

Prediction of Suitable Habitat for Lycophytes and Ferns in Northeast China: A Case Study on *Athyrium brevifrons*

LI Yan^{1, 2, 3}, CAO Wei¹, HE Xingyuan^{1, 2, 3, 4}, CHEN Wei^{1, 2, 3, 4}, XU Sheng^{1, 2, 4}

(1. Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China; 2. University of Chinese Academy of Sciences, Beijing 100049, China; 3. Shenyang Arboretum, Chinese Academy of Sciences, Shenyang 110016, China; 4. Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China)

Abstract: Suitable habitat is vital for the survival and restoration of a species. Understanding the suitable habitat range for lycophytes and ferns is prerequisite for effective species resource conservation and recovery efforts. In this study, we took *Athyrium brevifrons* as an example, predicted its suitable habitat using a Maxent model with 67 occurrence data and nine environmental variables in Northeast China. The area under the curve (AUC) value of independent test data, as well as the comparison with specimen county areal distribution of *A. brevifrons* exhibited excellent predictive performance. The type of environmental variables showed that precipitation contributed the most to the distribution prediction, followed by temperature and topography. Percentage contribution and permutation importance both indicated that precipitation of driest quarter (Bio17) was the key factor in determining the natural distribution of *A. brevifrons*, the reason could be proved by the fern gametophyte biology. The analysis of high habitat suitability areas also showed the habitat preference of *A. brevifrons*: comparatively more precipitation and less fluctuation in the driest quarter. Changbai Mountains, covering almost all the high and medium habitat suitability areas, provide the best ecological conditions for the survival of *A. brevifrons*, and should be considered as priority areas for protection and restoration of the wild resource. The potential habitat suitability distribution map could provide a reference for the sustainable development and utilisation of *A. brevifrons* resource, and Maxent modelling could be valuable for conservation management planning for lycophytes and ferns in Northeast China.

Keywords: *Athyrium brevifrons*; lycophytes and ferns; Maxent; suitable habitat; Northeast China; gametophyte

Citation: LI Yan, CAO Wei, HE Xingyuan, CHEN Wei, XU Sheng, 2019. Prediction of Suitable Habitat for Lycophytes and Ferns in Northeast China: A Case Study on *Athyrium brevifrons*. *Chinese Geographical Science*, 29(6): 1011–1023. <https://doi.org/10.1007/s11769-019-1085-4>

1 Introduction

Suitable habitat provides necessary conditions for survival and reproduction of species. Predicting the distribution of suitable habitats for species has become increasingly important in many fields especially in conservation biology (Manel et al., 2001; Balbontin, 2005). To develop effective conservation strategies, prediction of suitable habitats is widely used and applied for numerous species conservation studies with different taxa

and regions (Davies et al., 2008; Galparsoro et al., 2009; Giordano et al., 2010; Amici et al., 2015; Li et al., 2016, 2019). Identifying suitable habitat for a species can focus the search extent as well as map out potential sites for population restoration, maximise survival of the species, and conserve and manage the native habitats in a rational manner (Li et al., 2015; Campbell and Hilderbrand, 2017). French et al. (2018) quantified habitat suitability of Atlantic halibut and linked the suitability to stock abundance and distribution: this is a significant

Received date: 2019-01-03; accepted date: 2019-03-13

Foundation item: Under the auspices of National Key Research and Development Program of China (No. 2016YFC0500300), National Natural Science Foundation of China (No. 41675153)

Corresponding author: HE Xingyuan. E-mail: hexy@iae.ac.cn; XU Sheng. E-mail: shengxu703@126.com

© Science Press, Northeast Institute of Geography and Agroecology, CAS and Springer-Verlag GmbH Germany, part of Springer Nature 2019

step for future management of the fishery for this species. Cook et al. (2010) re-evaluated suitable habitat for reintroducing the eastern barred bandicoot and suggested that limited resources be focussed on the most suitable sites. Priority areas for species reintroduction and habitat restoration can be located by predicting suitable habitats for species in conservation biology, and this provides a good way to make decisions and maximise the cost-effectiveness of restoration work (Benito Garzón et al., 2006; Olsson and Rogers, 2009).

Species distribution models (SDMs) are popular methods for predicting geographical distribution and exploring the habitat preference of species. Multiple types of SDMs have been developed (bioclimatic envelope (BIOCLIM), domain distance (DOMAIN), generalized linear models (GLMs), generalised additive models (GAMs), genetic algorithm for rule-set production (GARP), etc.) and applied in the prediction of species distribution with different research purposes (MacKenzie et al., 2002; Zaniewski et al., 2002; Gu and Swihart, 2004; Pearce and Boyce, 2006; Carnaval and Moritz, 2008; Baldwin, 2009; Nieto-Lugilde et al., 2015). An array of SDM methods for modelling presence-only data has been developed (Elith et al., 2011), and among them the Maximum entropy (Maxent) model (Phillips et al., 2006; Phillips and Dudik, 2008) is widely used (Radosavljevic and Anderson, 2014; West et al., 2016). Maxent has been applied extensively, from finding correlates between species occurrences, mapping current distributions, predicting climate change impact on the distributions of species, to large-scale biodiversity mapping applications for both government and non-government organisations (Elith et al., 2011; Zhang et al., 2014). In recent years, there are many applications of Maxent in the prediction of plants' suitable habitats, such as *Trioza erythrae* (Richard et al., 2018), *Picea smithiana* (Zhang, et al., 2011), medicinal plants (Yi et al., 2016; Shen et al., 2017) and so on, but it is seldom used in lycophyte and fern habitat prediction.

Lycophytes and ferns are spore-bearing vascular plants which are significant groups in the evolutionary history of land plants (Zhang et al., 2013), and have important and unique values for food, medicine, garden, industry, agriculture, and so on. Diversity conservation of lycophytes and ferns is an important aspect of biodiversity conservation. Due to their susceptibility to environment change, the current situation of the lycophytes

and ferns is not so optimistic: Brummitt et al. (2015; 2016) assessed 972 species randomly selected from all lineages of lycophyte and fern diversity from International Union for Conservation of Nature (IUCN), and indicated that 16% of lycophyte and fern species are globally threatened with extinction. Dong et al. (2017) evaluated the extinction risk of 1372 species of lycophytes and ferns in China according to IUCN criteria, and found that 13.27% of the species are threatened with extinction. In recent years, the conservation of lycophytes and ferns has focused more on the suitability of habitats. Bruni et al. (2013) evaluated the extinction risk for the aquatic fern *Marsilea quadrifolia*, indicated active conservation strategies (such as relocation and reintroduction) needing to be implemented to improve the survival rate thereof. To a species on the edge of extinction such as island endemic fern *Anogramma ascensionis*, Baker et al. (2014) proposed rehabilitation of areas suitable for reintroduction as an important step in an integrated conservation plan, and invasive species will be eradicated from potential sites as part of the preparatory work, therefore, the research on suitable habitats is prerequisite for the effective conservation and utilisation of lycophyte and fern species.

Athyrium brevifrons Nakai ex Tagawa is a perennial herb of the family Athyriaceae, which mainly distributed in Northeast China and its surrounding areas (Fu, 1995; Wang et al., 1999; Wu et al., 2013). It is one of the most popular edible wild herbs exported abroad all year round (Dong and Wang, 1991; Liu and Li, 1995). It is also a traditional Chinese herbal medicine. Modern medical studies have confirmed that *A. brevifrons* not only has an anti-inflammatory effect to prevent pneumonia (Han et al., 2018), but also is a promising agent with anti-cancer properties which significantly suppressed tumour growth (Qi et al., 2015, 2017). Another study has isolated nine new compounds from *A. brevifrons* for the first time in recent years (Liu et al., 2016). These compounds may contribute to the medical effects of *A. brevifrons*, however, due to the sensitivity of lycophytes and ferns to environmental change, along with increasing of market demand and habitat destruction, the wild *A. brevifrons* resource has gradually decreased. It is necessary to conserve and enlarge the distribution extent of *A. brevifrons*, therefore we take *A. brevifrons* as an example to make the conservation planning for lycophytes and ferns resources in Northeast China. When

taking measures to protect and reintroduce of *A. brevifrons* resource, two questions should be addressed first: 1) what is the most suitable area for *A. brevifrons* distribution in Northeast China? 2) What environmental factors have the greatest influence on the distribution of *A. brevifrons*? To answer these questions, a Maxent model was used to predict the suitable habitat of *A. brevifrons* and to determine the key factors affecting its distribution, providing a theoretical basis for the protection and restoration of wild *A. brevifrons* resource in Northeast China.

2 Materials and Methods

2.1 Study area

The study area is located in Northeast China and covers three provinces (Heilongjiang Province, Jilin Province, and Liaoning Province) and the eastern part of Inner Mongolia (Hulunbuir City, Tongliao City, Chifeng City, and Hinggan League). There are three main mountain ranges running from west to east in the area (38°43'N–53°33'N and 115°31'E–135°5'E, Da Hinggan Mountains, Xiao Hinggan Mountains, and Changbai Mountains, Fig. 1). In winter the weather is cold and dry, and is often controlled by the Mongolian high. In summer the weather is hot and rainy, and is affected by oceanic air masses (Xu, 1986). With the change in temperature condition from south to north, the vegetation types therein are quite different. Deciduous broad-leaved forest occurs in the warm temperate zone, mixed coniferous broad-leaved forest in the temperate zone, and coniferous forests in the cold temperate zone. These forests provide good potential sites for lycophytes and ferns to grow.

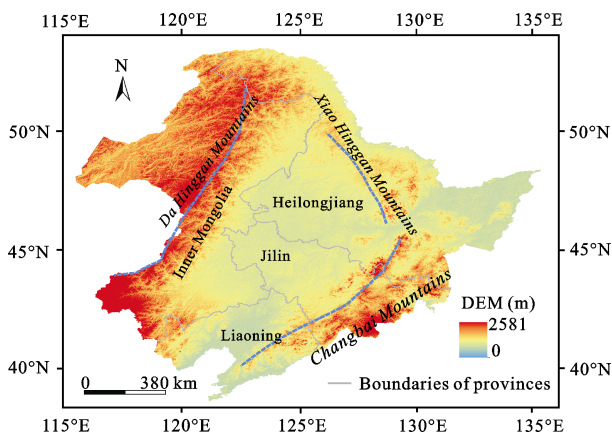


Fig. 1 The study area showing mountain ranges in Northeast China

2.2 Occurrence data processing

The occurrence data are also called presence-only data which are effective for modelling species distribution for many species in various regions (Elith et al., 2006). The occurrence data of *A. brevifrons* were obtained in two ways: the field investigation data during 2008–2012, and herbarium data (Northeast Biological Herbaria of Institute of Applied Ecology, Chinese Academy of Sciences). We took two steps to process these data: firstly, we utilized the ‘Baidu coordinate pick-up system’ (<http://api.map.baidu.com/lbsapi/getpoint/index.html>) to extract and verify the latitude and longitude coordinates of each fern record according to the description of distribution location, and discarded those with incomplete or uncertain descriptions of their distribution locations. Secondly, because co-located or nearby records are often spatially auto-correlated samplings (Phillips et al., 2017), to meet the IPP’s (Inhomogeneous Poisson Process) assumption of independent samples for Maxent, records within 10 km of each other were removed randomly (Boria et al., 2014). In the end, 67 occurrence records (33 herbarium records and 34 investigated records) remained for further analysis and 64 occurrence records were excluded.

2.3 Environmental variable selection and processing

Considering the biological meanings and topographic effects on the distribution of *A. brevifrons*, 22 environmental variables were chosen in the research, including: 1) 19 bioclimatic variables (Fick and Hijmans, 2017) with 30" spatial resolution (Version 2.0) were obtained from WorldClim website (www.worldclim.org), which represent annual trends, seasonality, and extreme or limiting environmental factors with more biological meanings. Bioclimatic variables, which became available since 1984, are the most common source for SDMs studies especially for Maxent (Booth et al., 2014; Booth, 2018) and, 2) elevation (Digital Elevation Model, DEM) with 30 m resolution was downloaded from the Geospatial Data Cloud website (www.gscloud.cn). The DEM data were used to generate slope and aspect using ArcGIS 10.2. Topographic variables (elevation, slope and aspect) were resampled to the same 30" spatial resolution as for bioclimatic variables.

To avoid the impact of high cross-correlations, principal

component analysis (PCA) and multi-collinearity test were used for selecting the variables involved in model operation. PCA was applied to 19 bioclimatic variables (Appendix 1) to get the loading coefficients of each variable (Cui et al., 2018). The multi-collinearity test (IBM SPSS Statistics 24) was performed on the 22 variables (Appendix 2). Only those variables with higher loading coefficients were included in the model when the absolute Pearson correlation coefficient $|r| \geq 0.8$ (Yang et al., 2013; Jia et al., 2017). Finally, nine environmental variables, including six bioclimatic variables (Bio1 (annual mean temperature), Bio3 (isothermality), Bio5 (max temperature of warmest month), Bio7 (temperature annual range), Bio15 (precipitation seasonality) and Bio17 (precipitation of driest quarter)) and three topographic variables (elevation, slope and aspect) were selected for Maxent prediction (Appendix 2).

2.4 Modelling procedure

Maxent (Phillips et al., 2018) was chosen to predict suitable habitat for *A. brevifrons*. Maxent is a powerful machine learning technique requiring only occurrence data and environmental layers for modelling. We chose cross-validation in the settings and the number of replicate runs was set to 10. The jack-knife test was chosen and other parameters set to their default values. Variable importance was estimated by two heuristic tests (percentage contribution and permutation importance) and the jack-knife test in Maxent (Phillips et al., 2006; Elith et al., 2011; Phipps et al., 2017). In the end, the prediction result from Maxent was reclassified in ArcGIS according to arbitrarily defined probability classes (Khafaga et al., 2011; Lu et al., 2012; Remya et al., 2015).

2.5 Evaluation of model performance

The objective of model evaluation is to assess model generality, and cross-validation is preferable based on the predictive accuracy in applications of Maxent (Merow et al., 2013; Estallo et al., 2018). Ten-fold cross validation was used to partition the occurrence data randomly into ten equal-size ‘folds’ for training and testing, and models were created by leaving out each fold in turn, then the left-out folds were used for test evaluation (Li et al., 2016; Lathrop, et al, 2018). Training accuracy refers to the goodness of fit of the model, while testing refers to the capability of the model prediction of the occurrence data not used in training,

and is considered as an independent means with which to evaluate model performance (Estallo et al., 2018). The area under the curve (AUC) of Receiving Operating Characteristic (ROC) curves has been widely used in Maxent as a measure of model accuracy performance (Merow et al., 2013). AUC ranks between 0 and 1; $AUC \leq 0.5$ shows that the model prediction is no better or worse than random; 0.5–0.7 indicates poor performance; 0.7–0.9 represents moderate/excellent performance; and > 0.9 demonstrates exceptional performance (Wang et al., 2007; Peterson et al., 2011; Vilar et al., 2016; West et al., 2016). Finally, we sorted out the distribution range of *A. brevifrons* county area according to the herbarium specimen collections which were not used in the prediction, and compared it with the predicted result, which could be used as an alternative for evaluating the prediction performance of the model.

3 Results

3.1 Analysis of AUC and variables’ contributions

The average AUC was 0.901 ± 0.066 (mean \pm SD) with ten-fold cross-validation, showing the model’s good performance in the prediction of suitable habitat for *A. brevifrons* (Fig. 2).

Our results showed the most important environmental variables affecting the distribution of *A. brevifrons* were related to precipitation (60.6% contribution, 63.3% permutation importance), followed by temperature-related variables and topography-related variables according to the heuristic tests (Table 1). Three environmental variables (Bio17 (precipitation of driest quarter), Bio3

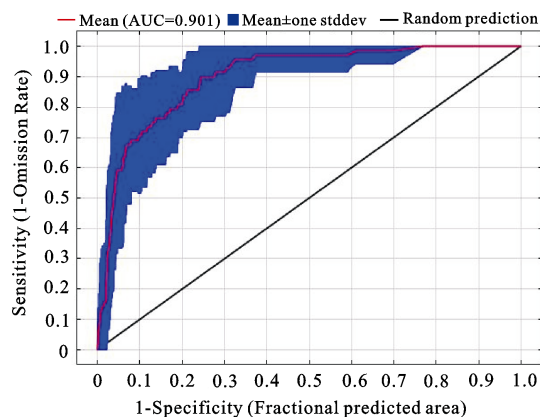


Fig. 2 The value of the area under the curve (AUC) with replicate runs for *A. brevifrons* in Northeast China

Table 1 The mean contributions of environmental variables using heuristic tests (percentage contribution and permutation importance) to the prediction of suitable habitat

Type	Variable	Contribution (%)		Permutation importance (%)	
		Variable	Type	Variable	Type
Precipitation	Bio17	58.6	60.6	56.6	63.3
	Bio15	2.0		6.7	
Temperature	Bio3	22.2	36.1	13.2	35.6
	Bio7	6.5		9.8	
	Bio5	5.1		9.3	
	Bio1	2.3		3.3	
Topography	Aspect	1.5	3.3	0.6	1.1
	Elevation	1.1		0.1	
	Slope	0.7		0.4	

Notes: 'Bio1' is 'annual mean temperature'; 'Bio3' is 'isothermality'; 'Bio5' is 'max temperature of warmest month'; 'Bio7' is 'temperature annual range'; 'Bio15' is 'precipitation seasonality'; 'Bio17' is 'precipitation of driest quarter'

(isothermality), and Bio7 (temperature annual range)) together contributed 87.3 % to contribution and 79.6 % to permutation importance. Precipitation of driest quarter (Bio17) contributed 58.6 % (56.6 % permutation importance) to the prediction, and was the key variable in determining suitable habitat.

Our result of jack-knife testing regularised training gains (Fig. 3) showed precipitation of driest quarter (Bio17) was the key variable affecting prediction of suitable habitat for *A. brevifrons*, followed by Bio15. Bio17 contributed the highest gain when used in isola-

tion, and thus reduced it the most when omitted.

3.2 Assessment of habitat suitability of *A. brevifrons*

The result of Maxent occurrence probability of *A. brevifrons* was reclassified into four classes according to arbitrarily defined probability classes in ArcGIS 10.2 (Fig. 4). The high and medium habitat suitability classes occupied 5.73% and 3.99% respectively (119 787 rasters and 83 507 rasters) of the whole study area. The low habitat suitability class accounted for 23.68% (495 005

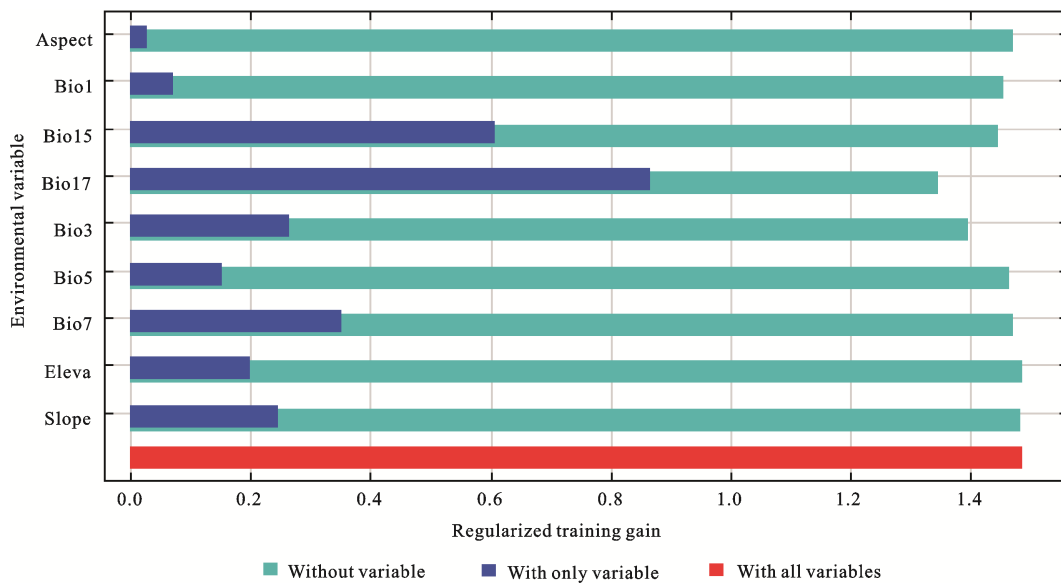


Fig. 3 Results of jack-knife analysis of environmental variable importance for the distribution of *A. brevifrons* in Northeast China. 'Bio1' is 'annual mean temperature'; 'Bio3' is 'isothermality'; 'Bio5' is 'max temperature of warmest month'; 'Bio7' is 'temperature annual range'; 'Bio15' is 'precipitation seasonality'; 'Bio17' is 'precipitation of driest quarter'; 'Eleva' refers to elevation

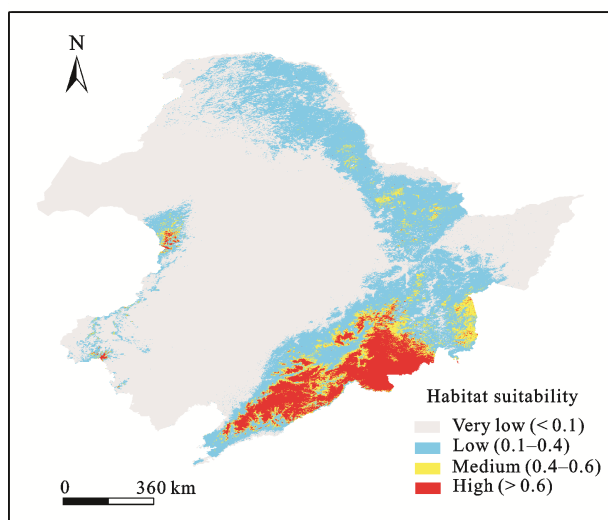


Fig. 4 Predicted distribution of suitable habitat for *A. brevifrons* in Northeast China

rasters), while the very low class covered 66.60% (1 392 297 rasters). The distributions of suitable areas (high habitat suitability, medium habitat suitability, and low habitat suitability) were mainly clustered on the Changbai Mountains and Xiao Hingan Mountains: southern parts of the Changbai Mountains contained highly, and moderately, suitable habitats making it the best area for natural distribution of *A. brevifrons*.

Variable means and coefficients of variations (CV) are listed in Table 2. The key environmental variable (Bio17) and the other three variables (Bio15, Bio3, and Bio7) were chosen according to the results of heuristic tests and the jack-knife test (Table 1, Fig. 3). Generally, means of Bio17 and Bio3 in high and medium suitability classes were higher than in low and very low suitability classes, while means of Bio15 and Bio7 show the opposite tendency. The changes of each variable's means were different in four habitat suitability classes. From the lowest mean (10.46) to the highest mean (26.27), the percentage of Bio17 increased 151%, but the mean percentage increase or decrease in three variables (Bio15, Bio3, and Bio7)

was much smaller compared with Bio17. The suitability class was affected more by Bio17 than other variables (Bio15, Bio3, and Bio7). The analysis indicated that Bio17 was the key environmental variable controlling the spatial distribution pattern of habitat suitability. The smallest CVs of four variables all appeared in high suitability class areas, which showed that the fluctuations therein were the smallest among the four suitability classes.

4 Discussion

4.1 Model performance evaluation

AUC analysis is an important measure of model prediction performance: it is the probability that a randomly chosen presence site is ranked above a random background site (Phillips et al., 2006). Models with values above about 0.75 are considered potentially useful (Elith, 2000; Phillips and Dudik, 2008). Studies also have shown that the AUC values of species with broad distribution scope tend to be lower (Evangelista et al., 2008; Yang et al., 2013). In our study, independent test data were used to assess model prediction, and Maxent provided an excellent performance (Fig. 2).

The regional information recorded in the specimens can reflect the approximate distribution of plants. Therefore, specimens of *A. brevifrons* in Northeast Biological Herbaria of Institute of Applied Ecology, Chinese Academy of Sciences were collated, and using 'county' as an index we plotted the distribution range map of the specimen collections. The county area distribution of *A. brevifrons* can generally reflect the natural distribution of *A. brevifrons* in Northeast China (Fig. 5). In our study, the predicted distribution range of suitable habitat (Fig. 4) for *A. brevifrons* with 30" spatial resolution was consistent with the county area distribution (Fig. 5) of *A. brevifrons*, evincing the high accuracy of the prediction.

Table 2 Four variables' mean and coefficient of variation (CV) within each habitat suitability class of *A. brevifrons* in Northeast China

Environmental variables (Unit)	Very low		Low		Medium		High	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Bio17 (mm)	10.46	53.25	17.40	25.69	23.00	31.13	26.27	23.79
Bio15 (%)	112.75	9.20	101.85	5.31	99.54	5.96	100.46	3.36
Bio3 (%)	23.76	9.68	23.88	5.86	24.43	4.22	25.26	4.12
Bio7 (°C)	52.48	7.83	53.00	8.36	49.00	6.41	47.00	4.43

Notes: 'Bio3' is 'isothermality'; 'Bio7' is 'temperature annual range'; 'Bio15' is 'precipitation seasonality'; 'Bio17' is 'precipitation of driest quarter'

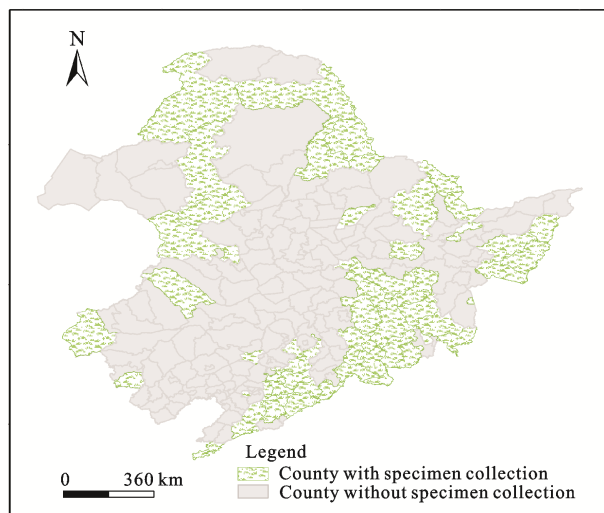


Fig. 5 Distribution of counties with specimen collection of *A. brevifrons* in Northeast China

4.2 The impact of chief variables on natural distribution

The type of environmental variables showed that precipitation contributed the most to the distribution prediction, followed by temperature, and topographic contribution the least. Topographic variables may affect the distribution of plants over a small-scale landscape, but on a large scale, they may be minimal, the reason could be that topographic variables exert their influences on plants indirectly (Vormisto et al., 2004; Nettesheim et al., 2014). The high habitat suitability areas have comparatively more precipitation and with less fluctuation in the driest quarter, but very low habitat suitability areas showed the opposite tendency.

The study shows that among all the bioclimatic variables related to the natural distribution of *A. brevifrons*, precipitation-related variables are more important than temperature-related variables, and precipitation of driest quarter (Bio17) is the key factor in determining the distribution. *A. brevifrons* is less drought-resistant than other common ferns in North China (Wu et al., 2014). Its life cycle alternates between two generations, sporophyte generation and gametophyte generation (Sheffield, 1994; Banks, 1999). Water plays a key role in the gametophyte generation from the germination of spores to the formation of juvenile sporophytes on gametophytes. The gametophyte has only small rhizoids which increase the risk when exposed to water stress. We believe that precipitation of driest quarter determines the

survival probability of gametophytes on a large-scale landscape. Peck et al. (1990) revealed that the greatest mortality of gametophytes was related to increased exposure to drought. Therefore, the colonizing stages of ferns (gametophyte and juvenile sporophyte) have much greater risks of mortality than mature sporophytes (Peck et al., 1990; Greer and McCarthy, 2000). Gametophyte generation plays the central role in the life cycle, for the sporophyte ultimately owes its existence to gametophytes (Testo and Watkins, 2013). Sato (1992) investigated the population mortality of overwintered gametophytes of *A. brevifrons*, analysed the main environmental factors and a safe-microsite for gametophyte establishment in nature. The results showed that spring mortality was highly correlated with water stress. With the decrease of soil moisture content after snow-melt in spring, the overwintering gametophytes were sensitive to water stress even a short drought period, and the mortality increased significantly. The gametophytes are not sufficiently drought-tolerant to survive the spring in the immature stage. Therefore, he suggested that spring desiccation might be a factor in reducing or limiting the natural distribution of gametophyte populations. Our results are consistent with those of Sato and those in the aforementioned empirical literature.

The ecology of lycophytes and ferns is complex given the reliance on independent gametophytes and sporophytes with unique habitat requirements (Canestraro et al., 2014). The biological features make lycophytes and ferns more sensitive to the environmental variables. Understanding gametophyte biology is critical to understanding fern sporophyte distributions (Watkins et al., 2007). Lycophytes and ferns in Northeast China are mesotherm and have many ecological types according to the classification by Lu and Chen (2013); because of their different ecological types, the environmental variables affecting the distribution of lycophytes and ferns might be different. So, it is valuable to consider both generations of the life cycle in the studies for further analysis of the impact of environmental variables on their natural distribution.

4.3 Suitable habitat assessment and conservation

A. brevifrons is a fern with homology of food and traditional Chinese medicine. With increasing demand in domestic and foreign markets, large-scale mass harvesting has led to a decrease in the distribution of wild *A.*

brevifrons resources. Especially in recent years, the local villagers have dug up whole rhizomes in mountainous areas with an abundant *A. brevifrons* distribution, and transplanted them in greenhouses. The rhizomes were discarded after picking all the edible petioles. Normally, a productive plant is 10–100 years old, however, after open acquisition and years of successive digging, the productivity is extremely low, resources are significantly depleted, and *A. brevifrons* has withered in significant numbers (Dong and Wang, 1991).

Protective development of the wild *A. brevifrons* resource is urgent, because the extensive exploitation of resources has been exacerbating the fierce conflict between ecological protection and economic development (He and Yu, 2016). The application of models provides an effective technical means for protective development. As with the widely-applied SDMs, the Maxent model can evaluate the potential distribution range of a species (West et al., 2016) and promising results were even obtained for endangered species with limited occurrence data (Pearson et al., 2007; Kumar and Stohlgren, 2009; Zhang et al., 2011). Our model results show the spatial habitat suitability of *A. brevifrons*, which is in line with the actual distribution (Fig. 5) of *A. brevifrons*. Our habitat suitability map of *A. brevifrons* could aid the conservation and restoration of *A. brevifrons*. From the regional-scale prediction of habitat suitability distribution for *A. brevifrons*, we find that Changbai Mountains provide the best ecological conditions for the survival of *A. brevifrons* as mountain areas with conifer-broadleaf forest and broadleaf forest provide the appropriate under-canopy environment. Therefore, we suggest that ecological conservation of the population in this area should be enhanced. In addition, under-canopy cultivation in medium or even low suitability habitats should be implemented to restore the *A. brevifrons* population. The cultivation not only improves ecological efficiency, reduces the harvest of wild *A. brevifrons* resources, but also increases the economic benefits of forests and the income of forest farmers.

Understanding the overall geographical distribution and suitable habitat range of species is prerequisite to effective species conservation, management, and recovery efforts (Pearce and Boyce, 2006; Lu et al., 2012). Firstly, the conservation efficiency can be improved by considering the centralized protection of species distributed in the most suitable habitat when formulating poli-

cies for species conservation; secondly, the suitable habitat is the best ecological condition for population restoration and expansion, and the analysis of habitat suitability can provide a reference for species *ex-situ* conservation and reintroduction; finally, the analysis of suitable habitats provides a clear range of species distribution, which forms the basic data and decision basis for resource surveys. Therefore, it is important to prioritise habitat suitability for conservation, evaluation, and utilisation of lycophytes and ferns. Our results showed the potential habitat suitability distribution map which could provide a reference for the sustainable development and utilisation of the *A. brevifrons* resource. While the Maxent method is efficient, as used in this study for predicting suitable habitat and analysing the impact of chief variables, it could be applied to other lycophyte and fern species to evaluate their habitat suitability and allow conservation management planning thereof. We hope that this study could provide a reference for the utilisation and diversity conservation of lycophytes and ferns in Northeast China or even as a larger scale.

5 Conclusions

This study predicted the suitable habitat for *A. brevifrons* using a Maxent model with 67 occurrence data and nine environmental variables in Northeast China. The type of environmental variables showed that precipitation contributed the most to the distribution prediction. Precipitation of driest quarter (Bio17) was the key factor in determining the natural distribution of *A. brevifrons*, the reason could be the greatest mortality of fern gametophytes under water stress. The Changbai Mountains, which covered almost all the high and medium habitat suitability areas, provided the best ecological conditions for the survival of *A. brevifrons*, should be considered as the priority area for protection and restoration of the wild resource.

Acknowledgement

Part of the occurrence data were provided by Northeast Biological Herbaria of Institute of Applied Ecology, Chinese Academy of Sciences. We express sincere thanks to Prof. Chang Yu and Prof. Tao Dali for the revisions and comments, and Prof. Xiong Zaiping for the advice to GIS.

References

- Amici V, Eggers B, Geri F et al., 2015. Habitat suitability and landscape structure: a maximum entropy approach in a mediterranean area. *Landscape Research*, 40(2): 208–225. doi: 10.1080/01426397.2013.774329
- Baker K, Lambdon P, Jones E et al., 2014. Rescue, ecology and conservation of a rediscovered island endemic fern (*Anogramma ascensionis*): *ex situ* methodologies and a road map for species reintroduction and habitat restoration. *Botanical Journal of the Linnean Society*, 174(3): 461–477. doi: 10.1111/boj.12131
- Balbontín J, 2005. Identifying suitable habitat for dispersal in Bonelli's eagle: an important issue in halting its decline in Europe. *Biological Conservation*, 126(1): 74–83. doi: 10.1016/j.biocon.2005.04.023
- Baldwin R A, 2009. Use of maximum entropy modeling in wildlife research. *Entropy*, 11(4): 854–866. doi: 10.3390/e11040854
- Banks J A, 1999. Gametophyte development in ferns. *Annual Review of Plant Physiology and Plant Molecular Biology*, 50: 163–186. doi: 10.1146/annurev.arplant.50.1.163
- Benito Garzón M, Blazek R, Neteler M et al., 2006. Predicting habitat suitability with machine learning models: the potential area of *Pinus sylvestris* L. in the Iberian Peninsula. *Ecological Modelling*, 197(3–4): 383–393. doi: 10.1016/j.ecolmodel.2006.03.015
- Booth T H, Nix H A, Busby J R et al., 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Diversity and Distributions*, 20(1): 1–9. doi: 10.1111/ddi.12144
- Booth T H, 2018. Why understanding the pioneering and continuing contributions of BIOCLIM to species distribution modelling is important. *Austral Ecology*, 43(8): 852–860. doi: 10.1111/aec.12628
- Boria R A, Olson L E, Goodman S M et al., 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling*, 275: 73–77. doi: 10.1016/j.ecolmodel.2013.12.012
- Brummitt N, Bachman S P, Aletrari E et al., 2015. The sampled red list index for plants, phase II: ground-truthing specimen-based conservation assessments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1662): 20140015. doi: 10.1098/rstb.2014.0015
- Brummitt N, Aletrari E, Syfert M M et al., 2016. Where are threatened ferns found? Global conservation priorities for pteridophytes. *Journal of Systematics and Evolution*, 54(6): 604–616. doi: 10.1111/jse.12224
- Bruni I, Gentili R, De Mattia F et al., 2013. A multi-level analysis to evaluate the extinction risk of and conservation strategy for the aquatic fern *Marsilea quadrifolia* L. in Europe. *Aquatic Botany*, 111: 35–42. doi: 10.1016/j.aquabot.2013.08.005
- Campbell C A, Hilderbrand R H, 2017. Using maximum entropy to predict suitable habitat for the endangered dwarf wedge-mussel in the Maryland Coastal Plain. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(2): 462–475. doi: 10.1002/aqc.2699
- Canestraro B K, Moran R C, Watkins J E, 2014. Reproductive and physiological ecology of climbing and terrestrial *Polybotrya* (Dryopteridaceae) at the La Selva biological station, Costa Rica. *International Journal of Plant Sciences*, 175(4): 432–441. doi: 10.1086/675576
- Carnaval A C, Moritz C, 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, 35(7): 1187–1201. doi: 10.1111/j.1365-2699.2007.01870.x
- Cook C N, Morgan D G, Marshall D J, 2010. Reevaluating suitable habitat for reintroductions: lessons learnt from the eastern barred bandicoot recovery program. *Animal Conservation*, 13(2): 184–195. doi: 10.1111/j.1469-1795.2009.00320.x
- Cui Shaopeng, Luo Xiao, Li Chunwang et al., 2018. Predicting the potential distribution of white-lipped deer using the Max-Ent model. *Biodiversity Science*, 26(2): 171–176. (in Chinese)
- Davies A J, Wisshak M, Orr J C et al., 2008. Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep Sea Research Part I: Oceanographic Research Papers*, 55(8): 1048–1062. doi: 10.1016/j.dsr.2008.04.010
- Dong Shiyong, Zuo Zhengyu, Yan Yuehong et al., 2017. Red list assessment of lycophytes and ferns in China. *Biodiversity Science*, 25(7): 765–773. (in Chinese)
- Dong Yuan, Wang Jianzhong, 1991. Exploitation, Utilization and protection of wild plant resources under forest in Northeast China. *Resources Science*, (2): 41–45. (in Chinese)
- Elith J, 2000. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. In: Ferson S, Burgman M (eds). *Quantitative Methods for Conservation Biology*. New York: Springer, 39–58.
- Elith J, Graham C H, Anderson R P et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2): 129–151. doi: 10.1111/j.2006.0906-7590.04596.x
- Elith J, Phillips S J, Hastie T et al., 2011. A statistical explanation of MaxEnt for ecologists. *Biodiversity Research*, 17(1): 43–57. doi: 10.1111/j.1472-4642.2010.00725.x
- Estallo E L, Sangermano F, Grech M et al., 2018. Modelling the distribution of the vector *Aedes aegypti* in a central Argentine city. *Medical and Veterinary Entomology*, 32(4): 451–461. doi: 10.1111/mve.12323
- Evangelista P H, Kumar S, Stohlgren T J et al., 2008. Modelling invasion for a habitat generalist and a specialist plant species. *Diversity and Distributions*, 14(5): 808–817. doi: 10.1111/j.1472-4642.2008.00486.x
- Fick S E, Hijmans R J, 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12): 4302–4315. doi: 10.1002/joc.5086
- French K J, Shackell N L, den Heyer C E, 2018. Strong relationship between commercial catch of adult Atlantic halibut (*Hippoglossus hippoglossus*) and availability of suitable habitat for juveniles in the Northwest Atlantic Ocean. *Fishery Bulletin*,

- 116(2): 107–121. doi: 10.7755/FB.116.2.1
- Fu Peiyun, 1995. *Clavis Plantarum Chinae Boreali-Orientalis (Editio Secunda)*. Beijing: Science Press, 35. (in Chinese)
- Galparsoro I, Borja Á, Bald J et al., 2009. Predicting suitable habitat for the European lobster (*Homarus gammarus*), on the Basque continental shelf (Bay of Biscay), using Ecological-Niche Factor Analysis. *Ecological Modelling*, 220(4): 556–567. doi: 10.1016/j.ecolmodel.2008.11.003
- Giordano P F, Navarro J L, Martella M B, 2010. Building large-scale spatially explicit models to predict the distribution of suitable habitat patches for the Greater rhea (*Rhea americana*), a near-threatened species. *Biological Conservation*, 143(2): 357–365. doi: 10.1016/j.biocon.2009.10.022
- Greer G K, McCarthy B C, 2000. Patterns of growth and reproduction in a natural population of the fern *Polystichum acrostichoides*. *American Fern Journal*, 90(2): 60–76. doi: 10.2307/1547415
- Gu W D, Swihart R K, 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation*, 116(2): 195–203. doi: 10.1016/S0006-3207(03)00190-3
- Han X Z, Ma R, Chen Q et al., 2018. Anti-inflammatory action of *Athyrium multidentatum* extract suppresses the LPS-induced TLR4 signaling pathway. *Journal of Ethnopharmacology*, 217: 220–227. doi: 10.1016/j.jep.2018.02.031
- He Xingyuan, Yu Jinghua, 2016. Technology and demonstration of ecological protection and exploitation and utilization of biological resources in northeast forest region. *Acta Ecologica Sinica*, 36(22): 7028–7033. (in Chinese)
- Jia Xiang, Ma Fangfang, Zhou Wangming et al., 2017. Impacts of climate change on the potential geographical distribution of broadleaved Korean pine (*Pinus koraiensis*) forests. *Acta Ecologica Sinica*, 37(2): 464–473. (in Chinese)
- Khafaga O, Hatab E E, Omar K, 2011. Predicting the potential geographical distribution of *Nepeta septemcrenata* in Saint Katherine Protectorate, South Sinai, Egypt using Maxent. *Academia Arena*, 3(7): 45–50.
- Kumar S, Stohlgren T J, 2009. Maxent modeling for predicting suitable habitat for threatened and endangered tree *Canacomyrica monticola* in New Caledonia. *Journal of Ecology and Natural Environment*, 1(4): 94–98.
- Lathrop R G, Niles L, Smith P et al., 2018. Mapping and modeling the breeding habitat of the Western Atlantic Red Knot (*Calidris canutus rufa*) at local and regional scales. *The Condor*, 120(3): 650–665. doi: 10.1650/CONDOR-17-247.1
- Li G Q, Du S, Guo K, 2015. Evaluation of limiting climatic factors and simulation of a climatically suitable habitat for Chinese sea buckthorn. *PLoS One*, 10(7): e0131659. doi: 10.1371/journal.pone.0131659
- Li G Q, Du S, Wen Z M, 2016. Mapping the climatic suitable habitat of oriental arborvitae (*Platycladus orientalis*) for introduction and cultivation at a global scale. *Scientific Reports*, 6: 30009. doi: 10.1038/srep30009
- Li N, Wang Z, Xia L et al., 2019. Effects of long-term coastal reclamation on suitable habitat and wintering population size of the endangered Red-crowned Crane, *Grus japonensis*. *Hydrobiologia*, 827(1): 21–29. doi: 10.1007/s10750-017-3341-x
- Liu Baodong, Li Xinhong, 1995. Resources of economic plant pteridophyte in Northeast China. *Chinese Wild Plant Resources*, (4): 36–38. (in Chinese)
- Liu Dongmei, Sheng Jiwen, Wang Sihong et al., 2016. Chemical constituents from *Athyrium multidentatum* rhizome and their reducing capacity. *Chinese Journal of Experimental Traditional Medical Formulae*, 22(21): 59–62. (in Chinese)
- Lu C Y, Gu W, Dai A H et al., 2012. Assessing habitat suitability based on geographic information system (GIS) and fuzzy: a case study of *Schisandra sphenanthera* Rehd. et Wils. In Qinling Mountains, China. *Ecological Modelling*, 242: 105–115. doi: 10.1016/j.ecolmodel.2012.06.002
- Lu Shugang, Chen Feng, 2013. On the pteridophyte ecological types. *Journal of Yunnan University (Natural Sciences Edition)*, 35(3): 407–415. (in Chinese)
- MacKenzie D I, Nichols J D, Lachman G B et al., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8): 2248–2255. doi: 10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2
- Manel S, Williams H C, Ormerod S J, 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, 38(5): 921–931. doi: 10.1046/j.1365-2664.2001.00647.x
- Merow C, Smith M J, Silander J A Jr, 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36(10): 1058–1069. doi: 10.1111/j.1600-0587.2013.07872.x
- Nettesheim F C, Damasceno E R, Sylvestre L S, 2014. Different slopes of a mountain can determine the structure of ferns and lycophytes communities in a tropical forest of Brazil. *Anais da Academia Brasileira de Ciências*, 86(1): 199–210. doi: 10.1590/0001-3765201495912
- Nieto-Lugilde D, Lenoir J, Abdulhak S et al., 2015. Tree cover at fine and coarse spatial grains interacts with shade tolerance to shape plant species distributions across the Alps. *Ecography*, 38(6): 578–589. doi: 10.1111/ecog.00954
- Olsson O, Rogers D J, 2009. Predicting the distribution of a suitable habitat for the white stork in Southern Sweden: identifying priority areas for reintroduction and habitat restoration. *Animal Conservation*, 12(1): 62–70. doi: 10.1111/j.1469-1795.2008.00225.x
- Pearce J L, Boyce M S, 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology*, 43(3): 405–412. doi: 10.1111/j.1365-2664.2005.01112.x
- Pearson R G, Raxworthy C J, Nakamura M et al., 2007. ORIGINAL ARTICLE: Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, 34(1): 102–117. doi: 10.1111/j.1365-2699.2006.01594.x
- Peck J H, Peck C J, Farrar D R, 1990. Influences of life history attributes on formation of local and distant fern populations. *American Fern Journal*, 80(4): 126–142. doi: 10.2307/1547200

- Peterson A T, Soberón J, Pearson R G et al., 2011. *Ecological Niches and Geographic Distributions*. Princeton: Princeton University Press, 172.
- Phillips S J, Anderson R P, Schapire R E, 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3–4): 231–259. doi: 10.1016/j.ecolmodel.2005.03.026
- Phillips S J, Dudík M, 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31(2): 161–175. doi: 10.1111/j.0906-7590.2008.5203.x
- Phillips S J, Anderson R P, Dudík M et al., 2017. Opening the black box: an open-source release of Maxent. *Ecography*, 40(7): 887–893. doi: 10.1111/ecog.03049
- Phillips S J, Dudík M, Robert E S, 2018. Maxent software for modeling species niches and distributions (Version 3.4.1). Available at: http://biodiversityinformatics.amnh.org/open_source/maxent/.
- Phipps W L, Diekmann M, MacTavish L M et al., 2017. Due South: a first assessment of the potential impacts of climate change on Cape vulture occurrence. *Biological Conservation*, 210: 16–25. doi: 10.1016/j.biocon.2017.03.028
- Qi G Y, Yang L Q, Xiao C X et al., 2015. Nutrient values and bioactivities of the extracts from three fern species in China: a comparative assessment. *Food & Function*, 6(9): 2918–2929. doi: 10.1039/C5FO00510H
- Qi G Y, Liu Z G, Fan R et al., 2017. *Athyrium multidentatum* (Doll.) Ching extract induce apoptosis via mitochondrial dysfunction and oxidative stress in HepG2 cells. *Scientific Reports*, 7(1): 2275. doi: 10.1038/s41598-017-02573-8
- Radosavljevic A, Anderson R P, 2014. Making better MAXENT models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography*, 41(4): 629–643. doi: 10.1111/jbi.12227
- Remya K, Ramachandran A, Jayakumar S, 2015. Predicting the current and future suitable habitat distribution of *Myristica dactyloides* Gaertn. using MaxEnt model in the Eastern Ghats, India. *Ecological Engineering*, 82: 184–188. doi: 10.1016/j.ecoleng.2015.04.053
- Richard K, Abdel-Rahman E M, Mohamed S A et al., 2018. Importance of remotely-sensed vegetation variables for predicting the spatial distribution of African citrus Triozid (*Trioza erytreae*) in Kenya. *International Journal of Geo-Information*, 7(11): 429. doi: 10.3390/ijgi7110429
- Sato T, 1992. Size dependency of gametophytes decay in *Athyrium brevifrons* Nakai during spring desiccation. *Ecological Research*, 7(1): 1–7. doi: 10.1007/BF02348591
- Sheffield E, 1994. Alternation of generations in ferns: mechanisms and significance. *Biological Reviews*, 69(3): 331–343. doi: 10.1111/j.1469-185X.1994.tb01275.x
- Shen Tao, Zhang Ji, Yang Qing et al., 2017. Ecology suitability study of *Gentiana rhodantha* in Yunnan-Guizhou Plateau. *Chinese Pharmaceutical Journal*, 52(20): 1816–1823. (in Chinese)
- Testo W L, Watkins J E Jr, 2013. Understanding mechanisms of rarity in Pteridophytes: competition and climate change threaten the rare fern *Asplenium scolopendrium* var. *americanum* (Aspleniaceae). *American Journal of Botany*, 100(11): 2261–2270. doi: 10.3732/ajb.1300150
- Vilar L, Gómez I, Martínez-Vega J et al., 2016. Multitemporal modelling of socio-economic wildfire drivers in central Spain between the 1980s and the 2000s: comparing generalized linear models to machine learning algorithms. *PLoS One*, 11(8): e0161344. doi: 10.1371/journal.pone.0161344
- Vormisto J, Tuomisto H, Oksanen J, 2004. Palm distribution patterns in Amazonian rainforests: what is the role of topographic variation? *Journal of Vegetation Science*, 15(4): 485–494. doi: 10.1111/j.1654-1103.2004.tb02287.x
- Wang Yunsheng, Xie Bingyan, Wan Fanghao et al., 2007. Application of ROC curve analysis in evaluating the performance of alien species' potential distribution models. *Biodiversity Science*, 15(4): 365–372. (in Chinese)
- Wang Zhongren, Zhang Xianchun, Zhu Weiming et al., 1999. *Flora Reipublicae Popularis Sinicae*, vol. 3(2). Beijing: Science Press, 162–165. (in Chinese)
- Watkins J E Jr, Mack M K, Mulkey S S, 2007. Gametophyte ecology and demography of epiphytic and terrestrial tropical ferns. *American Journal of Botany*, 94(4): 701–708. doi: 10.3732/ajb.94.4.701
- West A M, Kumar S, Brown C S et al., 2016. Field validation of an invasive species Maxent model. *Ecological Informatics*, 36: 126–134. doi: 10.1016/j.ecoinf.2016.11.001
- Wu F, Wang M M, Xi Z et al., 2014. Study on drought stress of six common ferns in North China. *Acta Horticulturae*, 1035: 113–124. doi: 10.17660/ActaHortic.2014.1035.13
- Wu Z Y, Raven P H, Hong D Y, 2013. *Flora of China*, Vol. 2–3. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press, 452, 466–467.
- Xu Wenduo, 1986. The relation between the zonal distribution of types of vegetation and the climate in Northeast China. *Acta Phytocologica et Geobotanica Sinica*, 10(4): 254–263. (in Chinese)
- Yang X Q, Kushwaha S P S, Saran S et al., 2013. Maxent modeling for predicting the potential distribution of medicinal plant, *Justicia adhatoda* L. in Lesser Himalayan foothills. *Ecological Engineering*, 51: 83–87. doi: 10.1016/j.ecoleng.2012.12.004
- Yi Y J, Cheng X, Yang Z F et al., 2016. Maxent modeling for predicting the potential distribution of endangered medicinal plant (*H. riparia* Lour) in Yunnan, China. *Ecological Engineering*, 92: 260–269. doi: 10.1016/j.ecoleng.2016.04.010
- Zaniewski A E, Lehmann A, Overton J M, 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling*, 157(2–3): 261–280. doi: 10.1016/s0304-3800(02)00199-0
- Zhang Jiping, Zhang Yili, Liu Linshan et al., 2011. Predicting potential distribution of Tibetan Spruce (*Picea smithiana*) in Qomolangma (Mount Everest) national nature preserve using maximum entropy niche-based model. *Chinese Geographical Science*, 21(4): 417–426. doi: 10.1007/s11769-011-0483-z
- Zhang M G, Zhou Z K, Chen W Y et al., 2014. Major declines of

woody plant species ranges under climate change in Yunnan, China. *Diversity and Distributions*, 20(4): 405–415. doi: 10.1111/ddi.12165

Zhang Xianchun, Wei Ran, Liu Hongmei et al., 2013. Phylogeny and classification of the extant lycophytes and ferns from China. *Chinese Bulletin of Botany*, 48(2): 119–137. (in Chinese)

Appendix 1 Loading coefficients of principal component analysis (PCA) on 19 bioclimatic variables for *A. brevifrons* in Northeast China

Variables	Principal component			
	PC1	PC2	PC3	PC4
Bio17	0.93	0.27	0.09	−0.15
Bio19	0.93	0.27	0.09	−0.15
Bio14	0.92	0.16	0.21	−0.13
Bio12	0.85	0.50	0.00	0.11
Bio18	0.84	0.47	0.01	0.23
Bio16	0.84	0.47	0.01	0.23
Bio13	0.82	0.43	0.12	0.33
Bio7	−0.45	−0.88	0.05	0.10
Bio4	−0.50	−0.83	0.14	0.18
Bio6	0.45	0.81	0.35	−0.09
Bio2	−0.12	−0.81	−0.43	−0.18
Bio9	0.45	0.79	0.39	−0.08
Bio11	0.46	0.79	0.38	−0.08
Bio5	0.10	0.03	0.97	0.01
Bio10	0.11	0.24	0.96	0.10
Bio8	0.12	0.24	0.95	0.11
Bio1	0.35	0.62	0.70	−0.01
Bio3	0.43	0.06	−0.68	−0.38
Bio15	0.06	−0.11	0.22	0.93
Contribution rate	36.05%	29.47%	23.47%	7.40%
Cumulative contribution rate	36.05%	65.52%	88.99%	96.39%

Notes: 'Bio1' is 'annual mean temperature'; 'Bio2' is 'mean diurnal range'; 'Bio3' is 'isothermality'; 'Bio4' is 'temperature seasonality'; 'Bio5' is 'max temperature of warmest month'; 'Bio6' is 'min temperature of coldest month'; 'Bio7' is 'temperature annual range'; 'Bio8' is 'mean temperature of wettest quarter'; 'Bio9' is 'mean temperature of driest quarter'; 'Bio10' is 'mean temperature of warmest quarter'; 'Bio11' is 'mean temperature of coldest quarter'; 'Bio12' is 'annual precipitation'; 'Bio13' is 'precipitation of wettest month'; 'Bio14' is 'precipitation of driest month'; 'Bio15' is 'precipitation seasonality'; 'Bio16' is 'precipitation of wettest quarter'; 'Bio17' is 'precipitation of driest quarter'; 'Bio18' is 'precipitation of warmest quarter'; 'Bio19' is 'precipitation of coldest quarter'

Appendix 2 The Pearson correlation coefficients (r) among environmental variables in the multicollinearity test for *A. brevifrons* in Northeast China

Variables	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	Eleva	Slope	Aspect
Bio1*	1																					
Bio2	-0.82	1																				
Bio3*	-0.25	0.40	1																			
Bio4	-0.60	0.62	-0.47	1																		
Bio5*	0.75	-0.39	-0.53	0.04	1																	
Bio6	0.91	-0.82	0.08	-0.88	0.42	1																
Bio7*	-0.67	0.73	-0.33	0.98	-0.02	-0.92	1															
Bio8	0.86	-0.61	-0.60	-0.11	0.96	0.57	-0.20	1														
Bio9	0.92	-0.82	0.05	-0.85	0.47	0.99	-0.89	0.60	1													
Bio10	0.86	-0.62	-0.60	-0.11	0.96	0.57	-0.21	1.00	0.61	1												
Bio11	0.93	-0.81	0.07	-0.86	0.46	1.00	-0.90	0.60	0.99	0.61	1											
Bio12	0.60	-0.53	0.34	-0.81	0.11	0.77	-0.80	0.23	0.76	0.23	0.77	1										
Bio13	0.63	-0.56	0.18	-0.70	0.22	0.73	-0.71	0.35	0.73	0.35	0.74	0.96	1									
Bio14	0.55	-0.37	0.25	-0.58	0.26	0.62	-0.57	0.31	0.62	0.31	0.63	0.83	0.79	1								
Bio15*	0.11	-0.12	-0.39	0.23	0.25	-0.05	0.17	0.30	-0.03	0.29	-0.03	0.07	0.31	-0.04	1							
Bio16	0.59	-0.52	0.31	-0.77	0.13	0.74	-0.76	0.25	0.74	0.25	0.74	0.99	0.98	0.80	0.19	1						
Bio17*	0.55	-0.39	0.36	-0.70	0.17	0.68	-0.67	0.23	0.67	0.24	0.68	0.90	0.84	0.97	-0.10	0.87	1					
Bio18	0.59	-0.52	0.31	-0.77	0.13	0.74	-0.76	0.25	0.74	0.25	0.74	0.99	0.98	0.79	0.20	1.00	0.87	1				
Bio19	0.55	-0.39	0.36	-0.70	0.17	0.68	-0.67	0.23	0.67	0.24	0.68	0.90	0.84	0.97	-0.10	0.87	1.00	0.87	1			
Eleva*	-0.30	0.08	0.57	-0.38	-0.69	0.02	-0.33	-0.62	-0.02	-0.62	-0.01	0.29	0.20	0.02	-0.12	0.29	0.13	0.29	0.13	1		
Slope*	0.30	-0.46	0.02	-0.43	-0.06	0.41	-0.48	0.08	0.40	0.08	0.40	0.57	0.59	0.37	0.19	0.58	0.41	0.58	0.41	0.26	1	
Aspect*	0.04	-0.20	-0.21	0.00	-0.02	0.04	-0.05	0.06	0.04	0.06	0.03	-0.04	0.01	-0.21	0.19	-0.01	-0.18	-0.01	-0.18	0.03	0.16	1

Notes: 'Bio1' is 'annual mean temperature'; 'Bio2' is 'mean diurnal range'; 'Bio3' is 'isothermality'; 'Bio4' is 'temperature seasonality'; 'Bio5' is 'max temperature of warmest month'; 'Bio6' is 'min temperature of coldest month'; 'Bio7' is 'temperature annual range'; 'Bio8' is 'mean temperature of wettest quarter'; 'Bio9' is 'mean temperature of driest quarter'; 'Bio10' is 'mean temperature of warmest quarter'; 'Bio11' is 'mean temperature of coldest quarter'; 'Bio12' is 'annual precipitation'; 'Bio13' is 'precipitation of wettest month'; 'Bio14' is 'precipitation of driest month'; 'Bio15' is 'precipitation seasonality'; 'Bio16' is 'precipitation of wettest quarter'; 'Bio17' is 'precipitation of driest quarter'; 'Bio18' is 'precipitation of warmest quarter'; 'Bio19' is 'precipitation of coldest quarter'; 'Eleva' is 'elevation'; 'Slope' is the variable selected for Maxent prediction