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Article

Incredible Host Diversity and Regional Potential Distribution of an Oriental Parasitic Plant (*Taxillus yadoriki*)

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Abstract: This study investigates the host diversity and characteristics of the rare parasitic plant Silverberry-like taxillus (*Taxillus yadoriki*). Seogwipo, Jeju Island, where *T. yadoriki* grows naturally, was examined to clarify the diversity of host species, their location, and the part of the tree where *T. yadoriki* is attached. A total of 687 host trees were found. *Taxillus yadoriki* was intensively distributed in the lowlands below 200 m a.s.l. The host trees belonged to 40 species, four varieties, three cultivars, and two hybrids from 32 genera and 21 families, of which 23 taxa were identified as host plants for the first time in this study. Incredibly, this plant was found to be able to parasitize a variety of plants from 12 orders. *Taxillus yadoriki* was found to be parasitic in three orders of Gymnosperms, Ginkgoales, Cupressales, and Pinales, as well as nine orders of Angiosperms, including Magnoliales, Rosales, and Ericales. Rosaceae was the most diverse at 18.0%, and most species were broad-leaved and arboreal. Among them, *Cryptomeria japonica* and *Litsea japonica* had the highest frequency of parasitization and *T. yadoriki* was mainly attached to the upper part of the main tree and the main branch; as a result, *T. yadoriki* was distributed and showed specificity in the position of disturbance on the host. *T. yadoriki*'s specific distribution model was built as a Maxent program. The area under the curve of the receiver operation characteristic was 0.948 ± 0.026 (mean ± standard deviation), and the performance of the constructed model was excellent. Of the total eight environmental factors, density of artistic forest and meant temperature of coldest quarter accounted for 75.3% of the total importance, which was the main distribution determinant of species. In the average distribution probability map of *T. yadoriki*, the critical probability for determining distribution was calculated to be 0.2898 ± 0.1018. Accordingly, the distribution of species is predicted to expand from Jeju Island to the entire southern and southeastern coasts.

Keywords: climate change; host plants diversity; Jeju Island; mistletoe; *Taxillus yadoriki*

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1. Introduction

More than 4750 species of parasitic plants have been identified to date, comprising approximately 20 families, representing approximately 1% of all flowering plants [1–3]. These species have a wide global distribution and are found in all biomes. According to the type, parasitic plants can be categorized as obligate, facultative, hemi-, holo-, stem-, or root- [4–6]. More than 40 species in seven families grow naturally in Korea, and various types grow naturally in all climate zones, from the subtropical to the subarctic zones. Korean parasitic plants include *Orobanche coerulescens*, *Aeginetia indica*, and *Cuscuta japonica*, which are fully parasitic plants (Obligate), *Monotropastrum humile* and *Monotropa hypopithys*, which are saprophytes, and mistletoe, which is hemiparasitic [7,8]. Among them, hemiparasitic plants are both parasitic and photosynthetic and survive by attaching parasitic roots to the host plant to obtain moisture and nutrients [2,9]. Mistletoes that grow naturally in Korea include *Viscum* and *Korthalsella* in Santalaceae and Loranthus and *Taxillus* in Loranthaceae (Table 1). The genus *Viscum* includes *Viscum album* var. *lutescens* and *Viscum album* for. *rubroauranticum*, which grow naturally in cool and temperate deciduous broad-leaved tree forests and are known to be parasitic on Fagaceae, Betulaceae, and Aceraceae. *Korthalsella japonica* is distributed in temperate and subtropical regions and is parasitic on Theaceae, Oleaceae, and Lauraceae. *Loranthus tanakae* is mainly distributed in deciduous broad-leaved tree forests in central and northern temperate regions and is parasitic on Fagaceae and Betulaceae. Finally, *T. yadoriki* is mainly distributed in evergreen broad-leaved tree forests in temperate and subtropical regions and is parasitic on Lauraceae, Fagaceae, and Theaceae [10–14]. However, little is still known about the host plant diversity and ecological characteristics of the parasitic species.

Table 1. Diversity of some parasitic plants in Korea.

Family	Genus	Species	Climate Zone	Host Diversity
Santalaceae	*Viscum*	*V. album* var. *lutescens*	Cool-temperate zone	Fagaceae, Betulaceae, Aceraceae etc.
		V. album f. *rubroauranticum*	Cool-temperate zone	Fagaceae, Betulaceae etc.
	Korthalsella	*K. japonica*	Warm-temperate and subtropical zone	Theaceae, Oleaceae, Lauraceae, etc.
Loranthaceae	*Loranthus*	*L. tanakae*	Cool-temperate zone	Fagaceae, Betulaceae etc.
	Taxillus	*T. yadoriki*	Warm-temperate and subtropical zone	Lauraceae, Taxodiaceae, Fagaceae etc.

Taxillus yadoriki, the target species of this study, is a mistletoe with a restricted distribution in Japan and Korea in Northeast Asia, and in Korea it grows naturally only on Jeju Island [11,13,15]. Due to the species' narrow distribution range and small population size, it is designated as a critically endangered species by the Korea Forest Service and as Near Threatened according to the Ministry of Environment's Red List Categories [16,17]. Due to the parasitic nature of the plant, which inhibits the growth of the host plant, it is recognized as an invasive plant to be removed from orchards and artificial forests that are managed for special purposes [18,19].

Like many other mistletoes, *T. yadoriki* has a long history of use in folk botany as a medicinal plant [14]. Recent studies have confirmed that it contains anti-cancer and anti-inflammatory substances. Notably, the diversity and content of medicinal substances in parasitic plants have been found to vary greatly depending on the type of host plant [20–22]. These results suggest that the potential of *T. yadoriki* as a medicinal plant is expected to vary depending on the host plant diversity. However, data on the host plant diversity of *T. yadoriki* are limited.

Therefore, this study determines the distribution status of *T. yadoriki* in Korea, as well as the diversity and host characteristics of its host plants. The host plant diversity identified for the first time in this study was described through comparison with the literature. Furthermore, by confirming which part is preferred when attaching to the host plant, we intend to not only reveal the attachment characteristics but also use it as basic information for management. In addition, we plant to use existing distribution information to derive environmental factors that determine the distribution of species and use these to analyze potential distribution sites for species. Our results will help to enhance the utilization potential of *T. yadoriki*, whose medicinal components vary depending on the host plant, and serve as a basis for the stable conservation and management of rare plants.

2. Materials and Methods

2.1. Field Research

Jeju Island (Jeju Special Self-Governing Province) is the southernmost part of the Korean Peninsula and has an area of approximately 1850 km^2. It is and oval-shaped island that is wide form east to west. The climate is characterized by high temperature and precipitation in summer and low temperature and dry climate in winter (Figure 1).

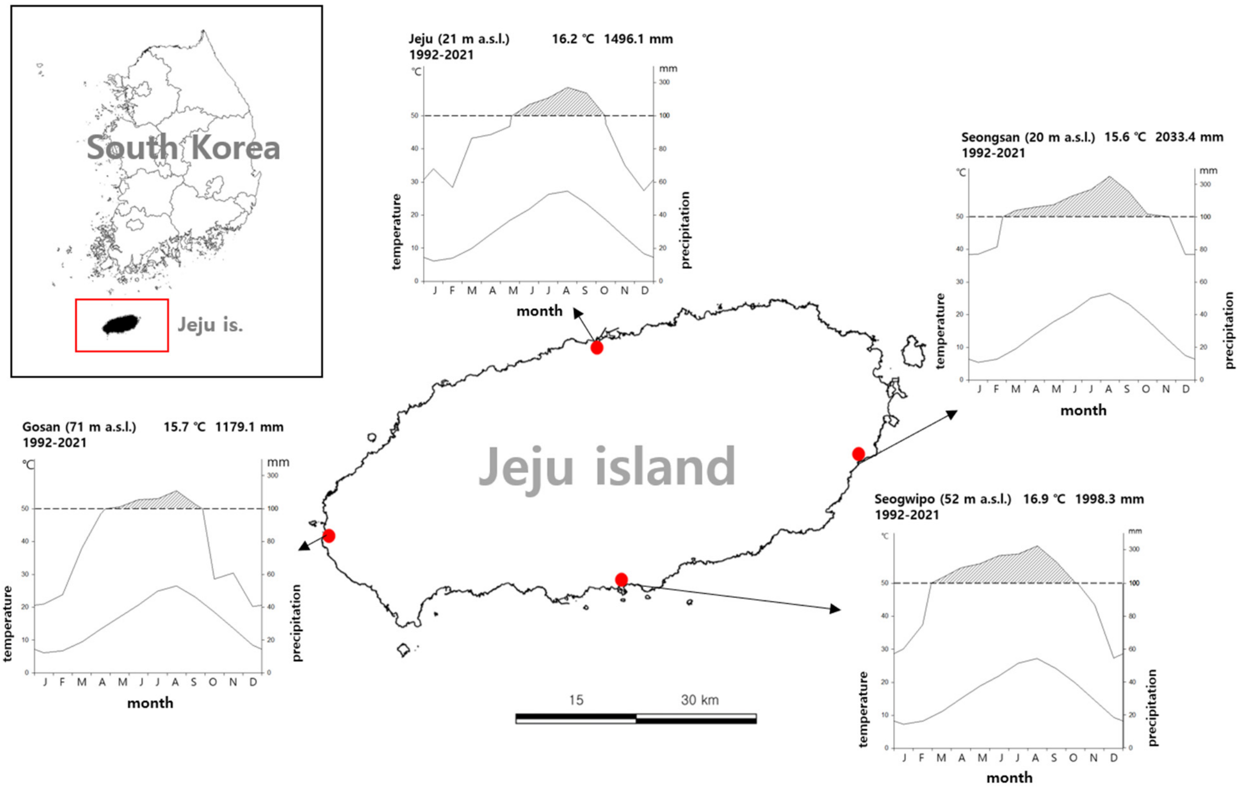

Figure 1. Geography and bioclimate of the study area (1992–2021).

A total of eight field surveys were conducted from January to May 2021 on Jeju Island: 4 times in January, 3 times in February, and 1 time in May. The entire island was surveyed to determine the distribution range of the species, and GPS values were calibrated and recorded for the points where the species distribution was confirmed. Field identifications were made to determine host plant diversity, and photographic data, including geographic information, were stored. When precise identification through specimens was required, species were collected, evidence specimens were prepared, and the specimens were deposited in the Warm Temperate and Subtropical Forest Research Center herbarium after identification. The scientific names of the species were based on the Korean Standardized Inventory of Plants [17], and the original color Korean Flora [23] and original color Korean Standardized Flora [24] were considered. To identify the characteristics of the species' attachment to the host plant, we carefully recorded the attached position and ecological characteristics of the host plant. The positions of attachment were categorized as trunk, branch, and twig according to the characteristics of the branch and recorded as the upper part, middle part, and lower part according to the position in the tree. The host plant was categorized according to taxonomic position, growth form [25], and disseminule forms [26].

2.2. Distribution Modeling

2.2.1. Data Collection

A species distribution model was created to identify potential distribution sites using the current distribution location of *T. yadoriki*. The scope of application of the species distribution model was limited to Jeju Island, and the coordinates collected through field surveys were used for analysis of species distribution information. The environmental data consisted of major climate data considering the characteristics of the native habitat of *T. yadoriki* and land cover data reflecting the habitat and host plant characteristics. For climate data, WorldClim ver. 2.1 bioclimatic variables (30″ × 30″) were used [27]. WorldClim consists of 19 variables that affect biological distribution.

For land cover data, the Ministry of Environment's land cover map was used [28]. The land cover map was reorganized into six legends, considering the diversity and density of plants that *T. yadoriki* can host for each legend. Then, after creating a grid with the same pixel size as the climate data, the area of the land cover legend reconstructed from each grid was calculated, and then the density (0–1) was calculated as a percentage (Figure S1). The types and descriptions of the reconstructed land cover are as follows: (1) Barren land, being an area where vegetation is not covered; among the legends of the land cover map, 'used area' and 'barren' are included. (2) Artificial grassland, being an artificial grassland; this area occasionally includes artificially planted trees. (3) Natural grassland, being a natural grassland; this area occasionally includes artificially planted trees as well as rare, native trees, and includes natural grasslands and wetlands among the land cover map legends. (4) Artificial forest, being an artificially created forest composed mainly of an orchard cultivated on Jeju Island and a windproof planting forest surrounding it; forest density is relatively high, but diversity is low. (5) Natural forest, being Jeju Island's native vegetation area; this area includes evergreen forests and coniferous forests and consists of high-density trees. (6) Aquatic area, being an area composed of water including rivers and lakes.

2.2.2. Data Processing and Selection

The collected environmental data were cropped to Jeju Island, the scope of the model, with QGIS ver. 3.28.12 and converted to rasters with a resolution of $30'' \times 30''$ [QGIS.org, Zürich, Swiss] [29], and correlation analysis was performed with the cor.test function in R ver. 4.3.2 to consider collinearity among variables [R Core Team, Vienna, Austria] [30–32]. The correlation of climate variables in Jeju Island was high among annual and quarterly temperature and precipitation data (B01, B05, B06, B08, B09, B10, B11, B12, B13, B14, B16, B15, B17, B18, B19) and temperature deviation data (B02, B03, B04, B07) (Table S1). In our variable selection, we wanted to reflect the characteristics of a temperate plant. Therefore, we selected 'Mean temperature of coldest quarter' for annual and quarterly temperature and precipitation data, and 'Temperature annual range' for temperature anomaly data. Meanwhile, the land cover variables were independent, so all variables were selected. In the end, eight variables were used in the modeling (Figure S1).

2.2.3. Modeling

We believe that our island-wide field surveys have identified the majority of *T. yadoriki* distributions on Jeju Island, but there may still be residual potential *T. yadoriki* distributions. Therefore, we used the maximum entry model algorithm, which allows effective modeling even with occurrence data [33,34].

The maximum entry model algorithm was performed with Maxent software ver. 3.4.4 (New York, NY, USA) [35]. During modeling, parameters were adjusted for model validation and ecological interpretation. 'Replicated run type' was set to 'Crossvalidate' and 'Replicates' was set to '10' for 10-fold cross validation. 'Create response curves' and 'Do jacknife to measure variable importance' were enabled to explore the relationship between *T. yadoriki* and its environment. 'Output format' was set to 'Logistic'. The performance of the constructed model was evaluated by the area under the curve of the receiver operation characteristic. It has a value of 0.5–1, and the closer it is to 1, the better the model [36–38]. The model variables were evaluated using importance. In the calculated average distribution probability map, if the probability was higher than the maximum test sensitivity plus specificity logistic threshold, it was judged as a potential distribution possible area [39].

3. Results and Discussion

3.1. Distribution Range of Native Species

The native distribution of *T. yadoriki* was limited to the Seogwipo area on Jeju Island, and the distribution was confirmed at 687 points. *T. yadoriki* was found at altitudes ranging from 7 to 194 m above sea level, with an average altitude of 67.4 m, and was concentrated in the lowlands. The horizontal distribution range was confirmed from Andeok-myeon Andeok valley area (33°15′26″ N 126°21′23″ E), the westernmost part, to Namwon-eup (33°15′50″ N 126°37′9″ E), the easternmost part, and from Yeongcheon-dong area (33°17′55″ N 126°35′32″ E), the northernmost part to Songsan-dong area (33°14′20″ N 126°36′5″ E), the southernmost part (Figure 2). The average annual temperature (1992–2021) at the Seogwipo ASOS site (52 m above sea level) adjacent to the distribution site was 16.9 °C with an annual precipitation of 1989.3 mm (Figures 1 and 2, [40]), and the area is considered to have a subtropical climate with a temperature index of 199.6. The region has the warmest climate in Korea, being the only region where the average daily temperature in winter is not below zero [40].

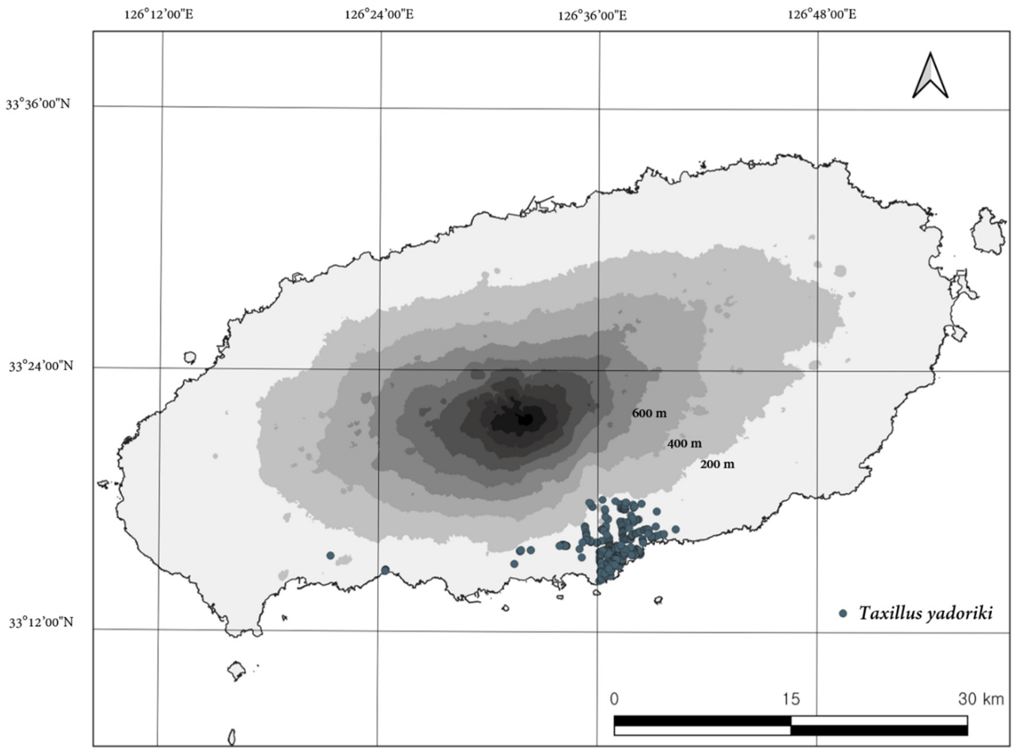

Figure 2. Distribution of *T. yadoriki* in Jeju, Republic of Korea.

Parasitized trees and locations were diverse, including street trees, windbreaks, landscape trees, fruit trees, and natural forests, but high frequencies were found in croplands, roadsides, and garden green areas where anthropogenic activities are intensive. Most of these species occur as stand-alone trees or exhibit a linear distribution, and in many cases, are vegetated landscapes that play various roles, such as local bird migration corridors, refuges, and sanctuaries. Due to these native distribution characteristics, *T. yadoriki* has one of the narrowest distribution ranges among mistletoe species in Korea, which contrasts with other mistletoe species that are mainly distributed in natural forests composed of long- to old-growth trees [11,41–43].

3.2. Host Plant Diversity and Species Characteristics

T. yadoriki was found to be able to parasitize a variety of plants from 12 orders. The identified host plants belonged to 49 taxa (40 species, four varieties, three cultivars, and two hybrids) in 32 genera and 21 families. Phylogenetically, *T. yadoriki* was found to be parasitic in three orders of Gymnosperms, Ginkgoales, Cupressales, and Pinales, as well as nine orders of Angiosperms, including Magnoliales, Rosales, and Ericales. Although these host plants show great differences in the structural aspect of sap movement, the fact that these species can parasitize is a very specific phenomenon. In detail, three taxa, three genera, and three families (*Ginkgo biloba*, *Cryptomeria japonica*, and *Torreya nucifera*) in Gymnosperma and 46 taxa, 28 genera, and 17 families of Lauraceae, Fagaceae, and Rosaceae in Dicotyledon among Angiosperma were identified as host plants. This was 3.3 times higher than the host plant diversity of 15 taxa, 14 genera, and eight families recorded in previous studies in Korea for *T. yadoriki*. We identified 23 taxa of new host plants [17,20,44,45]. This value was also the highest host plant diversity compared to other mistletoes in Korea, confirming that *T. yadoriki* utilizes a wide range of host plants in Korea (Table 2). Internationally, *T. yadoriki* host plant diversity is known for 57 taxa, 53 species, three variants, and one hybrid in 38 genera and 26 families (Table 3). Of these, 24 families have species in common with Korea. However, seven families, including Illiciaceae, Moraceae, and Myrtaceae; 12 genera, including *Ficus*, *Ulmus*, and *Litsea*; and 25 taxa, including *Torreya nucifera*, *Eriobotrya japonica*, *Cornus kousa*, and *Nerium oleander*, were identified as host plants only in Korea, and our report first records their host potential. Among the foreign host plants, *Quercus gilva*, *Q. acuta*, *Carpinus tschonoskii*, *Toxicodendron succedaneum*, *Symplocos prunifolia*, and *Pittosporum tobira* are species that grow naturally in Korea and are likely to contribute as host plants in Korea, although parasitism was not confirmed in this study [10,12,46,47].

Table 2. Host plant diversity of *T. yadoriki* in Korea (○: first record).

Order	Family	Scientific Name	Newly Discovered
Ginkgoales	Ginkgoaceae	*Ginkgo biloba* L.	○
Cupressales	Cupressaceae	*Cryptomeria japonica* (Thunb. ex L.f.) D.Don	
Pinales	Taxaceae	*Torreya nucifera* (L.) Siebold & Zucc.	○
Fagales	Fagaceae	*Castanopsis sieboldii* (Makino) Hatus.	
		Quercus acutissima Carruth.	
		Quercus glauca Thunb.	
		Quercus mongolica var. *crispula* H.Ohashi	○
		Quercus serrata Murray	
Magnoliales	Ulmaceae	*Aphananthe aspera* (Thunb.) Planch.	
		Celtis sinensis Pers.	
		Ulmus parvifolia Jacq.	○
	Moraceae	*Ficus erecta* Thunb.	○
		Ficus erecta var. *sieboldii*	○
	Magnoliaceae	*Magnolia kobus* DC.	
		Magnolia obovata Thunb.	○
	Illiciaceae	*Illicium anisatum* L.	○
	Lauraceae	*Actinodaphne lancifolia* Meisn.	
		Cinnamomum camphora (L.) J.Presl	
		Cinnamomum yabunikkei H.Ohba	
		Litsea japonica (Thunb.) Juss.	
		Machilus thunbergii Siebold & Zucc. ex Meisn.	
		Neolitsea aciculata (Blume) Koidz.	
		Neolitsea sericea (Blume) Koidz.	
Rosales	Theaceae	*Camellia japonica* L.	
		Camellia sasanqua Thunb.	
		Camellia × *williamsii* W.W.Sm.	○
		Eurya emarginata (Thunb.) Makino	○
		Eurya japonica Thunb.	
	Hamamelidaceae	*Distylium racemosum* Siebold & Zucc.	
	Rosaceae	*Eriobotrya japonica* (Thunb.) Lindl.	
		Prunus mume (Siebold) Siebold & Zucc.	
		Prunus persica (L.) Stokes	○
		Prunus salicina Lindl.	○
		Prunus serrulata f. *spontanea* Chin S.Chang	
		Prunus spachiana f. *ascendens* Kitam.	○
		Prunus × *yedoensis* Matsum.	
		Pseudocydonia sinensis C.K.Schneid.	○
		Pyrus pyrifolia var. *culta* Nakai	○

Table 2. *Cont.*

Order	Family	Scientific Name	Newly Discovered
Geraniales	Rutaceae	*Citrus natsudaidai* Hayata	○
		Citrus unshiu Marcow.	○
Sapindales	Aceraceae	*Acer palmatum* Thunb.	
		Acer palmatum var. *sanguineum* Nakai	○
Myrtales	Myrtaceae	*Acca sellowiana* Burret	○
	Elaeagnaceae	*Elaeagnus umbellata* Thunb.	○
Cornales	Cornaceae	*Cornus kousa* F.Buerger ex Hance	○
Ericales	Ericaceae	*Rhododendron yedoense* f. *poukhanense* Sugim. ex T.Yamaz.	○
	Ebenaceae	*Diospyros kaki* Thunb.	
Gentianales	Styracaceae	*Styrax japonicus* Siebold & Zucc.	
	Apocynaceae	*Nerium oleander* L.	○

Table 3. Comparison of host plant diversity between Korea and other countries (+: present).

Family	Scientific Name	Korea	Others [a]
Ginkgoaceae	*Ginkgo biloba* L.	+	·
	Cryptomeria japonica (Thunb. ex L.f.) D.Don	+	+
Cupressaceae	*Metasequoia glyptostroboides* Hu et W.C.Cheng	·	+
Taxaceae	*Torreya nucifera* (L.) Siebold & Zucc.	+	·
Salicaceae	*Populus angulata* Aiton	·	+
Betulaceae	*Carpinus tschonoskii* Maxim.	·	+
Fagaceae	*Castanea crenata* Siebold et Zucc.	·	+
	Castanopsis cuspidata (Thunb.) Schottky	·	+
	Castanopsis sieboldii (Makino) Hatus.	+	+
	Lithocarpus edulis (Makino) Nakai	·	+
	Quercus acuta Thunb.	·	+
	Quercus acutissima Carruth.	+	+
	Quercus gilva Blume	·	+
	Quercus glauca Thunb.	+	+
	Quercus mongolica var. *crispula* (Blume) H.Ohashi	+	·
	Quercus phillyraeoides A. Gray	·	+
	Quercus salicina Blume	·	+
	Quercus serrata Murray	+	+
Ulmaceae	*Aphananthe aspera* (Thunb.) Planch.	+	+
	Celtis sinensis Pers.	+	+
	Ulmus parvifolia Jacq.	+	·
	Zelkova serrata (Thunb.) Makino	·	+
Moraceae	*Ficus erecta* Thunb.	+	·
	Ficus erecta var. *sieboldii*	+	·
Magnoliaceae	*Magnolia kobus* DC.	+	+
	Magnolia obovata Thunb.	+	·
Illiciaceae	*Illicium anisatum* L.	+	·
Lauraceae	*Actinodaphne acuminata* (Blume) Meisn.	·	+
	Actinodaphne lancifolia (Siebold & Zucc.) Meisn.	+	+
	Cinnamomum camphora (L.) J.Presl	+	+
	Cinnamomum yabunikkei H.Ohba	+	+
	Litsea japonica (Thunb.) Juss.	+	·
	Machilus japonica Siebold et Zucc. ex Blume	·	+
	Machilus thunbergii Siebold & Zucc. ex Meisn.	+	+
	Neolitsea aciculata (Blume) Koidz.	+	+
	Neolitsea sericea (Blume) Koidz.	+	+

Table 3. *Cont.*

Family	Scientific Name	Korea	Others [a]
Theaceae	*Camellia japonica* L.	+	+
	Camellia japonica var. *macrocarpa* Masam.	·	+
	Camellia sasanqua Thunb.	+	+
	Camellia × *williamsii* W.W.Sm.	+	·
	Cleyera japonica Thunb.	·	+
	Eurya emarginata (Thunb.) Makino	+	·
	Eurya japonica Thunb.	+	+
	Ternstroemia gymnanthera (Wight et Arn.) Bedd.	·	+
Hamamelidaceae	*Distylium racemosum* Siebold & Zucc.	+	+
Pittosporaceae	*Pittosporum tobira* (Thunb.) W.T.Aiton	·	+
Rosaceae	*Eriobotrya japonica* (Thunb.) Lindl.	+	·
	Prunus mume (Siebold) Siebold & Zucc.	+	+
	Prunus persica (L.) Stokes	+	·
	Prunus salicina Lindl.	+	·
	Prunus serrulata Lindl. f. *spontanea* (E.H.Wilson) Chin S.Chang	+	+
	Prunus spachiana (Lavallée ex Ed.Otto) Kitam. f. *ascendens* (Makino) Kitam.	+	·
	Prunus × *yedoensis* Matsum.	+	+
	Pseudocydonia sinensis (Thouin) C.K.Schneid.	+	·
	Pyrus pyrifolia var. *culta* (Makino) Nakai	+	·
Euphorbiaceae	*Mallotus japonicus* (L.f.) Müll.Arg.	·	+
Rutaceae	*Citrus natsudaidai* Hayata	+	·
	Citrus unshiu (Yu.Tanaka ex Swingle) Marcow.	+	·
Anacardiaceae	*Toxicodendron succedaneum* (L.) Kuntze	·	+
Aceraceae	*Acer morifolium* Koidz.	·	+
	Acer palmatum Thunb.	+	+
	Acer palmatum var. *matsumurae* (Koidz.) Makino	·	+
	Acer palmatum var. *sanguineum* Nakai	+	·
Aquifoliaceae	*Ilex integra* Thunb.	·	+
Celastraceae	*Euonymus japonicus* Thunb.	·	+
Elaeocarpaceae	*Elaeocarpus sylvestris* var. *ellipticus* (Thunb.) H. Hara	·	+
Elaeagnaceae	*Elaeagnus pungens* Thunb.	·	+
Elaeagnaceae	*Elaeagnus umbellata* Thunb.	+	·
Myrtaceae	*Acca sellowiana* (O.Berg) Burret	+	·
Cornaceae	*Cornus kousa* F.Buerger ex Hance	+	·
	Cornus macrophylla Wall.	·	+
Araliaceae	*Schefflera heptaphylla* (L.) Frodin	·	+
Ericaceae	*Rhododendron kaempferi* Planch.	·	+
	Rhododendron tashiroi Maxim.	·	+
	Rhododendron yedoense Maxim. f. *poukhanense* (H.Lév.) Sugim. ex T.Yamaz.	+	·
Myrsinaceae	*Ardisia sieboldii* Miq.	·	+
Primulaceae	*Myrsine seguinii* H.Lév.	·	+
Ebenaceae	*Diospyros kaki* Thunb.	+	+
	Diospyros morrisiana Hance	·	+
Styracaceae	*Styrax japonicus* Siebold & Zucc.	+	+
Symplocaceae	*Symplocos prunifolia* Siebold et Zucc.	·	+
Apocynaceae	*Nerium oleander* L.	+	·

[a] Species pool of others summarized form references [10,12,46,47].

The newly identified host plants in this study include 17 genera, including *Torreya*, *Cornus*, *Elaeagnus*, and *Magnolia*, and 25 taxa, including *Ginkgo biloba*, *Prunus spachiana* f. *ascendens*, *Ulmus parvifolia*, *Elaeagnus umbellata*, and *Illicium anisatum*. The diversity of host plants varies by family, with nine taxa (18.0%) in Rosaceae, six taxa (12.0%) in Lauraceae, and five taxa (10.0%) in Theaceae. However, there are 13 taxa in one genus and one family, accounting for 26.0% of the total, suggesting that the phylogenetic dependence on host plants is not high.

The growth form of the host plant was dominated by arboreal and sub-arboreal trees with 40 taxa (80.0%) and was parasitic on shrubby trees (10 taxa, 20.0%), including *Elaeagnus umbellata*, *Litsea japonica*, and *Ficus erecta* Thunb. (Table 4). The average height of the host tree was 6.2 m, with a range of sizes from 1.5 to 15 m.

Table 4. Ecological characteristics of host plants and parasitic character of *T. yadoriki*.

Character		**Type**	**Proportion (%)**
Host character	Life form	Tree	82.0
		Shrub	18.0
	Leaf functional group	Deciduous broad-leaved tree	50.0
		Evergreen broad-leaved tree	44.0
		Deciduous, coniferous tree	2.0
		Evergreen coniferous tree	4.0
	Distribution	Native	66.0
		Non-native	34.0
Parasitic character	Position adhered to	Top	31.7
		Middle	62.7
		Bottom	5.5
	Type of branch adhered to	Trunk	21.3
		Branch	58.1
		Twig	20.7

Among the host plants, native, cultivated, and planted species accounted for 66.0%, 18.0%, and 16.0%, respectively. The highest dispersal type of host plant was animal dispersal, with 60.0% (30 taxa). Coniferous and evergreen broad-leaved trees and deciduous broad-leaved trees accounted for 6.0%, 44.0%, and 50.0%, respectively. Species with a relatively high frequency of parasitization by *T. yadoriki* were Cryptomeria japonica (189 sites), *Litsea japonica* (109 sites), *Prunus* × *yedoensis* (88 sites), *Machilus thunbergii* (66 sites), *Neolitsea sericea* (61 sites), and *Camellia japonica* (23 sites). Meanwhile, there were some species with high occurrence in the study area but that were not identified as parasitic, such as *Ilex rotunda*, *Pinus thunbergii*, *Melia azedarach*, *Elaeocarpus sylvestris* var. *ellipticus*, and *Cinnamomum camphora* (one individual). Mistletoe has host specificity and preference through the evolutionary process of speciation [5,48–50], and some species are thought to have host-plant exclusivity of *T. yadoriki*.

3.3. Attachment Characteristics within the Host Plant

Attachment of *T. yadoriki* was identified on host plants of 48 taxa, 39 species, four varieties, three cultivars, and two hybrids from 31 genera and 21 families.

The distribution of the attachment location of *T. yadoriki* based on the host plant's tree type was 62.7% (431 individuals) in the middle part, 31.7% (218 individuals) in the upper part, and 5.5% (38 individuals) in the lower part. The distribution of branch types with parasitic attachment was highest at 58.1% (399) on the branch, followed by 20.7% (142) on the twig and 21.3% (146) on the trunk (Table 5). Different tree species showed differences in attachment characteristics. For *Cryptomeria japonica*, a candelabra-type tree with a relatively upright trunk and a long main stem, *T. yadoriki* was mainly distributed in the trunk and middle part. Zelkova-type trees with widely spreading branches, *Quercus acutissima*, *Quercus glauca*, *Quercus serrata*, *Magnolia kobus*, *Neolitsea sericea*, showed attachment of *T. yadoriki* on these branches, while other shrubby species with relatively small tree heights showed a predominant attachment of *T. yadoriki* to the upper part and main branches.

Table 5. Diversity, frequency and ecological characters of host plant of *T. yadoriki* in Korea (* new record).

	Sp. Code	Freq	L/F	L/T	Seas	Nat		Sp. Code	Freq	L/F	L/T	Seas	Nat
1	CrJa	189	T	Co	EG	E	26	IlAn *	2	T	Br	EG	N
2	LiJa	109	S	Br	EG	N	27	NeAc	2	T	Br	EG	N
3	PrxYe	88	T	Br	SG	N	28	PrPe *	2	T	Br	SG	P
4	MaTh	65	T	Br	EG	N	29	QuSe	2	T	Br	SG	N
5	NeSe	61	T	Br	EG	N	30	UlPa *	2	T	Br	SG	N
6	CaJa	23	T	Br	EG	N	31	AcSe *	1	S	Br	EG	P
7	MaKo	22	T	Br	SG	N	32	AcPav.s *	1	T	Br	SG	P
8	AcPa	19	T	Br	SG	E	33	ApAs	1	T	Br	SG	N
9	CeSi	17	T	Br	SG	N	34	CaxWi *	1	T	Br	EG	P
10	DiKa	15	T	Br	SG	P	35	CaSa	1	T	Br	EG	P
11	QuQl	11	T	Br	EG	N	36	CiCa	1	T	Br	EG	N
12	DiRa	6	T	Br	EG	N	37	CiNa *	1	T	Br	EG	P
13	PrSpf.a *	6	T	Br	SG	N	38	CoKo *	1	T	Br	SG	N
14	CiYa	5	T	Br	EG	N	39	ElUm *	1	S	Br	SG	N
15	PsSi *	5	T	Br	SG	P	40	EurJa	1	S	Br	EG	N
16	PrSa *	4	T	Br	SG	P	41	FiEr *	1	S	Br	SG	N
17	StJa	4	T	Br	SG	N	42	FiErv.s *	1	S	Br	SG	N
18	ErJa	3	T	Co	EG	P	43	MaOb *	1	T	Br	SG	P
19	NeOl *	3	S	Br	EG	P	44	PrMu	1	T	Br	SG	P
20	RhYef.p *	3	S	Br	EG	E	45	PrSef.s	1	T	Br	SG	N
21	AcLa	2	T	Br	EG	N	46	PyPyv.c *	1	T	Br	SG	P
22	CaSi	2	T	Br	EG	N	47	QueAc	1	T	Br	SG	N
23	CiUn *	2	T	Br	EG	P	48	QuMov.c *	1	T	Br	SG	N
24	EuEm *	2	S	Br	EG	N	49	ToNu *	1	T	Co	EG	N
25	GiBi *	2	T	Co	SG	P		Total	697				

These attachment traits are thought to be highly correlated with the characteristic that *T. yadoriki* dispersal is driven by avian feeding. The tendency to attach is considered to occur at a high frequency in areas with high branch density and suitable conditions for birds. It is necessary to conduct further studies on the bird diversity involved in the dispersal of *T. yadoriki,* the effects of bird feeding and digestion on germination, the external morphological characteristics of seed attachment sites on seed germination and settlement, and pharmacological activity, depending on the host plant.

3.4. Species Distribution Model

T. yadoriki's specific distribution model was built as a maximum entry algorithm. The area under the curve of the receiver operation characteristic was 0.948 $\pm$ 0.026 (mean $\pm$ standard deviation), and the performance of the constructed model was excellent. Of the total eight environmental factors, 'density of artistic forest' and 'meant temperature of coldest quarter' accounted for 75.3% of the total importance, which was the main distribution determinant of *T. yadoriki* (Figure 3). The most important distribution determinant was 'density of artistic forest' (52.3% $\pm$ 2.0%). And mean temperature of coldest quarter was the second most important determinant of distribution (23.0% $\pm$ 4.3%). The distribution probability of species tended to be proportional to the 'density of artificial forest'. The distribution probability of *T. yadoriki* then increased rapidly when the 'mean temperature of coldest quarter' was above 5–6 °C.

In the average distribution probability map of species, the critical probability for determining distribution was calculated to be 0.2898 $\pm$ 0.1018. Therefore, *T. yadoriki* is predicted to be distributed throughout the south and southeast coasts of Jeju Island (Figure 4).

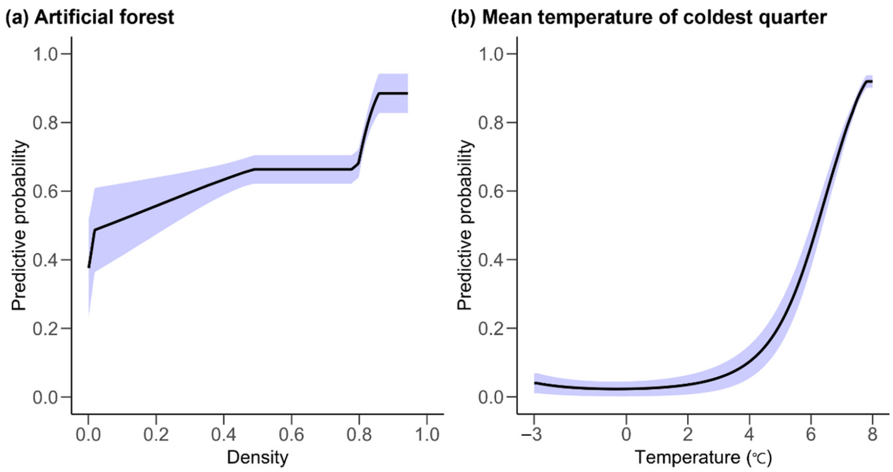

Figure 3. The response curve showing the density of artificial forests (**a**) and mean temperature of coldest quarter (**b**), which are the main distribution factors of *Taxillus yadoriki*. The line represents the mean, and the blue ribbon represents the standard deviation.

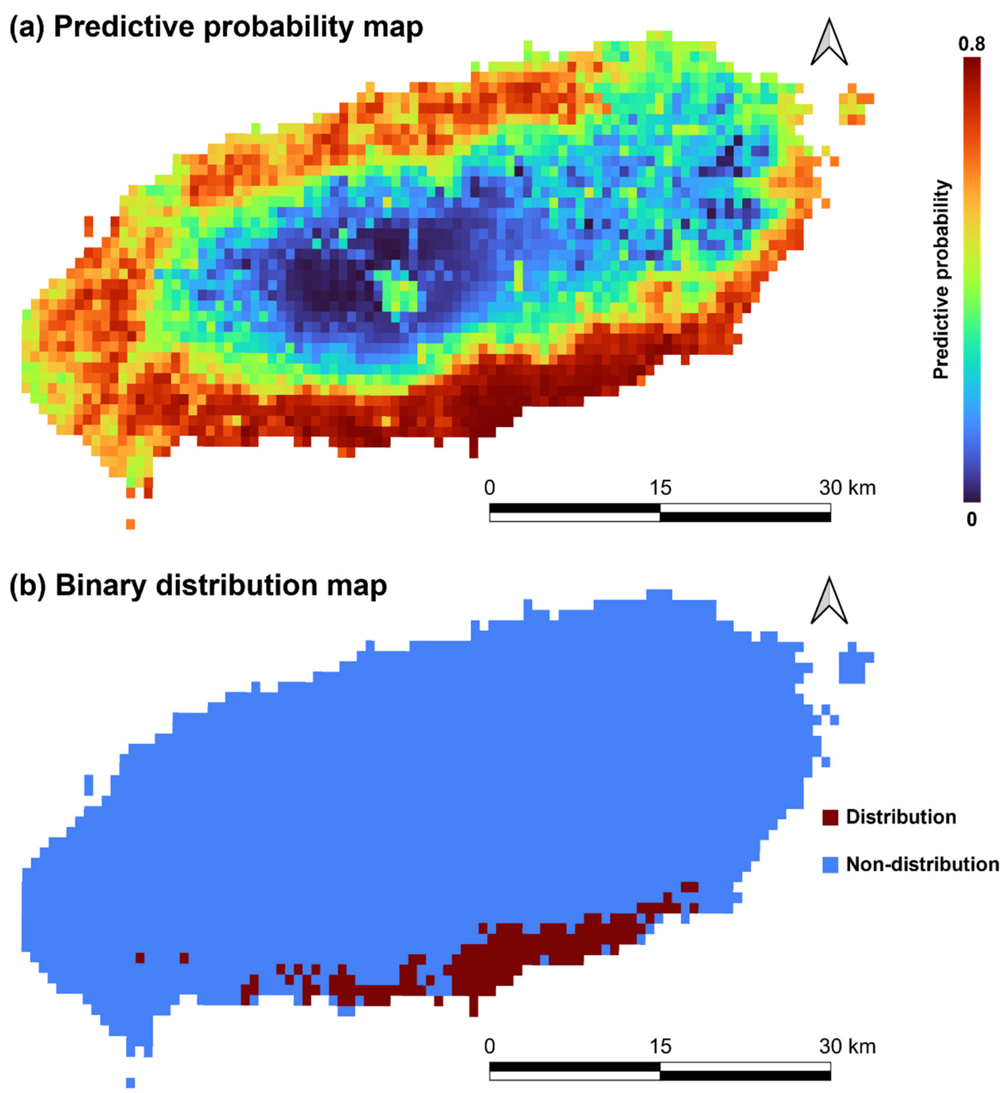

Figure 4. Probability map (**a**) and binarized distribution map (**b**) predicted by Maxent of *Taxillus yadoriki* in Jeju Island. Binarization was done with maximum test sensitivity plus specificity logistic threshold.

The constructed species distribution model was complementary to the field research results. In the modeling, *T. yadoriki* preferred artificial forests. This reflects the field surveys' preference for small, human-managed forests and populations over natural forests, and is consistent with the characteristics associated with dispersal by small birds. For these small birds, artificial forests, such as orchards, provide protection from their natural enemies, large animals, while also providing an abundance of food [51,52]. The proportional relationship between the probability of distribution of *T. yadoriki* and the mean temperature of the coldest quarter also reflects the fact that the areas where *T. yadoriki* occurred in field surveys do not drop below freezing in winter. The model refines this further and suggests a quantitative distribution limit temperature of 5–6 °C. Finally, the species distribution model predicts that the distribution of *T. yadoriki* extends beyond the southern and southwestern distributions of Jeju Island, as well as the southern and southeastern coasts, which were the areas investigated by field researchers. This is because the low-elevation coastal plain of Jeju Island, with the exception of the northeast, is covered by operational orchards, providing physical habitat for *T. yadoriki*, but its distribution is limited by the lowest temperatures of the year.

4. Conclusions

The host plants of *Taxillus yadoriki* were diverse, including 49 taxa, 32 genera, and 21 families. Twenty-three host plants were identified for the first time. In Korea, *T. yadoriki* was limited to the Seogwipo area and was mainly parasitic on street trees and landscape trees subjected to anthropogenic disturbance. While the host plant species diversity was high, the frequency of occurrence was particularly high for certain species, including *Cryptomeria japonica* and *Litsea japonica*. *T. yadoriki* was commonly attached to both woody and broadleaf host plants, with the most frequent attachment location being the middle part of the host plant and the most frequent attachment site being the branch. In addition, as there were tree species not specifically parasitic in the area where they grow naturally, they were determined to have host specificity and exclusivity. The field survey results were supported using a species distribution model, and potential distribution areas were predicted. *T. yadoriki* requires the presence of woody plants on which it can parasitize, as well as temperatures that do not fall below freezing throughout the year in habitats subject to artificial disturbance. Accordingly, it was predicted that the distribution would expand to the south and southeast coasts of Jeju Island, which is suitable for the distribution determinants. Further studies are needed to analyze the potential distribution and cultivation sites of *T. yadoriki*, which is highly valued as a medicinal plant, as well as the variation of pharmacological activity according to the host plant, alongside cultivation technology and management techniques.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f15050799/s1, Table S1: Summary of Correlations between 25 environmental variables. Figure S1: Diversity in environmental factors used in species distribution model for *Taxillus yadoriki* in Jeju Island.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available since these are research data conducted as a project for obtaining specific research results and intellectual property rights at the Nation Institute of Forest Science. When the project is completed, it is planned to be publicly provided through the institution's original and independent system.

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