.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f12111580/s1>, Figure S1: Collection locations of *Fomitiporia torreyae* (blue circle) and *Fomitiporia punctata* (orange circle) used in the Maxent analyses; Table S1: Latitude and longitude data of the collection locations of *Fomitiporia torreyae* and *Fomitiporia punctata* used in Maxent analyses.

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Data Availability Statement: The latitude and longitude data used in this study are available in Table S1. Other data presented in this study are available on request from the corresponding author.

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