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Predicting the climate niche of *Puccinia abrupta* var. *partheniicola* using maximum entropy for strategic biological control of *Parthenium hysterophorus* in India

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Abstract

Puccinia abrupta var. *partheniicola* is a rust fungus specific to *Parthenium hysterophorus*, a globally invasive weed causing ecological and health problems. As a potential classical biocontrol agent, understanding the rust's ecological distribution is crucial. This study applies MaxEnt species distribution modelling to assess the current and potential distribution of *P. abrupta* var. *partheniicola* in India, using nineteen global occurrence records and bioclimatic variables from the WorldClim database. MaxEnt excels at modelling species presence under environmental constraints, making it ideal for rare species like *P. abrupta* var. *partheniicola*, where absence data are limited. The model revealed high habitat suitability in northwestern India (Punjab, Haryana, western Uttar Pradesh), moderate to high suitability in central, eastern and southern regions, and low suitability in the Thar Desert, Gujarat and Coastal Plains. Precipitation of the driest month (bio14) and isothermality (bio3) were key drivers, with bio3 showing the highest permutation importance, indicating sensitivity to thermal stability. Mean temperature of the driest quarter (bio9) was the most informative predictor in jackknife analysis. The model performed exceptionally well (AUC = 0.995), confirming high predictive accuracy. Omission rate and predicted area analyses further validated strong calibration. These findings highlight thermal and moisture factors as critical determinants of the rust's distribution. The study underscores MaxEnt's value in forecasting pathogen spread and guiding sustainable biological control of *P. hysterophorus*. Future work should integrate fine-scale climatic data and assess potential impacts under climate change scenarios.

Keywords: Bioclimatic variables, DIVA-GIS, MaxEnt, rust fungi, species distribution modelling, weed biocontrol

Introduction

Originally from tropical America, *Parthenium hysterophorus* L. (Asterales: Asteraceae), a globally invasive weed notorious for its rapid spread, ecological disruption and adverse impacts on agriculture and human health (Adkins and Shabbir, 2014; Sreerama Kumar, 2024), has swiftly invaded varied agro-ecological regions across India (Fig. 1). It is predominantly found in wastelands, along roadsides, at forest margins, and within agricultural fields, with notably high prevalence across states such as Maharashtra, Karnataka, Andhra Pradesh, Tamil Nadu and Uttar Pradesh. The weed's aggressive growth habit, prolific seed production and allelopathic capacity have collectively contributed to its

extensive colonisation and sustained persistence in both rural and urban environments (Mahadevappa, 2009).

Among the natural enemies of *P. hysterophorus* (commonly called parthenium weed), *Puccinia abrupta* var. *partheniicola* (H.S. Jacks.) Parmelee (Pucciniales: Pucciniaceae), an obligate biotrophic rust fungus, is distinguished by its host specificity and potential as a classical biocontrol agent (Evans, 1997; Dhileepan, 2007). It has been causing severe seasonal stress to parthenium weed in areas close to Bengaluru in Karnataka, India (Fig. 2), since 2023, is now regularly observed during the winter months, prompting molecular analyses, spatial mapping and long-term monitoring to harness it as a potential biocontrol agent (Sreerama Kumar, 2025). Known as the winter rust, understanding the ecological distribution and potential range expansion of *P. abrupta* var. *partheniicola* is critical for predicting its epidemiological behaviour under changing environmental conditions and for assessing its utility in biocontrol programmes.

Species distribution modelling (SDM) has become a powerful tool for predicting suitable habitats based on environmental variables and occurrence records (Farag *et al.*, 2025). Among SDM approaches, the maximum entropy (MaxEnt) method is widely regarded as one of the most robust, particularly when only presence data are available (Phillips *et al.*, 2006; Elith *et al.*, 2011). Rooted in information theory, MaxEnt estimates the probability distribution of species occurrence that is closest to uniform (maximum entropy), constrained by environmental conditions at known presence sites. This makes it especially suitable for rare or underreported species such as *P. abrupta* var. *partheniicola*, for which absence data are scarce.

By integrating occurrence records with bioclimatic variables, MaxEnt identifies areas of suitable habitat with minimal assumptions (Phillips and Dudík, 2008). It has been extensively applied in ecological niche modelling across taxa, including invasive plants, pathogens, and biocontrol agents (Peterson *et al.*, 2011; Bebber *et al.*, 2013). However, its use for rust fungi, particularly *P. abrupta* var. *partheniicola*, remains underexplored.

This study employs MaxEnt to evaluate the current and potential distribution of *P. abrupta* var. *partheniicola* across diverse climatic and ecological regions in India. Specifically, we aimed to: (i) identify key environmental factors shaping its distribution; (ii) predict areas of high suitability under present climate conditions; and (iii) assess implications for its role in the natural suppression of *P. hysterophorus*. The findings provide new insights into the ecological niche of this rust fungus and inform strategies for sustainable weed management and biocontrol deployment.

Materials and Methods

Nineteen global occurrence records for *P. abrupta* var. *partheniicola* were obtained from published records (CABI Compendium) and other sources. Nineteen bioclimatic variables of current climate scenario, at a spatial resolution of 2.5 arc minutes, were sourced from the WorldClim database (version 1.4; <http://www.worldclim.org>). Species distribution modelling was conducted using MaxEnt version 3.4.4 (http://biodiversityinformatics.amnh.org/open_source/maxent/). The model was configured with a convergence threshold of 100, a maximum of 5000 iterations, and 10,000 background points. To evaluate the relative contribution of each variable, a jackknife test was performed

using the background data. Model performance was assessed using the area under the curve (AUC) of the receiver operating characteristic (ROC) curve. AUC values range from 0 to 1, where higher values indicate greater predictive accuracy; values below 0.5 are considered to have limited predictive reliability. Potential distribution maps were generated based on probability values between 0 (indicating low likelihood of species presence) and 1 (indicating high likelihood of occurrence). DIVA-GIS version 7.5 (a free downloadable software from www.diva-gis.org) was used to generate the model using input ASCII file derived from MaxEnt analysis.

Results and Discussion

The MaxEnt modelling output provided a comprehensive spatial prediction of the current potential distribution of *P. abrupta* var. *partheniicola* in India, grounded in environmental suitability derived from bioclimatic variables. Suitability is expressed on a logistic scale from 0 (unsuitable) to 1 (highly suitable) and was classified into low (0.4–0.6), moderate (0.6–0.8) and high (0.8–1.0) habitat suitability categories. The generated suitability map (Fig. 3) revealed that the northwestern states — especially Punjab, Haryana and western Uttar Pradesh — exhibited the highest likelihood of *P. abrupta* var. *partheniicola* occurrence. These regions, characterised by semi-arid climates with distinct temperature fluctuations and dry winters, offer favourable conditions for pathogen development, as supported by prior epidemiological studies (Bhardwaj *et al.*, 2019; Bhardwaj *et al.*, 2024).

Central and eastern India, including Chhattisgarh, Odisha, Jharkhand and the Eastern Gangetic Plains, displayed moderate to high suitability, despite generally higher humidity levels. This suggests that seasonal windows of moisture deficit or microclimatic buffering could create localised niches suitable for disease proliferation. In southern India, localised high suitability zones in Karnataka, Maharashtra and Tamil Nadu, particularly across the Deccan Plateau and Western Ghats, point toward interactions between thermal consistency and seasonal moisture stress — conditions that align with previous findings on rust fungi's climatic sensitivity (Helfer, 2014).

The northeastern region, including Assam and surrounding states, showed pockets of moderate to high suitability, potentially linked to high isothermality and precipitation seasonality. Conversely, low suitability was predicted for the western Thar Desert, Eastern Coastal Plains and parts of Gujarat — likely due to excessive aridity or thermal extremes incompatible with the life cycle of *P. abrupta* var. *partheniicola*.

Variable Contributions and Environmental Drivers

The environmental variable contribution analysis (Table 1) highlighted precipitation of the driest month (bio14) as the dominant factor in terms of percent contribution (34.3%), suggesting its role in shaping the ecological limits of *P. abrupta* var. *partheniicola*. However, its permutation importance was minimal (0.2%), implying high influence during model training but limited predictive power when considered independently — likely due to collinearity with other precipitation-related variables (Elith *et al.*, 2011). In contrast, isothermality (bio3) showed both high percent contribution (14.2%) and overwhelming permutation importance (79.4%), indicating its pivotal role in capturing thermal stability — a key factor influencing pathogen survival and infectivity (Chen *et al.*, 2024). Isothermality reflects the ratio of daily to annual temperature oscillations, suggesting that the rust thrives in

regions with minimal diurnal fluctuations and relatively stable annual thermal regimes. Maximum temperature of the warmest month (bio5), while contributing 11.8% to model gain, had zero permutation importance, likely due to redundancy with other temperature variables. Meanwhile, mean temperature of the driest quarter (bio9) and precipitation of the wettest month (bio13) had moderate contributions but similarly low standalone predictive capacity.

Interestingly, mean diurnal range (bio2), despite a low percent contribution (0.5%), had a modest permutation importance (4.1%), indicating subtle yet meaningful effects on the rust distribution. Variables such as temperature seasonality (bio4), temperature annual range (bio7), and mean temperature of coldest quarter (bio11) exhibited negligible impact in both metrics, suggesting limited relevance to the current ecological niche of *P. abrupta* var. *partheniicola* under present climatic conditions.

Jackknife Test of Variable Importance

The jackknife test (Fig. 4) further reinforced the findings of the contribution analysis. When used in isolation, mean temperature of the driest quarter (bio9) yielded the highest regularised training gain, making it the single most informative predictor of the rust distribution. Its removal caused a significant decline in overall model performance, emphasising its indispensable role.

Similarly, isothermality (bio3) demonstrated substantial predictive capacity both when used alone and when excluded, underscoring its unique contribution. In contrast, variables such as annual mean temperature (bio1), mean temperature of wettest quarter (bio8) and mean temperature of coldest quarter (bio11) had limited individual importance, further validating their exclusion from simplified niche models. Precipitation of the driest month (bio14) showed moderate importance in the jackknife analysis, supporting its ecological relevance, albeit secondary to temperature-driven variables. The synergy between thermal stability and dry-season moisture appears to be the most critical environmental determinant of the rust's potential distribution. Response curves which show how each environmental variable affects the MaxEnt prediction are provided in Fig. 5.

Omission Rate and Predicted Area as a Function of Cumulative Threshold

Fig. 6 illustrates the relationship between omission rate and predicted area across a range of cumulative thresholds in a species distribution model. The omission rate refers to the proportion of known presence records that are incorrectly predicted as absent by the model. It is calculated for both training data (used to build the model) and, if available, test data (used to evaluate model performance). As the cumulative threshold increases, the model becomes more conservative in predicting suitable habitat, leading to a decrease in predicted area but a potential increase in omission rate. Ideally, the observed omission rate should align closely with the predicted omission, due to how the cumulative threshold is defined, i.e. based on the cumulative output values across the landscape. A close match between predicted and actual omission rates indicates good model calibration and reliability. Discrepancies might suggest overfitting (if training omission is low but test omission is high) or underfitting (if both omission rates are high even at lower thresholds).

The MaxEnt model demonstrated strong predictive accuracy for *P. abrupta* var. *partheniicola* in India, with area under the receiver operating characteristic (ROC) curve (AUC) values of

0.995 for the current climate scenario. These AUC values fall within the 0.9 to 1.0 range, which is considered indicative of excellent model performance.

Implications Ahead

The findings presented herein are consistent with global research highlighting the climatic sensitivity of rust fungi and the demonstrated utility of SDMs in forecasting plant disease forecasting (Aloyce, 2025; Ikeda and Osawa, 2020). In the case of *P. abrupta* var. *partheniicola*, the current modelling framework not only delineates contemporary zones favouring pathogen but also establishes a robust foundation for assessing the potential impacts of future climate change, particularly under scenarios characterised by heightened temperature variability and altered precipitation regimes.

Regions identified as favourable — specifically those located in northwestern, central and select southern areas — require prioritisation in terms of disease surveillance and targeted spread of the agent. Moreover, the strong predictive performance associated with bioclimatic variables bio3 and bio9 underscores the importance of incorporating fine-scale thermal and moisture dynamics in subsequent modelling efforts. Future studies may benefit from integrating remote sensing datasets and phenological observations to further refine predictive accuracy for *P. abrupta* var. *partheniicola*.

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Table 1. Estimates of relative contributions of the environmental variables to the MaxEnt model for *Puccinia abrupta* var. *partheniicola*

Variable	Current climate	
	Percent contribution	Permutation importance
Precipitation of driest month (bio14)	34.3	0.2
Isothermality (bio3)	14.2	79.4
Maximum temperature of warmest month (bio5)	11.8	0
Precipitation of wettest month (bio13)	8.0	5.7
Mean temperature of driest quarter (bio9)	4.8	0.7
Precipitation of driest quarter (bio17)	4.7	1.1
Annual mean temperature (bio1)	3.8	1.4
Annual precipitation (bio12)	3.7	2.6
Precipitation seasonality (bio15)	3.3	1.6
Minimum temperature of coldest month (bio6)	2.7	1.2
Precipitation of wettest quarter (bio16)	2.3	0.1
Precipitation of coldest quarter (bio19)	1.8	0
Precipitation of warmest quarter (bio18)	1.1	0.7
Mean temperature of warmest quarter (bio10)	1.1	0
Mean temperature of wettest quarter (bio8)	0.9	1.2
Temperature annual range (bio7)	0.8	0
Mean diurnal range (bio2)	0.5	4.1
Temperature seasonality (bio4)	0.2	0
Mean temperature of coldest quarter (bio11)	0	0

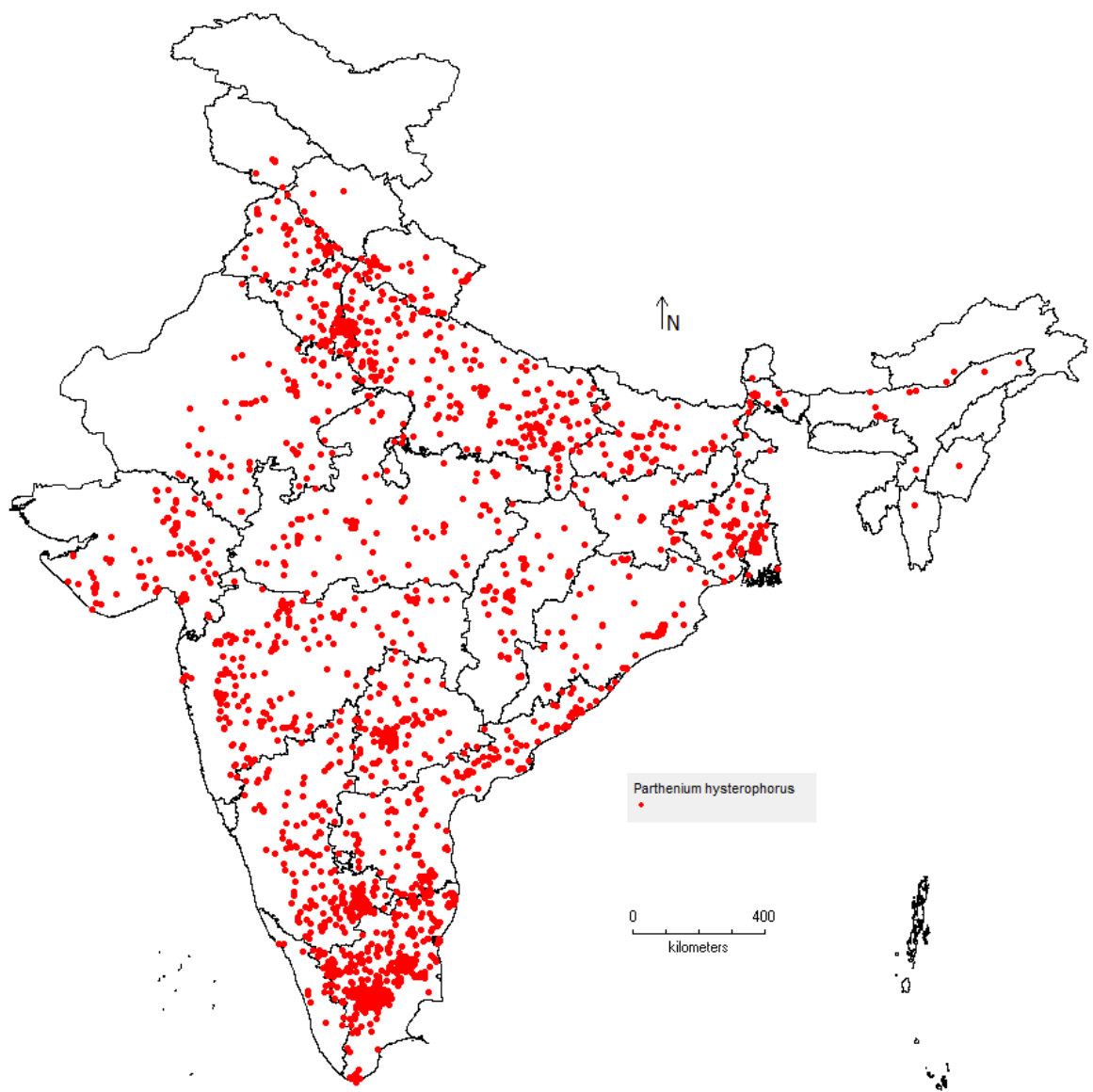


Fig. 1. Distribution of *Parthenium hysterophorus* in India (Data courtesy: GBIF.org)



Fig. 2. *Parthenium hysterophorus* exhibiting infection by *Puccinia abrupta* var. *partheniicola* along a roadside in Bengaluru Urban District, Karnataka, India (February 2023)

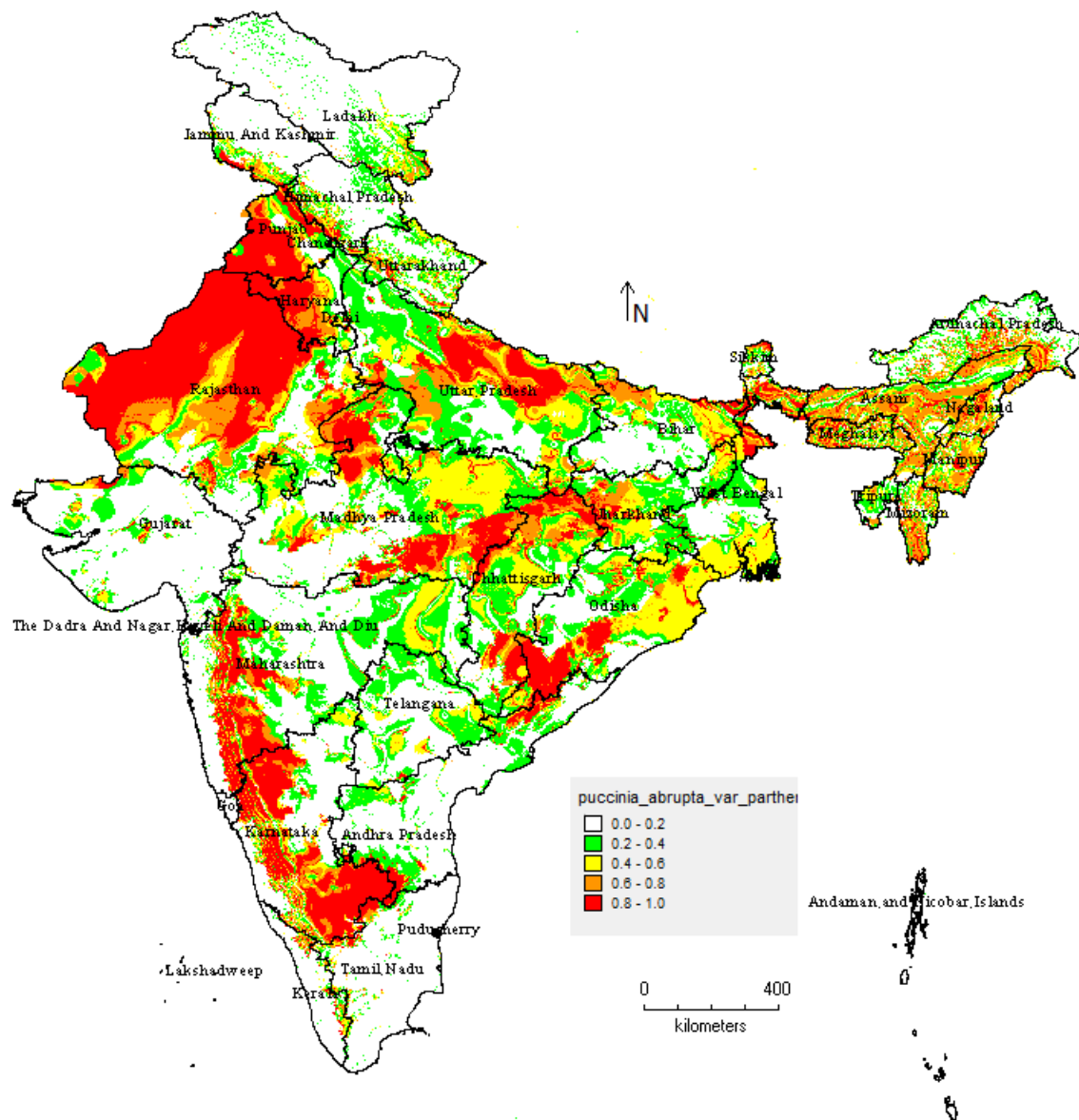


Fig. 3. MaxEnt model generated for the distribution of *Puccinia abrupta* var. *partheniicola*

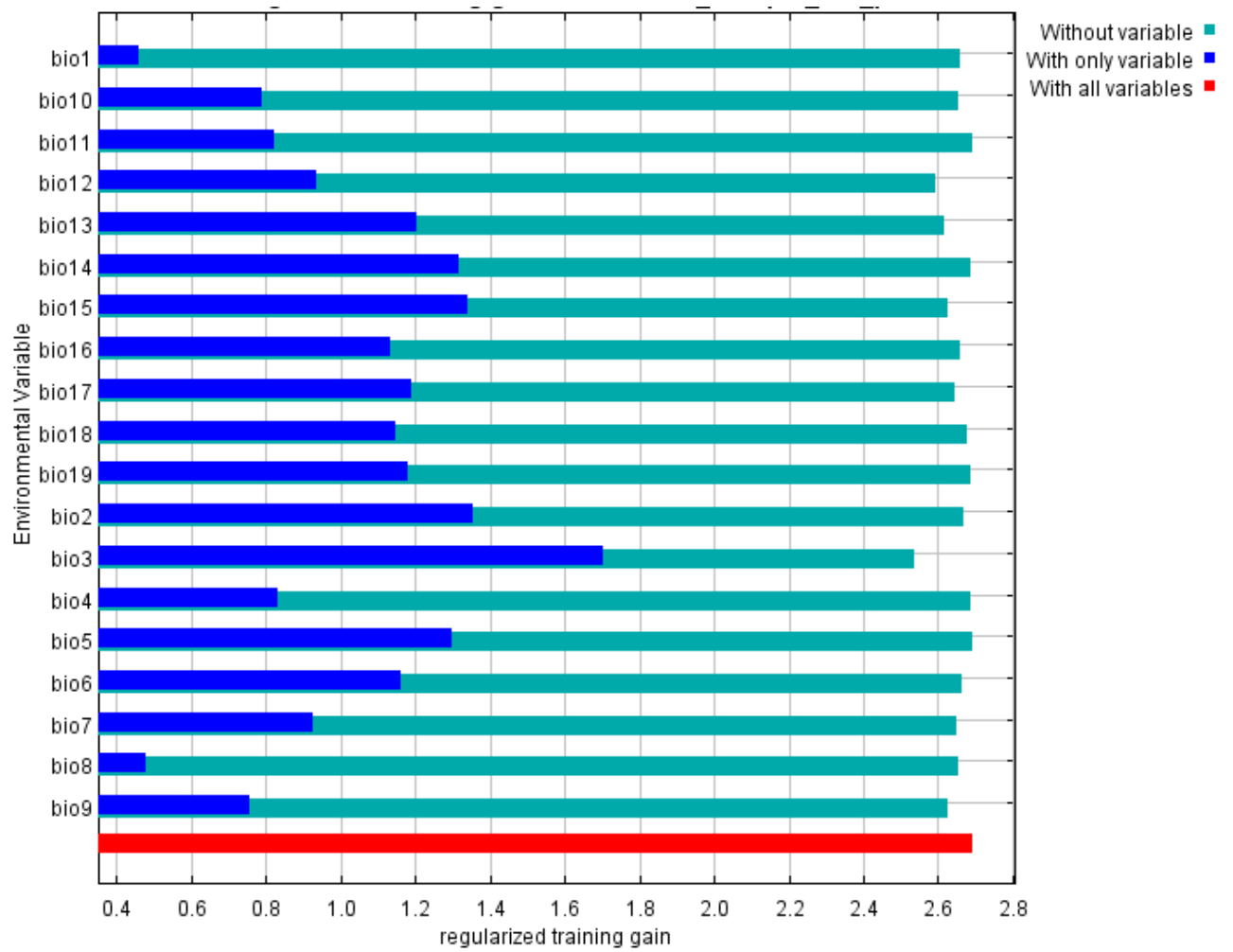
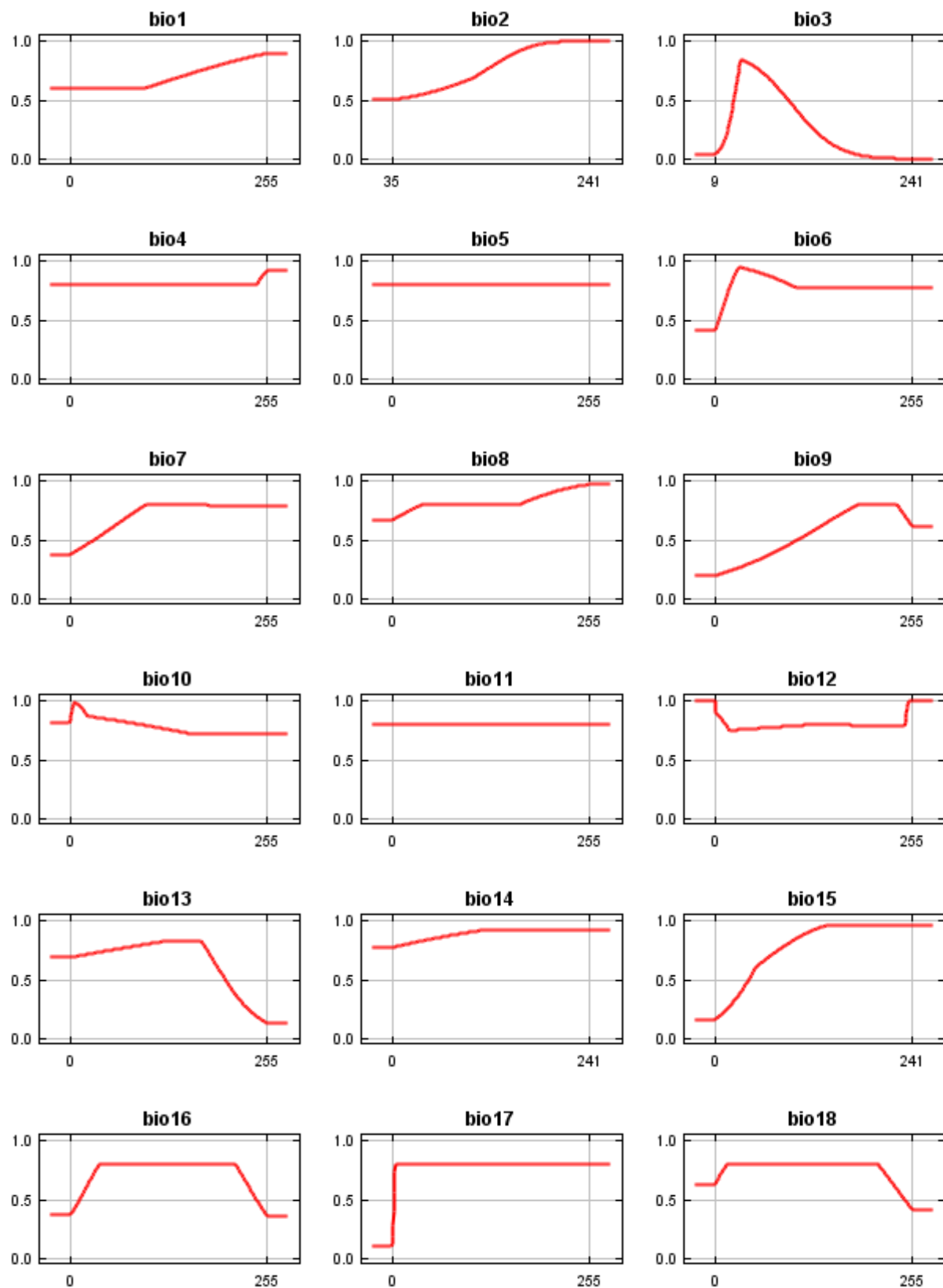


Fig. 4. Jackknife of regularised training gain for *Puccinia abrupta* var. *partheniicola*



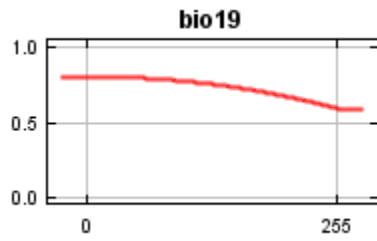


Fig. 5. Response curves which show how each environmental variable affects the MaxEnt prediction

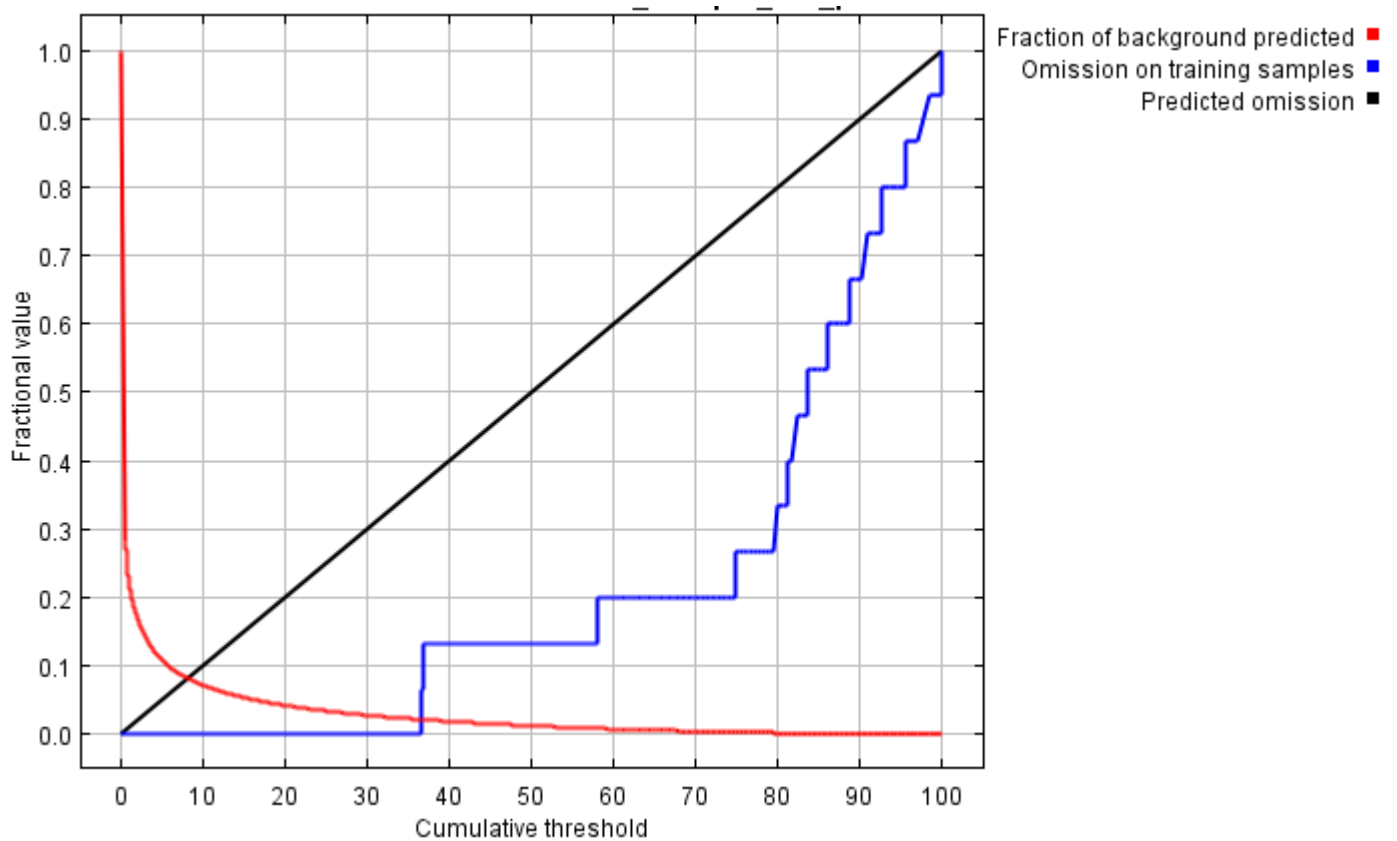


Fig. 6. Omission and predicted area for *Puccinia abrupta* var. *partheniicola*