1	
2	
3	
4	Predicting potential current distribution of Lycorma delicatula (Hemiptera: Fulgoridae)
5	using MaxEnt model in South Korea
6	
7	Hyeban Namgung ^{1¶,} Min-Jung Kim ^{2¶} , Sunghoon Baek², Joon-Ho Lee ^{2,3*} , Hyojoong Kim ^{1*}
8	
9	
10	
11 12	¹ Department of Biology, Kunsan National University, Gunsan 54150, Repubic of Korea
13 14	² Entomology program, Department of Agricultural Biotechnology, Seoul National University, Seoul 08826, Republic of Korea
15 16 17 18	³ Research Institute of Agriculture and Life Sciences, Seoul National University, Seoul 08826, Republic of Korea
19	*Corresponding author
20	E-mail: jh7lee@snu.ac.kr (JL), hkim@kunsan.ac.kr (HK)
21	
22	
23	[¶] These authors contributed equally to work
24	

25 **Abstract**

26 Lycorma delicatula (Hemiptera: Fulgoridae) is invasive insect in Korea which causes plant damages by sucking and sooty molds. Lycorma delicatula was first detected in South 27 28 Korea in 2004, where its introduction and spreading possibly were affected by human activityrelated factors. Here, we used MaxEnt to describe current distribution of L. delicatula in Korea 29 and tried to find out the impact of human influences for distribution. We used 143 sites of 30 31 occurrence data, 19 bioclimatic variables, duration of temperature below -11°C, average daily 32 minimum temperature in January, cumulative thermal unit variable, the distribution of grape 33 orchard variable and human footprint to create models. These models were estimated by two 34 sets of 24 candidates with feature combinations and regularization multipliers. In addition, 35 these two sets were created as models with and without footprint for how human influence affect to distribution. Model selection for optimal model was performed by selecting a model 36 37 with a lowest sum of each rank in small sample-size corrected Akaike's information criterion 38 and difference between training and test AUC. Model of LQ10 parameter combinations was selected as optimal models for both model sets. Consequently, both of distribution maps from 39 these models showed similar patterns of presence probability for L. delicatula. Both models 40 expected that low altitude regions were relatively more suitable than mountain areas in Korea. 41 Footprint might be limited for the distribution and L. delicatula might already occupy most of 42 available habitats. Human-related factors might contribute to spread of L. delicatula to 43 44 uninfected areas.

45

46 Introduction

47 Spotted lanternfly, *Lycorma delicatula* (Hemiptera: Fulgoridae), is an invasive species
 48 of which origin is the southern China and the countries in the subtropical zones of Southeast

Asia [1]. In Korea, L. delicatula was first detected in Cheonan in 2004 [2], and then expanded 49 50 across South Korea for more than a decade [3]. Since its first detection, the agricultural area, 51 mostly grapevine yards, damaged by L. delicatula increased rapidly from one ha in 2006, seven ha in 2007, 91 ha in 2008, 2,946 ha in 2009, to 8,378 ha in 2010 [4, 5]. According to 52 Park et al. [3], L. delicatula might disperse more frequently in the western region and its long-53 distance dispersal could be possible beyond the mountain range. These rapid spread might 54 55 be caused by human-related factors such as vehicles which mainly could transfer a host plant or other material with its egg masses [6]. 56

57 A few studies have been conducted for determining potential habitats and habitat suitability of L. delicatula. Jung et al. [7] estimated the potential habitats of L. delicatula in 58 Korea by using CLIMEX, which is a mechanistic modelling method based on physiological 59 traits and constraints [7]. The CLIMEX requires the biological parameters related with the 60 target insects such as optimal temperature, lower developmental threshold, lethal temperature, 61 optimal humidity and so on [8]. Nevertheless, information on the biological parameters for L. 62 63 delicatula was limited, and thus estimated potential habitats were not exactly matched with 64 the current distribution of L. delicatula in Korea. A correlative method, which relates 65 occurrence data of a species to environmental data statistically [9], seems to be better than deterministic methods (e.g., CLIMEX) because biological information for L. delicatula is limited 66 67 and human related factors cannot be applied to deterministic methods due to difficulty of 68 parameterization of them. As one of the correlative methods, MaxEnt could be applied to 69 describe current distribution of L. delicatula in Korea because it needs only presence data and 70 has high predictive accuracy [10, 11], although a few issues with MaxEnt modeling should be considered to increase prediction accuracy (e.g., sampling bias of occurrence data, types of 71 72 feature, model complexity, criteria of model selection, model evaluation method and etc.) 73 [12-15].

This study aims to select best combinations of parameters for application of presence data of *L. delicatula* and its surrounding environmental and human related variables in MaxEnt,

- to select variables affecting the current distribution, to find out the effects of anthropogenic
 factor, and to visualize current presence probability of *L. delicatula* in Korea.
- 78

79 Material and methods

80 Collection and preparation of presence data of *L. delicatula*

81 Total 143 presence data points of L. delicatula were collected from the published papers [6, 16-19] (15 points), the report of National Institute of Ecology (NIE) [20] (83 points), 82 and observation of this study (45 points). For developing distribution maps of L. delicatula, 83 84 data were divided into two data sets; one for training data for model calibration, and the other for test data for model validation or evaluation [9]. For training data, 83 data points of the NIE 85 86 report were selected because these data were collected for whole Korean territories with a 87 consistent sampling criteria during one year, in 2015. The other 60 points were used for test data. Both training and test data sets were analyzed to determine spatial patterns using 88 89 ArcGIS 10.1 [21] with the average nearest neighbor test, and all data were used in model 90 development because both data show a random distribution. Data with random distribution 91 are needed to avoid overestimating problem, which is caused by clustered occurrence data, 92 in species distribution models [22]

93

94 Environmental variables related to *L. delicatula*

Monthly temperature and precipitation data from 1981 to 2010 (30 years) were downloaded from the web site of the Korea Meteorological Administration (KMA). These weather data were collected from 73 meteorological stations operated nationwide by KMA, and then were interpolated by Inverse Distance Weighting (IDW) method for estimating temperature and precipitation with a grid size of 1 km. Nineteen bioclimatic variables [23] were created in DIVA-GIS 7.5 [24] using these data. These 19 variables were transformed to ASCII
 file format using SDMs tool [25] in ArcGIS 10.1.

102 To consider all variables related with occurrence of L. delicatula, published papers on 103 its ecology were reviewed (Table 1). Among them, two overwintering related variables, development related variable and main host (i.e., grape) distribution of *L. delicatula*, were used 104 as these variables expected to be directly related with occurrence of L. delicatula in Korea. 105 106 There were multiple studies [6, 26-28] that overwintering egg mortality of *L. delicatula* was affected by number of days with minimum temperature below -11°C and average daily 107 minimum temperature in January. Thus, these variables (i.e., under -11 Jan and 108 min tmp jan) were created with the same climatic data and interpolation method, and then 109 110 used for 19 bioclimatic variables. Cumulative thermal unit variable (i.e., Degree day) for 111 development of L. delicatula in locations of 73 meteorological stations of KMA was calculated and mapped by using average daily maximum and minimum temperatures of 30 years (1981-112 2010) and 11.13°C lower development threshold from Park's paper [6]. Even although L. 113 114 delicatula has diverse host plants [16], its adults showed high preference and fitness at grapes [16, 29]. Thus, distribution of grape orchard variable (i.e., Grape) was created from 1,916 115 dimensions of viticulture by regions (www.agrix.go.kr) with ordinary krigging method in ArcGIS 116 117 10.1.

118 **Table 1. Biological information of** *L. delicatula* **in published papers.**

Biological parameters	stage	Matched information	Reference
Lower development threshold	Egg	8.14	[30]
(°C)	Egg	11.13	[6]
Upper development threshold (°C)	Egg	31-33	[6]
Low lethal temperature (°C)	Egg	- 12.72	[28]
	Egg	- 16.51	[6]
Thermal requirements (DD)	Egg	355.4	[30]
	Egg	293.26	[6]
Hatching rate (factors)	Egg	Mean daily min temperature in Jan	[28] [6]

	_		
	Egg	Number of days below -11℃ in Jan	[26]
Peak time of occurrence in <i>A. altissima</i> (DD)	1st	270.71 ± 3.38	[6]
: base temperature (11.13 °C)	2nd	491.98 ± 7.15	
	3rd	619.31 ± 6.15	
	4th	907.60 ± 9.72	
	Adult	1820.65 ± 14.21	
Host plants in Korea (ea)	All stages	41 (38 trees and 3 herb plants)	[16]
Host preference (plant species)	Adult	Juglans mandshurica, Cedrela fissilis, Toona sinensis, Evodia danielii, Phellodendron amurense, Picrasma quassioides, Ailanthus altissima, Parthenocissus quinquefolia, Vitis amurensis, Vitis vinifera	[16], [29]
Hatching rate by different light conditions (8; 12; 16h)	Egg	Not significant	[31]
Cyclic behavior	Adult	Sex based dispersal	[6]
	Adult	Host preference cycle	[32]
preference of color (sticky trap)	All stages	Brown	[30]
Inhibition of growth of grape	4th	Significant	[31]
Parasitism rate of egg parasitoid in origin (%)	Egg	30	[33]
Sex ratio (%)	Adult	35-45	[6]
No. eggs in egg mass (ea)	Egg	32.7 ± 6.49	[31]
	Egg	40-50	[16]

¹¹⁹

126

Human foot print variable (i.e., footprint) [34] was also downloaded (<u>http://sedac.ciesin.columbia.edu/</u>) because distribution of *L. delicatula* might be affected by human activities [6].

Total 24 environmental variables (i.e., 19 bioclimatic variables, under_-11_Jan, min_tmp_jan, Degree day, Grape and footprint) were created to develop distribution model of *L. delicatula* In Korea.

127 Selection of environmental variables

Multi-collinearity test was conducted to eliminate correlated variables by Pearson's coefficient 'r' [35]. If multiple variables were correlated (|r | > 0.8), only one variable was selected based on biological relevance with *L. delicatula* ecology. From this process, 11 variables (bio03, bio05, bio11, bio12, bio13, bio15, bio17, under_-11_Jan, Degree day, grape and footprint) were selected among 24 variables.

133

134 Modelling procedure

135 As a default setting, MaxEnt offers six features (i.e., an expanded set of transformations of the original covariates [36] types, L (linear), Q (quadratic), P (product), T 136 (threshold), H (hinge), C (categorical), which are automatically selected by 'Auto features' 137 depending on the sample size of training data [37]. In addition, MaxEnt creates a distribution 138 139 model, using regularization multiplier (default value = 1), which mitigates model complexity or 140 overfitting, to make general interpretation [36]. Nevertheless, MaxEnt does not always create the best model by a given default parameter setting [38]. Therefore, to select the best model 141 we adjusted the parameters setting and developed 24 candidate models with different feature 142 143 combinations and regularization multipliers by using four feature combinations (LQ, LQP, LQH, 144 LQPH) and six regularization parameters (1, 2, 5, 10, 15, 20). For comparison, another set of 24 models trained by 10 variables except for footprint was also created with previously noted 145 feature combinations and regularization parameters to estimate habitat suitability excluded 146 147 possibility of propagation.

For selecting optimal parameter combination, small sample-size corrected Akaike's information criterion (i.e., AIC_c) [39] and area under the receiver operation characteristic curve (i.e., AUC) were used to compare candidate models. Because high training AUC (AUC calculated by training data) might be result of overfitting model, difference between training

and test AUC (AUC calculated by test data) were choose for model selection criteria. 152 153 Therefore, AIC_c and difference between training and test AUC (AUC_{diff}) were calculated in ENMTools [40] and MaxEnt. To consider both AUC_{diff} and AIC_c [12] for model selection, sum 154 of each rank in AUC_{diff} and AIC_c from the lowest value was used because smaller values of 155 AIC_c and AUC_{diff} represent a better model. If sum of rank of candidate models is equal, a model 156 with a smaller AIC_c score was selected. From these processes, optimal models were re-built 157 158 and importance of each variables evaluated with jackknife test and 10-fold cross-validation. 159 Each of two models were built with its own selected variables to describe current occurrence probability of *L. delicatula* in Korea. The maps of two models were visualized in ArcGIS 10.1. 160

- 161
- 162 **Results**

Selection of best parameter combinations in both models

164 **for MaxEnt application**

165 LQ10 (i.e., combination of feature types L and Q and regularization multiplier 10), 166 LQH10 (i.e., combination of feature types L, Q, and H and regularization multiplier 10), and 167 LQPH5 (i.e., combination of feature types L, Q, P, and H and regularization multiplier 5) were selected by having the lowest value of summing both ranks in AUC_{diff} and AIC_c for the model 168 without footprint (Fig 1. (A)). However, both LQ10 and LQH10 had same AIC_c values, and 169 these values of both parameter combinations were lower than one of LQPH5. Thus, LQ10 and 170 LQH10 were considered as the best models without footprint for L. delicatula. LQ10 and 171 LQH10 were also determined in the model with footprint (Fig 1. (B)). In both model selections, 172 173 LQ10 and LQH10 created exactly same model. Therefore, LQ10 parameter combinations of each model was selected to build the distribution model for L. delicatula. 174

175

176 **Fig 1. Sum of AUC_{diff} and AIC_c ranks for 24 candidate models.**

Sum of AUC_{diff} and AIC_{c} ranks of all candidate models (A) without footprint and (B) with footprint. Each AUC_{diff} and AIC_{c} were ranked in order of ascending power from values calculated in MaxEnt and ENMTools. Black and grey bar represent rank of AUC_{diff} and AIC_{c} respectively. Asterisk (*) represents final selected models.

181

182 Evaluation of developed models

Two MaxEnt executions (without footprint and with footprint) with LQ10 parameter 183 184 combination created models using five variables in each run (Table 2). The average AUC score calculated by 10-fold cross-validation with training data and 10 variables for the model 185 without footprint was 0.733 ± 0.064 (Table 2), indicating reasonable performance (AUC score 186 > 0.7; Peterson at al., 2011). When this model was evaluated with test data, the AUC score 187 188 was 0.747, representing reliable performance. Among five variables used in modelling, Bio 05 189 and Degree day were estimated as important variables in distribution model for L. delicatula 190 by occupying more than 90% contributions to determine the distribution model. This result was also obtained in jackknife test (Fig 2. (A) and Table 3). 191

Fig 2. Results of Jackknife test for relative importance of used variables in each final model.

Relative importance of (A) ten variables used in model without footprint and (B) 11 variables
used in model with footprint. Jackknife tests were executed with 10-fold cross-validation,
results were averaged values of each run.

197

198 **Table 2. Summary of description and performance of each two models.**

Model	Model description	Model performance

(LQ 10)	No. input variables	Used variables	No. parameters	Training AUC	Average AUC (mean±SD)	Test AUC
Without footprint	11	Bio 05 Bio 13 Bio 15 Degree day Grape	5	0.755	0.733 ± 0.064	0.747
With footprint	10	Bio 05 Bio 13 Degree day Footprint Grape	5	0.789	0.769 ± 0.045	0.773

199Training AUC and test AUC were calculated by training and test data of occurrence information200respectively. Average AUC was averaged AUC value of 10 test bins in result of 10-folds cross-

201 validation.

202

203	Table 3. Averaged percent contribution and permutation importance of environmental
204	variables for each two models.

	Without	footprint	With footprint		
Variables	Percent contribution	Permutation importance	Percent contribution	Permutation importance	
Footprint	-	-	51.4	27	
Bio 05	91.3	75.2	40.8	53.3	
Bio 15	4	1.9	-	-	
Degree day	2	16.5	2.4	15.4	
Grape	1.7	2.8	1.3	2.9	
Bio 13	1	3.3	0.1	1	

²⁰⁵

The model with footprint performed better than the model without footprint, showing that the average AUC score was 0.769 ± 0.045 and test AUC score was 0.773 (Table 2). This model was also created with five parameters from five variables regularized by LQ 10 combination. The footprint and Bio 05 were important variables predicting distribution of *L*.

210	delicatula (Fig 2 and Table 3). The response curve of footprint and Degree day showed that
211	probability of presence was increased linearly (Fig 3. (A) and (C)). Probability of presence was
212	exponentially increased according to the increase of Bio 05 (Fig 3. (B)).

213

Fig 3. Probability of presence of *L. delicatula* according to each environmental variable.

(A) Human foot print; (B) Max temperature of warmest month; (C) Cumulative thermal unit

216 (base temperature: 11.13°C); (D) Precipitation seasonality (coefficient of variation); (E)

217 Distribution of grape orchard; (F) Precipitation of wettest month

218

219 Current presence probability maps of *L. delicatula* in Korea

Both distribution maps including and excluding footprint variable well descripted current presence possibility of *L. delicatula* in Korea, showing similar patterns of presence probability (Fig 4). Both models expected that mountain areas were potentially unsuitable, whereas low altitude regions were relatively suitable in Korea (Fig 4). However, the model with footprint more specifically estimated regions of higher probability of presence rather than that without footprint (Fig 4).

226

Fig 4. Potential distribution map of *L. delicatula* estimated by two models in Korea.

Probability of presence (MaxEnt's logistic output) predicted by (A) model with footprint and (B)
 without footprint.

230

231 **Discussion**

Both models without and with footprint predicted well current presence possibility of 232 233 L. delicatula in Korea. Moreover, there was a strong correlation (r = 0.916) between two 234 models. This indicates that the effects of human-related factors might be limited for the current distribution of L. delicatula, which might already occupy most of available habitats in Korea. 235 However, the model with footprint showed higher prediction ability than that without footprint 236 by considering AUC values. From our results, we speculate that human-related factors might 237 238 contribute to spread of L. delicatula to uninfected areas rather than directly affection for habitat 239 suitability. Spear et al. [42] found strong relationship between human population density and richness of alien species, proposing human density as good predictor determining population 240 241 size of alien species. This human-mediated propagule pressure could assist successful 242 establishment of invasive species by supplying population above Allee threshold into new 243 areas [43]. As for L. delicatula, contribution of human factors for its dispersal could be 244 significant because its eggs were frequently found in packing, construction and agricultural 245 materials [6, 31]. Recently, L. delicatula was also found in Berks county of Pennsylvania, USA 246 [44, 45]. This introduction and spreading were also suspected by causing human-related factors such as packing materials and vehicles [44, 45]. Moreover, there was no record of L. 247 248 *delicatula* found in the DMZ (Demilitarized Zone) area [46, 47] even though physical distance was not far away from the observed areas. Therefore, human influence could be an important 249 250 factor in determining distribution of *L. delicatula*, especially in the early stage of invasion.

In both models with and without footprint, Bio 05 (i.e., maximum temperature during the warmest month) was the most important environmental factor to contribute the distribution of *L. delicatula*. This might be related to the origin of *L. delicatula* which is South China and Southeast Asia [48]. Because *L. delicatula* is poikilothermic, its development is increased as temperature increases up to its upper developmental threshold [49-51]. The mean maximum temperature during the warmest month in Korea was generally lower than the upper developmental threshold of *L. delicatula* [6, 52].

Degree day, another environmental factor made in this study, also contributes in 258 259 distribution modeling of *L. delicatula*. In response curve of Degree day variable, 50% presence 260 possibility of L. delicatula was determined around 1,900 DD similar to the accumulated degreedays (i.e., 1,821) of peak occurrence of *L. delicatula* adults in fields [6]. One-tailed binomial 261 tests [53] were applied to training and test data using 1,821 DD, the Degree day variable well 262 distinguished presence and pseudo-absence of L. delicatula significantly (p < 0.05) in both 263 264 training and test data. Therefore, degree-days would be suitable variable to predict potential 265 habitat of L. delicatula.

The other variables (i.e., Bio 13, Bio 15, and grape) used in modeling contribute a 266 small amount and discrimination ability of these variables for presence or absence of L. 267 delicatula was very low. The five variables related to winter temperature (Bio 06, Bio 09, Bio 268 10, under -11 Jan, and min tmp jan), which are supposed to determine the hatching rate of 269 270 L. delicatula, were not selected for the distribution model of L. delicatula. Although these variables were proposed as important variable determining annual population size in many 271 272 papers [6, 26-28], they did not explain distribution of *L. delicatula* in this study. This suggests 273 that low lethal temperature (i.e., around -12.7 °C to -16.5 °C) is over than average winter temperature in Korea, like Bio 05. As an example, there was no case that January mean 274 275 temperature was less than -11 °C in Seoul, one of coldest areas in Korea, during 38 years 276 (1981-2018), and quite high as -2.56 ± 1.951 °C (mean ± SD) than lower lethal temperature.

Both models in this study are closer to realized niche than fundamental one because these models were not built by deterministic method finding physiological traits of *L. delicatula*, but had correlative method with distribution and environmental variables [9]. These two models are strictly realized niche only in Korea, which include environmental variables in Korea and their unknown interaction [54]. Thus, extrapolation to other regions or predict of future distribution needs cautions. However, it could be still applicable to predict risk analysis for *L. delicatula* even in non-contaminated areas and countries having high risk of being invaded.

In conclusion, major variables related with occurrence of *L. delicatula* in Korea should be helpful for predicting its occurrence. Moreover, footprint variable might be applicable for making surveillance plan and deciding domestic quarantine stations in countries with early stages of invasion of *L. delicatula*, while remaining relevant variables with the occurrence of *L. delicatula* could be used for risk assessment in non-invaded countries

289

290

291 Acknowledgements

This work was carried out with the support of "Cooperative Research Program for Agriculture Science & Technology Development (Project No. PJ01257203)" Rural Development Administration, Republic of Korea. And this work was supported by Korea Environment Industry & Technology Institute (KEITI) through Exotic Invasive Species Management Program, funded by Korea Ministry of Environment (MOE) (2018002270005).

297

298

299

300 **References**

- Xiao G. Forest Insect of China. Forest Research Institute: Forest Research Institute;
 1991. 1361 p.
- Kim SS, Kim TW. *Lycorma delicatula* (White) (Hemiptera: Fulgoridae) in Korea. Lucanus.
 2005;5:9-10.
- Park M, Kim K-S, Lee J-H. Genetic structure of *Lycorma delicatula* (Hemiptera: Fulgoridae)
 populations in Korea: Implication for invasion processes in heterogeneous landscapes.
 Bull Entomol Res. 2013;103:1-11. doi: 10.1017/S0007485313000011.
- Lee SG. The grape orchards increase geometrically damage areas every year by
 Lycorma delicatula 2010. 27-9 p.
- 5. Lee GY, Kim SG, Kim IH, Kim GS. Seasonal occurrence of spot clothing wax cicada,

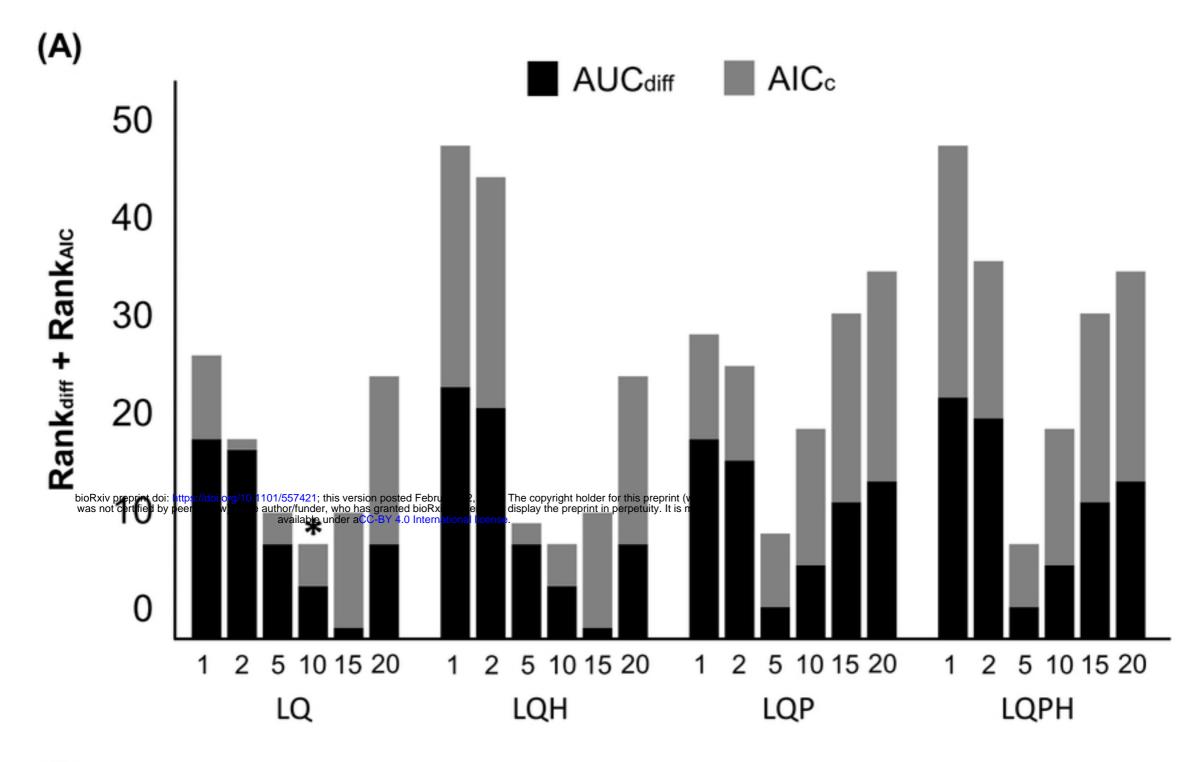
lycorma delicatula (Hemiptera: Fulgoridae) and It's control efficacy using EFAM at the vineyards. Korean J Pestic Sci. 2011;15(3):303-9.

- Bark M. Overwintering ecology and population genetics of *Lycorma delicatula* (Hemiptera:
 Fulgoridae) in Korea: Seoul national university granduate; 2015.
- Jung JM, Jung SH, Byeon DH, Lee WH. Model-based prediction of potential distribution
 of the invasive insect pest, spotted lanternfly *Lycorma delicatula* (Hemiptera: Fulgoridae),
 by using CLIMEX. J Asia Pac Biodivers. 2017. doi: doi.org/10.1016/j.japb.2017.07.001.
- Sutherst R, Maywald G, Kriticos D. CLIMEX® software version 3, User's Guide: CSIRO, Hearne Scientific Software Pty Ltd.; 2007.
- Elith J, H. Graham C, P. Anderson R, Dudík M, Ferrier S, Guisan A, et al. Novel methods improve prediction of species' distributions from occurrence data. Ecography. 2006;29(2):129-51. doi: doi.org/10.1111/j.2006.0906-7590.04596.x.
- 32310. Phillips SJ, Anderson RP, Schapire RE. Maximum entropy modeling of species324geographic325distributions.326https://doi.org/10.1016/j.ecolmodel.2005.03.026.
- 326 11. Ortega-Huerta AM, Peterson AT. Modeling ecological niches and predicting geographic
 327 distributions: A test of six presence-only methods. Rev Mex Biodivers. 2008;79:205-16.
- Warren DL, Seifert SN. Ecological niche modeling in Maxent: the importance of model
 complexity and the performance of model selection criteria. Ecol Appl. 2011;21(2):335 42. doi: doi.org/10.1890/10-1171.1.
- Merow C, Smith MJ, Silander JA. A practical guide to MaxEnt for modeling species'
 distributions: What it does, and why inputs and settings matter. Ecography.
 2013;36(10):1058-69. doi: doi.org/10.1111/j.1600-0587.2013.07872.x.
- Kramer-Schadt S, Niedballa J, Pilgrim JD, Schrder B, Lindenborn J, Reinfelder V, et al.
 The importance of correcting for sampling bias in MaxEnt species distribution models.
 Divers Distrib. 2013;19(11):1366-79.
- Radosavljevic A, Anderson RP. Making better Maxent models of species distributions:
 complexity, overfitting and evaluation. J Biogeogr. 2014;41(4):629-43. doi:
 doi.org/10.1111/jbi.12227
- Park JD, Lee SG, Shin SC, Kim JH, Park IG. Biological Characteristics of *Lycorma delicatula* and the Control Effects of Some Insecticides. Korean J Appl Entomol.
 2009;48(1):53-7.
- Kim SG, Lee KY, Shin YH, Kim GH. Chemical Control Effect Against Spot Clothing Wax
 Cicada, *Lycorma delicatula* (Hemiptera: Fulgoridae) Nymphs and Adults. Korean J Pestic
 Sci. 2010;14(4):440-5.
- 18. Han JM. Studies on Taxonomy of Korean Fulgoridae (Hemiptera) and Introduction of
 Lycorma delicatula to Korea: Chungbuk national university; 2010.
- Pyo SH. Characterization of the Life Cycle of *Lycorma delicatula* and the Effects of
 Organophosphate Treatment on th Cycle Stages of the Insect: Chungbuk national
 university; 2011.
- 20. Ecology NIo. Monitoring of Invasive Alien Species Designated by the Wildlife Protection
 Act (II). National Institute of Ecology: National Institute of Ecology, 2015.
- 353 21. ESRI. ArcGIS 10.1. ESRI. Redlands, California. USA. 2012.
- Boria RA, Olsonb LE, Goodman SM, Anderson RP. Spatial filtering to reduce sampling
 bias can improve the performance of ecological niche models. Ecol Modell. 2014;275:737. doi: dx.doi.org/10.1016/j.ecolmodel.2013.12.012.
- Ramirez-Villegas J, Bueno-Cabrera. Working with climate data and niche modeling:
 Creation of bioclimatic variables. International Center for Tropical Agriculture (CIAT), Cali,
 Colombia: International Center for Tropical Agriculture (CIAT), Cali, Colombia; 2009.
- 24. Hijmans RJ, Guarino G, Macathur P. DIVA-GIS. Version 7.5.0. Manual.
 <u>http://www.divagis.org</u>. 2012.
- 362 25. Brown JL, Bennett JR, French CM. SDMtoolbox 2.0: the next generation Python-based
 363 GIS toolkit for landscape genetic, biogeographic and species distribution model analyses.

364 PeerJ. 2017;5:e4095. doi: 10.7717/peerj.4095.

- 26. Lee YS, Jang MJ, Kim JY, Kim JR. The Effect of Winter Temperature on the Survival of
 Lantern Fly, *Lycorma delicatula* (Hemiptera: Fulgoridae) Eggs. Korean J Appl Entomol.
 2014;53(3):311-5.
- Jeong T-S, Hwang M-R, Moon Y-G, Lee J-H, Lee N-G, Kwon S-B, et al. Occurrence of
 Lycorma delicatula according to Temperature Changes of Winter Season in Gangwon
 Province. Korean Jouranl of Soil Zoology. 2015;19(1):52-6.
- 28. Lee J-S, Kim I-K, Koh S-H, Cho SJ, Jang S-J, Pyo S-H, et al. Impact of minimum winter
 temperature on *Lycorma delicatula* (Hemiptera: Fulgoridae) egg mortality. J Asia-Pacific
 entomology. 2011;14(1):123-5. doi: doi.org/10.1016/j.aspen.2010.09.004.
- Lee JE, Mun SR, An HG, Cho SR, Yang JG, Yoon CM, et al. Feeding Behavior of *Lycorma delicatula* (Hemiptera: Fulgoridae) and Response on Feeding Stimulants of Some Plants. Korean J Appl Entomol. 2009;48(4):467-77.
- 30. Choi D-S, Kim D-I, Ko S-J, Kang B-R, Park J-D, Kim S-G, et al. Environmentally-friendly
 control methods and forecasting the hatching time *Lycorma delicatula* (Hemiptera:
 Fulgoridae) in Jeonnam Province. Korean J Appl Entomol. 2012;51(4):371-6. doi:
 dx.doi.org/10.5656/KSAE.2012.09.0.022.
- 381 31. Song MK. Damageby *Lycorma delicatula* and chemical control in vineyards: Chungbuk
 382 national university; 2010.
- 383 32. Kim JG, Lee E-H, Seo Y-M, Kim N-Y. Cyclic Behavior of *Lycorma delicatula* (Insecta: 384 Hemiptera: Fulgoridae) on Host Plants. Journal of Insect Behavior. 2011;24(6):423. doi: 385 10.1007/s10905-011-9266-8.
- 386 33. Choi M-YYZ-QWX-YTY-LHZ-RKJHBYW. Parasitism Rate of Egg Parasitoid Anastatus
 387 orientalis (Hymenoptera: Eupelmidae) on Lycorma delicatula (Hemiptera: Fulgoridae) in
 388 Choi M-YYZ-QWX-YTY-LHZ-RKJHBYW. Parasitism Rate of Egg Parasitoid Anastatus
 387 orientalis (Hymenoptera: Eupelmidae) on Lycorma delicatula (Hemiptera: Fulgoridae) in
 388 Choi M-YYZ-QWX-YTY-LHZ-RKJHBYW. Parasitism Rate of Egg Parasitoid Anastatus
 388 orientalis (Hymenoptera: Eupelmidae) on Lycorma delicatula (Hemiptera: Fulgoridae) in
 388 Choi M-YYZ-QWX-YTY-LHZ-RKJHBYW. Parasitism Rate of Egg Parasitoid Anastatus
 388 orientalis (Hymenoptera: Eupelmidae) on Lycorma delicatula (Hemiptera: Fulgoridae) in
 388 Choi M-YYZ-QWX-YTY-LHZ-RKJHBYW. Parasitism Rate of Egg Parasitoid Anastatus
 388 orientalis (Hymenoptera: Eupelmidae) on Lycorma delicatula (Hemiptera: Fulgoridae) in
 388 Choi M-YYZ-QWX-YTY-LHZ-RKJHBYW. Parasitism Rate of Egg Parasitoid Anastatus
- 389 34. Gallardo B, Zieritz A, Aldridge DC. The importance of the human footprint in shaping the
 390 global distribution of terrestrial, freshwater and marine invaders. PloS one.
 391 2015;10(5):e0125801.
- 392 35. Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, et al. Collinearity: a review
 393 of methods to deal with it and a simulation study evaluating their performance. Ecography.
 394 2013;36(1):27-46. doi: doi.org/10.1111/j.1600-0587.2012.07348.x.
- 395 36. Elith J, Kearney M, Phillips S. The art of modelling range-shifting species. Methods Ecol
 396 Evol. 2010;1(4):330-42. doi: doi.org/10.1111/j.2041-210X.2010.00036.x.
- 397 37. Phillips SJ, Dudik M. Modeling of species distributions with Maxent: new extensions and
 398 a comprehensive evaluation. ECOGRAPHY. 2008;31(2):161-75.
- 399 38. Morales-Castilla I, Davies TJ, Pearse WD, Peres-Neto P. Combining phylogeny and co 400 occurrence to improve single species distribution models. Glob Ecol Biogeogr.
 401 2017;26(6):740-52. doi: doi.org/10.1111/geb.12580.
- 402 39. Akaike H. A new look at the statistical model identification. IEEE Trans Automat Contr.
 403 1974;19(6):716-23. doi: doi.org/10.1109/TAC.1974.1100705.
- 404 40. Warren DL, Glor RE, Turelli M. ENMTools: a toolbox for comparative studies of 405 environmental niche models. Ecography. 2010;33(3):607-11. doi: doi.org/10.1111/j.1600-406 0587.2009.06142.x.
- 407 41. Peterson AT, Sober, xf, n J, Pearson RG, Anderson RP, et al. Ecological Niches and
 408 Geographic Distributions (MPB-49): Princeton University Press; 2011.
- 409
 42. Spear D, Foxcroft LC, Bezuidenhout H, McGeoch MA. Human population density explains alien species richness in protected areas. Biological Conservation. 2013;159:137-47. doi: https://doi.org/10.1016/j.biocon.2012.11.022.
- 412 43. Drake JM, Lodge DM. Allee Effects, Propagule Pressure and the Probability of
 413 Establishment: Risk Analysis for Biological Invasions. Biol Invasions 2006;8:365. doi:
 414 doi.org/10.1007/s10530-004-8122-6.
- 44. Barringer L, Donovall L, Spichiger S-E, Lynch D, Henry D. The First New World Record
 of *Lycorma delicatula* (Insecta: Hemiptera: Fulgoridae). Entomol News. 2015;125:20-3.
 doi: doi.org/10.3157/021.125.0105.

- 418 45. Dara SK, Barringer L, Arthurs SP. *Lycorma delicatula* (Hemiptera: Fulgoridae): A New
 419 Invasive Pest in the United States. J Integr Pest Manag. 2015;6(1):20. doi:
 420 doi.org/10.1093/jipm/pmv021.
- 421 46. Ahn NH, Jeon MJ, Seo HY, Kim KG, Park SJ, Han SH. National List of Species of Korea 422 [Insect] (Insects of North Korea). Incheon: NIBR; 2013.
- 423 47. Ecology NIo. Biodiversity Synthesis Report of the DMZ area: National Institute of Ecology;
 424 2016.
- 48. Han JM, Kim HJ, Lim EJ, Lee SH, Kwon YJ, Cho SW. *Lycorma delicatula* (Hemiptera:
 Auchenorrhyncha: Fulgoridae: Aphaeninae) finally, but suddenly arrived in Korea.
 Entomol Res. 2008;38(4):281-6. doi: doi.org/10.1111/j.1748-5967.2008.00188.x.
- 428 49. Lactin DJ, Holliday NJ, Johnson DL, Craigen R. Improved Rate Model of Temperature429 Dependent Development by Arthropods. Environ Entomol. 1995;24(1):68-75. doi:
 430 doi.org/10.1093/ee/24.1.68.
- 431 50. Logan JA, Wollkind DJ, Hoyt SC, Tanigoshi LK. An Analytic Model for Description of
 432 Temperature Dependent Rate Phenomena in Arthropods 1. Environ Entomol.
 433 1976;5(6):1133-40. doi: doi.org/10.1093/ee/5.6.1133.
- 434 51. Briere J-F, Pracros P, Le Roux A-Y, Pierre J-S. A Novel Rate Model of Temperature435 Dependent Development for Arthropods. Environ Entomol. 1999;28:22-9. doi:
 436 doi.org/10.1093/ee/28.1.22.
- 437 52. Pearman PB, Guisan A, Broennimann O, Randin CF. Niche dynamics in space and time.
 438 Trends Ecol Evol. 2008;23(3):149-58. doi: doi.org/10.1016/j.tree.2007.11.005.
- 439 53. Pearson RG. Species' Distribution Modeling for Conservation Educators and Practitioners:
 440 Lessons in Conservation; 2010.
- 54. Kearney M, Porter W. Mechanistic niche modelling: combining physiological and spatial
 data to predict species' ranges. Ecol Lett. 2009;12(4):334-50. doi: doi.org/10.1111/j.14610248.2008.01277.x.



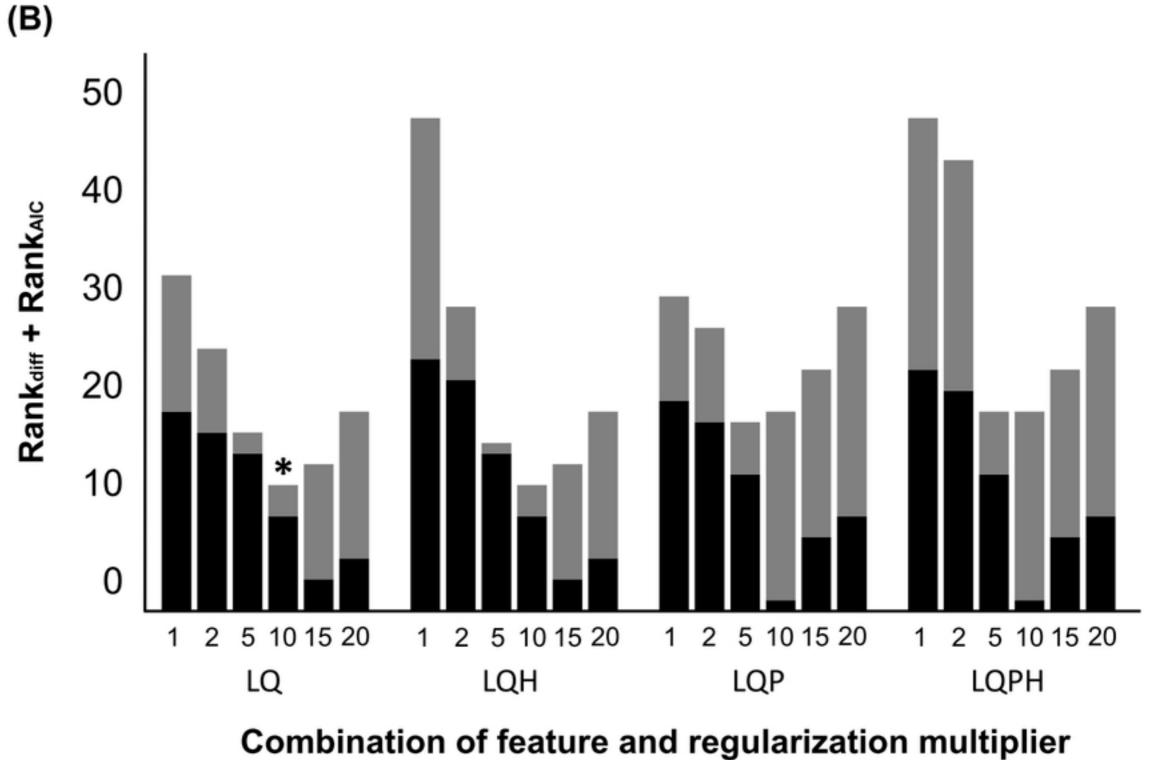


Figure 1

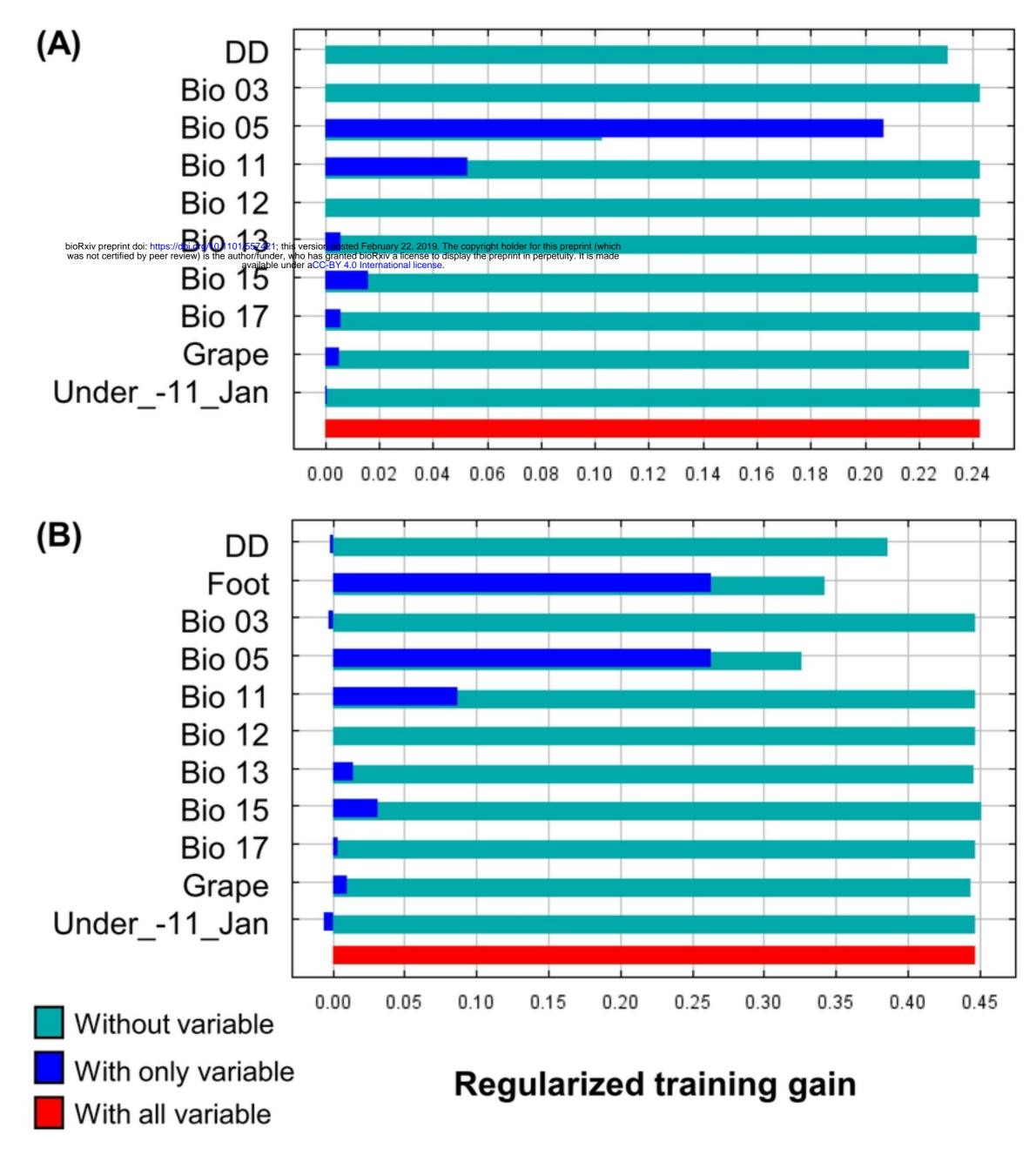


Figure 2

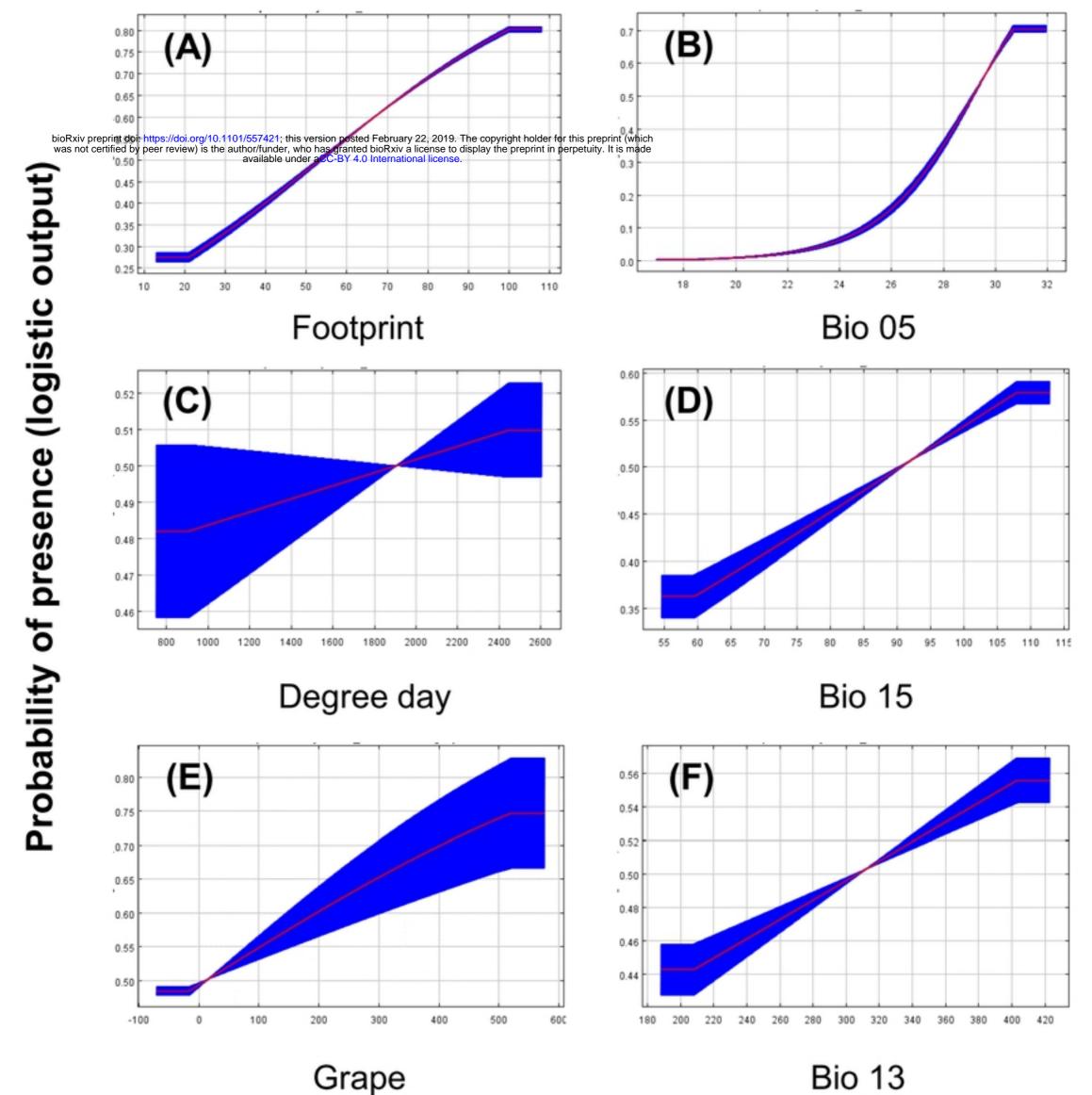


Figure 3

