

PREDICTIVE MODELING FOR BETTER UNDERSTANDING DISTRIBUTION AND SYSTEMATICS OF USEFUL ENCYRTIDS (HYMENOPTERA: CHALCIDOIDEA: ENCYRTIDAE)

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Received: 02.12.14; accepted: 29.01.15

Using a Maximum Entropy (Maxent) approach based on climate variables (~5 km resolution) we constructed predictive distribution models (PDM) of climate niches for eight encyrtid species (*Anagyrus pseudococci* (Girault), *A. aligarhensis* Agarwal and Alam, *A. dactylopii* (Howard), *A. sp. nr. pseudococci*, *Syrphophagus aphidivorus* (Mayr), *Ageniaspis fuscicollis* (Dalman), *Discodes coccophagus* (Ratzeburg), *Cerapterocerus mirabilis* Westwood (Hymenoptera: Chalcidoidea, Encyrtidae)) – all of them important in biological control as case studies for PDM. Models successfully predicted all of the known distribution for each species and identified additional suitable areas where each species could be used as a biological control agent. The results show that all the modeled species are highly associated with temperature variables. The mean annual temperature, minimal temperature of coldest month and isothermality are the most important determinants for the distribution of encyrtids. These parameters (and all other bioclimatic variables in general) are not fully independent and may confound the interpretation of variable importance. Modeling results showed that the distribution range of *A. sp. nr. pseudococci* falls within the ranges of two other *Anagyrus* species, except the extreme southeast, which could be the bias caused by improper taxon sampling. Here, we suggest that *A. sp. nr. pseudococci* should be considered as a synonym of *A. dactylopii* (Howard). In this study we show relatively fast and simple ways of using PDM for encyrtid species in the biological control planning and solving of taxonomic problems.

INTRODUCTION

Species of Encyrtidae (Hymenoptera: Chalcidoidea) are significant as biological control agents because many species regulate important pests of natural or agricultural ecosystems. This group has particular importance in parts of the world where natural control is preferred over pesticides for ecological, financial, or political reasons [1-3]. Understanding a species' response to environmental variability is paramount in the successful management of natural enemies [4-6], especially when natural enemies are being introduced to new locations for the purpose of biological control, making such knowledge a useful in the successful management of pests. Despite the acknowledged importance of encyrtids in pest control,

no extensive data sets have been developed on their distribution and ecology. For many of the described species, only a few exact localities are available and their broader distributions are usually unknown. In such cases it is not possible to plan biological control programs effectively. It is a widely accepted principle in biological control that agents (natural enemies) should be collected from climates that match the environments they will be introduced into as closely as possible [6]. This is difficult to achieve in practice, as a 'climate' is a term denoting many interacting environmental factors, and because the collection locations of a biological control agent may not represent the optimal climatic conditions for that species. Therefore, it is important to develop models for use either

in selecting search areas where biological control agents of particular interest might be found, or release areas most suitable for their introduction.

One of the best known methods for potential distribution analysis in the framework described above is a climate matching system called CLIMEX [7]. CLIMEX is a simple way to construct a species' actual and potential distribution by combining temperature and/or rainfall variables. However, this method has several important limitations. It neither allows for a rigorous statistical evaluation of derived models nor does it provide flexibility (i.e., the ability to manipulate or incorporate many types of variables). In addition, it is not free. Because of these drawbacks, use of CLIMEX is rather limited. Another approach, discussed below, is predictive modeling of species distribution (PDM), which is a statistical detection of the pattern of species distribution based on the observed occurrence and associated environmental variables [8]. PDM is widely used for predicting a species' potential distribution for several reasons [9]: PDM is increasingly acknowledged as an effective tool in biological control planning and in resolving systematic problems, as it aims to construct species-specific niche distribution maps [4,6,10-15]. In theory, PDM is particularly useful when the species is widespread and the occurrence data are scarce; however, modern PDM methods are unfortunately decreasing in power as data becomes scarcer and more artificially based [16]. The results of PDM are roughly equally dependent on the algorithms used and on the quality of the input data (occurrence and/or absence, predictor variables), and these input data are hardly (if ever) perfect. Because of these imperfections the results of PDM vary significantly between algorithms and studies [16-19].

Despite the popularity of PDM, this method is not commonly used to model encyrtid species distribution ranges. In this study, we highlighted a fast and relatively easy way to construct PDM for encyrtid species with different biological and ecological characteristics. The derived models we created were used to develop distributional maps, potentially useful in the search/release of target species in new locations. We also examined whether the distribution models could help resolve systematic problems associated with the allopatrically distributed cryptic species, particularly species in the genus *Anagyrus* Howard, 1896 (Hymenoptera: Chalcidoidea, Encyrtidae) (*A. pseudococci* (Girault, 1915), *A. sp. nr. pseudococci* and *A. dactylopii* (Howard, 1898)), which are the subject of ongoing debates about the validity of their systematic position [20-23].

OBJECTIVES AND METHODS

Target species and occurrence data

This study is a part of an ongoing project to develop a distributional database for encyrtid parasitoids and their

hosts in the Trans-Caucasian countries, Turkey, and Iran. Insect distribution data were collected from different published sources from Georgia, Armenia, Azerbaijan, Turkey and Iran [1,22,24-33]. The data were mapped with the help of ArcGIS 9.3 (ESRI, Redlands, CA, USA) and Google Earth v.6.2.2 (Google Inc.) based on UTM grid system (Appendix 1).

For this study we choose eight species, for which we constructed PDM models (Table 1; Appendix 1). Four species were from same genus (*Anagyrus pseudococci*, *A. dactylopii*, *A. sp. nr. pseudococci* and *A. aligarhensis* Agarwal & Alam, 1959) – all parasitoids of pseudococcids. First three species are very close to each other with their morphological and biological features, which make troubles for correct taxonomic identification and their successful use in biocontrol [23]. Another four parasitoid species were from different genera possessing different biological characteristics (the aphid parasitoid *Syrphophagus aphidivorus* Mayr, 1876, the lepidopteran parasitoid *Ageniaspis fuscicollis* (Dalman, 1820), *Discodes coccophagus* (Ratzeburg, 1848) (Hymenoptera: Chalcidoidea, Encyrtidae), a primary parasitoid of the scale *Sphaerolecanium prunastri* (Boyer De Fonscolombe, 1834) (Hemiptera: Coccoidea, Coccidae), and *Cerapterocerius mirabilis* Westwood, 1833 (Encyrtidae), a hyperparasitoid of parasitoids of several soft scales, such as *S. prunastri*, probably parasitizing *D. coccophagus*). *A. fuscicollis* and *S. aphidivorus* are widely distributed, almost cosmopolitan. *D. coccophagus* and *C. mirabilis* are important primary and secondary parasitoids of *S. prunastri* [34,35]. All species are important biocontrol agents and comparative study of the distribution of these species can provide new insights into their ecology.

Environmental variables

Apart from collecting representative occurrence data for species needing to be modeled, another major challenge with PDM is the selection of environmental variables. Use of accessible environmental variables is limited, and we do not know whether any particular variable or combination of variables determines species' distribution. However, based on the assumption that species distribution can be correlated with available variables, we used those that are available without strong preliminary inspection. Besides this, sometimes we need to define the probabilistic ecological niche dimension [36] within the framework of one or more classes of variables. This is the case when no preliminary assumption of the variable importance is needed. Rather, we seek all the potential areas where suitable combinations of analyzed variables (or the ecological niche – as defined by those variables) are met for any particular species [9,37]. The most intuitive and frequently used ecological variable class in PDM is climatic variables (i.e., temperature and rainfall combinations and derivatives), based on which

potential climatic niches are constructed. In recent years such climate databases have been developed for the whole world at various resolutions [38]. These climate databases contain 19 bioclimatic variables derived from monthly temperature and precipitation values, and are used to generate more meaningful and easily interpreted variables, such as annual and seasonal trends in temperature or precipitation and also possible limiting climate variables (e.g., temperature in coldest month, etc.; Table 1). To build potential PDMs (based on climate niche) for each target species, we used 19 bioclimatic variables with a spatial resolution of ~5 km. Detailed descriptions of each bioclimatic variable can be found in the data base website <http://worldclim.org>.

Selection of modeling techniques

Selecting the most suitable modeling method is not straightforward and is heavily dependent on the kind of data used, its quality, and the researcher's experience [39]. Normally, two classes of modeling algorithms are considered in constructing PDMs based on the input occurrence data: (1) only presence-based algorithms and (2) presence/absence-based algorithms. Theoretically, presence/absence methods are preferred in constructing PDMs because the input data provides information about unacceptable or nearly unacceptable conditions for the species under consideration. However, uncertainties concerning the validity of absence data (such as possible confounding biotic interactions which generally are not included in PDMs) can be important sources for uncontrolled bias in constructing PDMs. In contrast, models based solely on presence data are free from such uncertainties, although most such algorithms are less powerful [16]. Since only occurrence data are available for most species, presence-only modeling methods are especially important and popular. Many presence-only methods are currently available, but not all of them perform well consistently. For example, one of the well-known methods is BIOCLIM [40], which has gained popularity in recent years because of its simplicity. However, BIOCLIM has been shown to be not very powerful and prone to biases [41]. The most complicated methods are machine learning methods such as the entropy maximization approach – commonly known as Maxent [42]. The difficulty associated with such sophisticated methods is their “black box” nature, which means that the interpretation of the outputs is not straightforward [16].

In this study we used Maxent to model distributions of encyrtid species because of several advantages the method had: (1) there is a free and easy-to-use software package (MAXENT v.3. (<http://www.cs.princeton.edu/~schapire/maxent/>)) available; (2) it is one of the most frequently used and tested modeling methods (result of Google scholar search at 05.2013); (3) Maxent has been proven to be a

robust method against variable multi-collinearity (however, one must be careful in the interpretation of the outputs if the variables are highly correlated, and some authors suggest sieving such variables before calculation [43] and (4) Maxent uses a “hinge” function by which it can deal with piecewise linear responses of explanatory variables [44]. In general, Maxent has been shown to be a candidate for the best performing modeling algorithm available today [41,45–48].

Here, we briefly describe the conceptual characteristics of Maxent; a full description with comprehensive explanation can be found elsewhere [42,49]. Maxent is an algorithm that uses a comparison between presence and available background localities (randomly sampled pseudo-absence points) to make predictions of probability distribution for target species. The Maxent algorithm is designed for the incomplete distributional data in order to produce probability distribution across a study area; however, Maxent assumes that sampling localities contain unbiased information, which can otherwise become a source of uncontrolled biases in the final model [49]. Maxent maximally uses all the information included in presence localities (making no additional assumptions unsupported by the presence data) and finds a probability distribution maximally close to uniform. This is achieved by minimizing entropy between the probability distribution of presence localities and randomly selected background points [16,50]. Thus, Maxent is most suitable for modeling the distribution of species with few (around 10) presence points [51]. Maxent is able to handle continuous and categorical variables and it is also able to analyze complex functional relationships between predictor and response (linear, quadratic, threshold and piecewise (hinge) forms). All this makes Maxent one of the most powerful and intuitive modeling methods in determining niche conception [44,52].

In our study, the occurrence data used for model building for each of our species were well scattered (not clumped) within the respective distributional area, which makes the assumption of representativeness highly probabilistic. The number of available presence points was not less than 25 per species, excluding *A. dactylopii*, which had only 12 localities (Table 2).

Occurrence data and variable layers (ASCII raster formats) were imported in software MAXENT [49]. For model building, default options were used except the random background sampling limitations, which were set up to one pixel size radius for each occurrence such that no selected random localities could occur more closely. Five hundred iterations were performed with 20% of occurrences used as test data. Models were computed with the “logistic” option, which returns the map of continuous probabilities of prediction (ranging between 0 and 1) with a “hinge” option. For visualization purpose, we applied the threshold

to Maxent models at a value above which 95% of training localities occurred.

Model validation

Although there are several statistical measures to evaluate the performance of the model, no unbiased statistical evaluation is possible [53]. The best and most frequently used statistical means of model performance is considered the threshold independent discrimination measure - AUC (Area Under the ROC [Receiver Operating Characteristics] Curve) [54,55,56,57]. When $AUC = 0.5$, then model discriminatory ability is no better than random, whereas AUC values close to 1 means perfect performance of the model. In our case, we considered a model's performance to be good if its AUC values was close to 0.9 (or $AUC \sim 0.9$). With the pure statistics, which shows only mechanistic performance of the algorithm, we used expert knowledge (in the term "expert knowledge" we consider all the scientific information about the distribution of target species collectively) to additionally evaluate the quality of produced models. In regard to statistical evaluations, expert knowledge of a specific taxon under study can be very important in model building and evaluation [53,58]. Knowledge of a species' distribution pattern and its physiological and ecological requirements can contribute greatly in assessment, and in the future improvement of model performance. For this additional assessment we mapped the known distribution of each species by country (Fig. 1), which by itself is too rough to talk about a species' exact distribution. However, even such a rough map can still be used in model validation. In particular, we calculated the index for model performance - IMP as follows: $IMP = CNP / (CN - CM)$ where CN denotes the total number of countries where the species is known to exist, CM is the number of countries where model training samples are collected and CNP is the number of countries from where the species is known to occur but was not predicted by the model (See Table 1). The IMP index varies between 0 and 1. If $IMP = 0$ then the model prediction optimal, whereas an IMP approaching 1 indicates that the model prediction is not as good. The IMP index is not defined when CN equals CM, and hence can only be used when the number of countries with the presence points used in model training is less than the actual known distribution.

RESULTS AND ANALYSIS

Modeling results

In general, Maxent algorithm had very good performance, as the average AUC value (for test data) did not fall below 0.95 and had a low standard deviation (Table 2). Our study did not intend to analyze the details of the importance or response of each species to each variable; however, it should be noted that all the modeled species are highly associated with temperature variables (Table 1). Specifically, mean

annual temperature, minimal temperature of coldest month and isothermality are the most important determinants for the distribution of encyrtids. Clearly, these parameters (and all other bioclimatic variables in general) are not fully independent and may confound the interpretation of variable importance.

The IMP index showed very good results as well (i.e., correctly predicted a great deal of the known distribution for each species based on a relatively small sample) (Table 2). Hence, the derived models for each species are highly acceptable based on both evaluation methods used.

Informing biological control planning

The Maxent algorithm successfully predicted the species' actual distribution areas based on a small subset of occurrence localities, and gave important range extensions for several of them (Fig. 1). This in turn suggests that the area where such species is currently unknown can either be searched for a target species or subjected to biological control agents. One of the important questions during biological control planning is whether a biological control agent will establish and hence be effective against a particular pest. The bioclimate models are largely able to answer this question. As climate is the most important driver of species distribution [59], predictive models based on climate data should be at least standard starting procedure for biological control planning.

Despite the limited occurrence data used to build models for *A. fuscicollis*, *D. coccophagus*, and *A. aligarhensis*, the resulting models correctly predicted all countries where these species have so far been recorded (Table 2). Only a slight gap was detected in the predicted distribution of *C. mirabilis* where one country (South Africa) was not covered by the model (Fig. 1). However, this species has a Holarctic distribution pattern as well as its host species *D. coccophagus* [34,35] and the records from South Africa [60] (which is far outside the general distribution area of *C. mirabilis*) are doubtful and need reexamination. It should also be noted that Noyes [2] reported a possible bias in specimen identification from these regions.

Anagyrus aligarhensis is an important biological control agent that parasitizes pests such as *Nipaecoccus viridis* (Newstead), *Pseudococcus comstocki* (Kuwana), *Trionymus multivorus* (Kiritchenko) (Hemiptera: Coccoidea, Pseudococcidae) and other mealybugs [2]. The species is currently known to occur in 25 countries (Fig.). Our modeling gave quite trustworthy data for this species: all countries where *A. aligarhensis* has been previously recorded were covered by the model, and it predicted 44 additional countries for future introduction (both the AUC and IMP statistics performed well) (Table 2). Australia, New Zealand, and numerous African and South American countries can either be considered as not yet known distributional areas or as potential areas of introduction for pest control.

Similar results have been derived for two other species (*A. sp. nr. pseudococci* and *A. dactylopii*). Maxent provided detailed distribution for both species within their known ranges and predicted susceptible areas in other regions as well (Fig. 1). While the models can be useful in biological control, it is important to understand the systematics of this species (including *A. pseudococci*) as incorrectly identifying the species can lead to an uncontrolled bias in the distribution modeling.

The modeling results of the two remaining species were less perfect. Specifically, Maxent was not able to detect 6 and 7 countries (with known distribution) for *S. aphidivorus* and *A. pseudococci*, respectively (these two species also have the largest IMP index) (Table 2). Since the derived models are still informative and useful for biological control purposes, it will be important to determine the causes for the incongruence between the models and known distribution. The data for the distribution of *S. aphidivorus* in Mongolia, Sudan, Peru, and Cuba needs checking, as these countries have very different climates from other areas where this species occurs, suggesting possible identification mistakes. Although modeling shows lower climatic fit with previous records from Brazil, Kenya, India and Mexico, these records may also reflect biases in species identification. There are many data sets where parasitoid species were misidentified by various authors (2; Trjapitzin 1989). Guerrieri and Pellizzari [20] also mention the possible misidentification of *A. pseudococci*, used so widely in biological control programs worldwide, and suggest that in some cases the species identified as *A. nr. pseudococci* may in fact be *A. dactylopii*. We would suggest making a full revision of the distribution of these species before using them as biological control agents.

Possible solution for the systematics of the A. pseudococci species group

The systematics of the *A. pseudococci* species group is still controversial [22,23,61,62]. The morphological and molecular characteristics of *A. pseudococci*, *A. dactylopii* and *A. sp.nr. pseudococci* were discussed by Triapitsyn et al. [23], where molecular data has shown that *A. dactylopii* and *A. sp.nr. pseudococci* are more closely related than *A. pseudococci* with *A. sp.nr. pseudococci*, while the morphological characteristics (coloration of first funicular segment, frontovertex width) are the same. This opinion was later supported by Karamaouna et al. [21].

Distributional data about *A. dactylopii* indicates that the species occurs in the far south, east and southeastern Asia, Australia and Asia Minor. Meanwhile, a doubtful identification was recorded in Peru [2]. This distributional data is based on the work of Noyes and Hayat [22], however, information about Peru was not found in this work. The distribution area of *A. pseudococci* is wider and includes all of Africa, all of the Americas and almost all

of Eurasia whereas *A. sp. nr. pseudococci* is known from USA and few European and South-West Asian countries. Presumably, *A. dactylopii* is an Oceania-Asian “species”, while *A. pseudococci* can be described as Mediterranean. Noyes and Hayat [22] have previously discussed different races of these close related forms, such as Mediterranean, Asiatic, African, and Middle Eastern. Host species of both forms are almost the same, and the suggestion that there are some specific differences in their host specificity is not documented. The latest data on *A. sp. nr. pseudococci* shows that this “species” has a wider range of hosts [61] than previously thought [23]. The suspicion that *A. dactylopii* and *A. pseudococci* are conspecific is discussed in Noyes and Hayat [22]. Despite the fact that experiments to interbreed *A. pseudococci* and *A. dactylopii* populations have failed [22], this cannot be considered proof that they are different species. As Noyes and Hayat [22] state, the holotype of *A. dactylopii* consists only of a foreleg, making further comparison of new material with the holotype difficult. One of us (G. Japoshvili) has been working on this taxon for a long time and has had the chance to examine material from different parts of the world and from different museums; he has come to the conclusion that *A. sp.nr. pseudococci* is morphologically indistinguishable from *A. dactylopii* (unpublished material). Triapitsyn et al. [23] also noted the closeness of these “species”, and proposed that they could be clones of the same species, although the authors could not test this experimentally. It seems very probable that all these three “species” represent a monophyletic group of lineages (Triapitsyn et al. 2007; 21).

Our modeling results showed that the distribution of *A. sp. nr. pseudococci* falls in the distribution of two other “species” except in the extreme southeast Asia, which could also be a bias caused by improper taxon sampling. Based on all these observations we suggest *A. sp. nr. pseudococci* to be considered as a synonym of *A. dactylopii*, however further studies are needed to confirm this proposal.

CONCLUSION

Distribution data for encyrtids (many of them of high economic importance) are incomplete, which makes it difficult to properly and quickly plan biological control projects. Determining the actual and potential geographic distribution of certain species can lead to improved success when introducing natural enemies, as well as better predictions of the risk of accidental pest establishment [6,63]. Here, we showed that PDM, using freely available software and environmental data, can be successfully used in studies of the distribution of encyrtid species. Apart from using PDM in solving taxonomic problems, most importantly, areas potentially suitable for the effective use of these species as biological control agents can be predicted. The further improvement of the predictive ability

of the algorithm can be achieved either by incorporating other environmental predictors or increasing occurrence data of the target species being modeled.

ACKNOWLEDGMENT

We are grateful to Professor Roy Van Driesche for correcting and commenting on an earlier draft of the manuscript.

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ПРОГНОЗНОЕ МОДЕЛИРОВАНИЕ КЛИМАТА ПРИ РАСПРЕДЕЛЕНИИ И СИСТЕМАТИКЕ ПОЛЕЗНЫХ ЭНЦИРТИД (HYMENOPTERA: CHALCIDOIDEA: ENCYRTIDAE)

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Использование максимальной энтропии (MaxEnt) - подход, основанный на климатической переменчивости (с разрешением ~ 5 км). Были построены модели прогнозирования распределения (ДПМ) климатических ниш для восьми видов энциртид (*Anagyrus pseudococci*, *A. aligarhensis*, *A. dactylopii*, *A.sp.nr. pseudococci*, *Syrphophagus aphidivorus*, *Ageniaspis fuscicollis*, *Discodes coccophagus*, *Cerapterocerus mirabilis* (Hymenoptera: Chalcidoidea). Все они имеют значение в биологическом контроле. В нашем случае используются как модельные виды для исследования по PDM. Модели успешно предсказали все известные распределения для каждого вида и предложили дополнительные территории их возможного распространения, где каждый вид может быть использован в качестве агента биологической борьбы. Результаты показали, что все моделированные виды высоко привязаны к температурной высокой связности и температурной вариабельности. Средняя годовая температура, минимальная температура самого холодного месяца и изотермичность являются наиболее важными факторами, определяющими распределение энциртид. Эти параметры (и вся другая биоклиматическая изменчивость в целом) не являются полностью независимыми и могут запутать интерпретацию переменных значений. Результаты моделирования показали, что диапазон распределения *A. sp. nr. pseudococci* попадает в пределы двух других видов *Anagyrus*, за исключением крайнего юго-востока. Такой показатель может быть вызван неправильным определением вида. Предполагаем, что *A. sp.nr. pseudococci* следует рассматривать как синоним *A. dactylopii*. Предлагаем относительно быстрый и простой способ планирования биологического контроля и решения таксономических проблем для видов энциртид с использованием PDM.

Table 1. Bioclimatic variables used in the Maxent modeling.

BIO1 - Annual Mean Temperature
BIO2 - Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3 - Isothermality (BIO2/BIO7) (* 100)
BIO4 - Temperature Seasonality (standard deviation *100)
BIO5 - Max Temperature of Warmest Month
BIO6 - Min Temperature of Coldest Month
BIO7 - Temperature Annual Range (BIO5-BIO6)
BIO8 - Mean Temperature of Wettest Quarter
BIO9 - Mean Temperature of Driest Quarter
BIO10 - Mean Temperature of Warmest Quarter
BIO11 - Mean Temperature of Coldest Quarter
BIO12 - Annual Precipitation
BIO13 - Precipitation of Wettest Month
BIO14 - Precipitation of Driest Month
BIO15 - Precipitation Seasonality (Coefficient of Variation)
BIO16 - Precipitation of Wettest Quarter
BIO17 - Precipitation of Driest Quarter
BIO18 - Precipitation of Warmest Quarter
BIO19 - Precipitation of Coldest Quarter

Table 2. Indexes of model performance (AUC and IMP) are presented. CN - Number of countries with known distribution; CM - Number of countries used in PDM; OD – Occurrence data used in model building; CnP - Number of countries with known distribution but not predicted by the Maxent; CaP - Number of additionally predicted countries; AUC – Area Under the (ROC) Curve with standard deviation indicated in brackets; IMP – Index for Model Performance (see main text for more details).

Species	CN	CM	OD	CnP	CaP	AUC	IMP
<i>Ageniaspis fuscicollis</i>	41	8	30	0	23	0.99(0.003)	0.00
<i>Discodes Coccophagus</i>	25	8	27	0	24	0.97(0.016)	0.00
<i>Cerapteroceris mirabilis</i>	31	9	25	1	30	0.99(0.002)	0.05
<i>Anagyrus aligarhensis</i>	25	13	41	0	44	0.87(0.049)	0.00
<i>Anagyrus sp.nr.pseudococci</i>	6	5	12	0	46	0.94(0.038)	0.00
<i>Anagyrus dactylopii</i>	14	3	26	1	61	0.98(0.005)	0.09
<i>Syrphophagus aphidivorus</i>	44	6	38	6	32	0.98(0.007)	0.16
<i>Anagyrus pseudococci</i>	44	12	37	7	37	0.99(0.003)	0.19

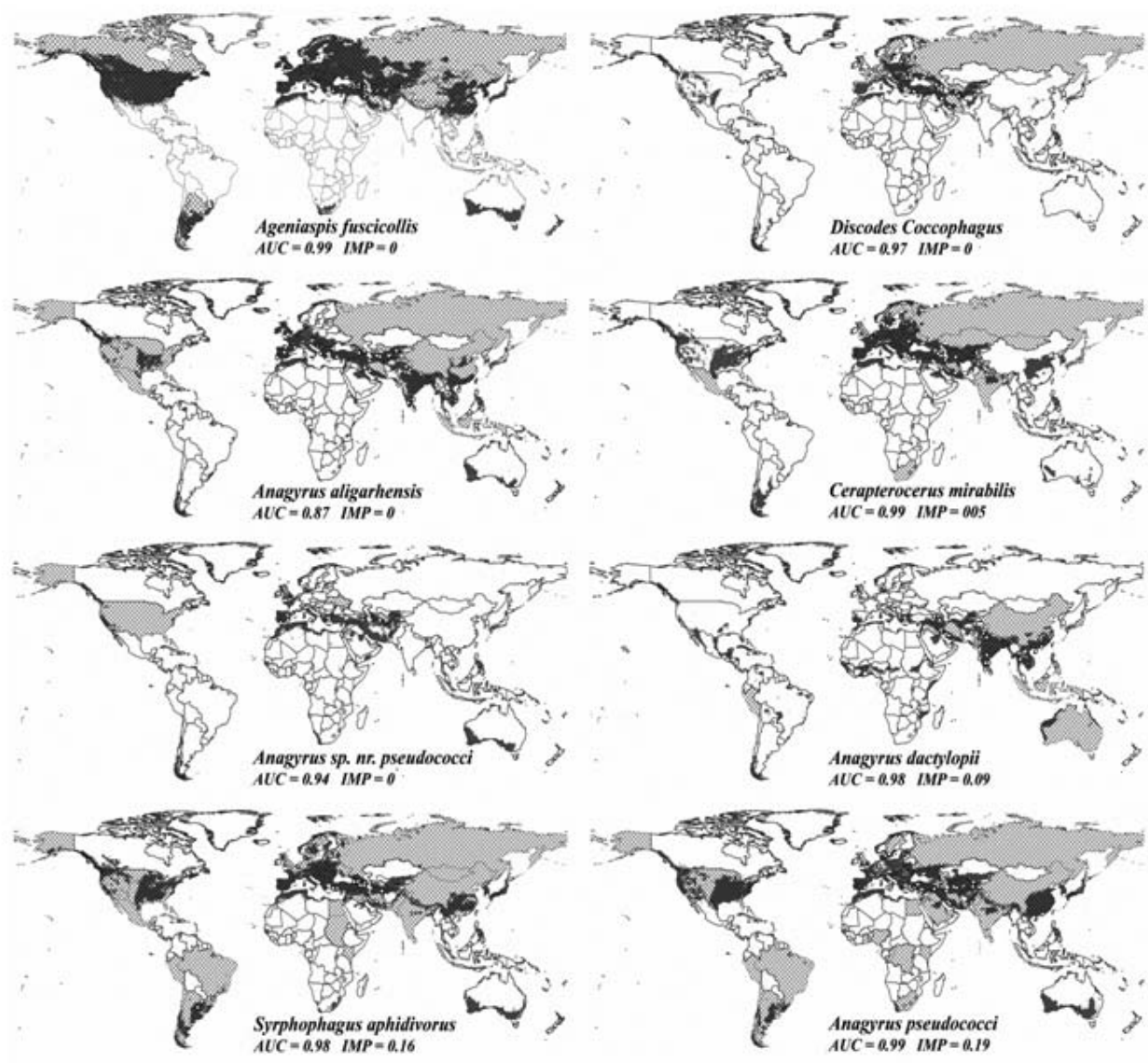


Fig. Predicted binary distribution maps for Encyrtidae species. Gridded area denotes known presence of target species in respective countries, while the black color indicates predicted distribution after applying the threshold (see main text for more details).