Eco-climatic matching to guide foreign exploration and optimal release strategies for biological control agents of *Rastrococcus iceryoides* in Africa and Asia

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Highlights

- India is a hotspot for biological control agents of *Rastrococcus iceryoides.*
- Eleven old and new *R. iceryoides* (host)-parasitoid associations were described.
- *Praleurocerus viridis* and *Anagyrus* chryos were the most promising parasitoids recorded.
- We predicted optimal suitability for parasitoid introduction into Africa and Southeast Asia.
- Predictive modelling are novel tools to support future classical biological control program.

Abstract

Rastrococcus iceryoides (Green) (Homoptera: Pseudococcidae) is a major invasive pest of several horticultural crops [in Africa and Asia, outside its native range in India], with damage levels ranging from 30% to complete crop failure. Due to lack of effective co-evolved parasitoids in the invaded regions, maximum entropy (MaxEnt) and genetic algorithm for ruleset production (GARP) were used to identify climatically suitable areas in India for foreign exploration. Based on the outcome of the predictive models, an extensive survey was conducted in 15 major mango growing regions in the state of Tamil Nadu, India. Thereafter, both models were used to identify climatic compatibility habitats in the invaded regions of *R. iceryoides*. Our results revealed ten host plants belonging to eight families with considerably low levels of infestation. The percentage parasitism established using mummified *R.*

iceryoides was relatively high ranging between 16.7 ± 1.4 to 91.3 ± 3.7%. Both old and new host-parasitoid associations were recorded with eleven parasitoid species described. Eight of the parasitoids recorded were new records of *R. iceryoides*. Among these parasitoids, *Praleurocerus viridis* Agarwal, *Anagyrus chryos* Noyes & Hayat and *Neoplatycerus tachikawai* Subba Rao were the most dominant and widespread parasitoid species, highly specific to *R. iceryoides* with percent parasitism of 53.2 ± 5.4, 31.3 ± 2.7 and 8.8 ± 2.9%, respectively. Using the occurrence data of the parasitoids, both models successfully identified optimal suitable habitats in Africa and Asia. Both models showed optimal performances with the value of the average area under the curve (AUC) of 0.98 for MaxEnt and 0.95 for GARP. However, the percentage contribution of the predictor variables that influenced the current and future predictions in the native and invaded range varied considerably. These findings demonstrate the importance of predictive modelling as novel tools to support future classical biological control program targeting *R. iceryoides* in the invaded regions. Our results provide important information to guide strategic planning for future classical biological control programmes.

Keywords: Native-range exploration; Co-evolved parasitoids prioritization; Classical biological control; Climate matching; Desktop GARP; MaxEnt

1. Introduction

Rastrococcus iceryoides (Green) (Homoptera: Pseudococcidae) is a highly polyphagous pest and attacks over 60 genera of plants in 36 families (Ben-Dov, 2012c, Williams, 2004). This pest is known to be native India and has been intercepted 25 times at U. S. ports-of-entry between 1995 and 2012, with specimens originating from China, India, Malaysia, and The Philippines (Williams, 1989, Williams, 2004). It is an invasive pest of utmost economic significance in Africa (Williams, 1989, Neuenschwander, 1993) and Asia (Tandon and Verghese, 1985) damaging fruits, twigs, and foliage of mango. Damage levels in heavily infested orchards have been reported to range from 30% to complete crop failure (Tanga, 2012). Fruits highly infested suffered largely from feeding damage rendering them either unmarketable or downgraded and unfit for export market (Tanga, 2012). Feeding pressure exerted on the mango plants has been well-documented as leading cause of defoliation, untimely drop of flowers, premature and severe dieback effect of young shoots (Tanga, 2012, Tanga et al., 2013b). In many cases, severe mealybug infestation on young undeveloped mango fruits led considerable reduction in size and weight loss compared to uninfested fruits (Pitan et al., 2002, Tobih et al., 2002, Tanga, 2012).

In invaded regions in Kenya, Tanzania and Malawi, commonly used control options applied by most of the growers to combat *R. iceryoides* infestation include cutting down heavily infested trees and burning them in addition to indiscriminate use of broad insecticidal canopy sprays (Tanga, 2012). Although, insecticidal sprays are largely practiced, this method of control is ineffective for the management of *R. iceryoides*, because the mealybug adults and nymphs can be covered in thick layers of waxy coating to varying extents shielding their body (Kairo et al., 2000, Tanga, 2012) and obscured in plant nooks and crannies where it is difficult to get through pesticide coverage. Eggs of *R. iceryoides* are usually enmeshed and protected in bushy waxy ovisac (Mansour et al., 2018), that are relatively waster proof and impermeable to most insecticides (Venkatesan et al. 2016). Also, European Union has introduced strict maximum residue level for exported fruits and vegetables, thus further compounded the excessive use of chemical pesticides. The increasing and inefficient utilization of insecticides by growers might increase the risk of development of insecticide resistance (Venkatesan et al., 2016).

Therefore, classical biological control using co-evolved natural enemies remains the most appropriate option for managing *R. iceryoides* (Garcia-Valente et al., 2009, Kairo et al., 2000, Moore, 2004, Roltsch et al., 2006). Surveys conducted in Kenya and Tanzania revealed six indigenous parasitoid species (*Anagyrus* aegyptiacus Moursi, *Agarwalencyrtus citri* Agarwal, Anagyrus *pseudococci* Girault, *Aenasius longiscapus* Compere, Leptomastrix *dactylopii* Howard, and Leptomastidea *tecta* Prinsloo) attacking *R. iceryoides*. Among these species, *A. pseudococci* was the most abundant species showing promising biocontrol potential with percentage parasitism ranging between 6 and 15% (Tanga, 2012). Given that the indigenous natural enemies in both countries provided negligible level of control, the need for importation of exotic natural enemies become crucial. In India, the native home of the pest, *Anagyrus* sp. nr *inopus* Noyes & Hayat, *Praleurocerus viridis* (Agarwal), *Allotropa* sp., and *Tetrastichus* sp., are the most important primary parasitoids, effectively suppressing *R. iceryoides* with percentage parasitism of more than 40% (Tandon and Lal, 1978, Tandon and Srivastava, 1980, Narasimham and Chacko, 1988). Hyperparasitoids such as *Coccophagus* sp., *Promuscidea unfasciativentris* Girault, and *Chartocerus* sp. have also been reported to parasitize the primary parasitoids at fairly low levels ((Tandon and Lal, 1978, Tandon and Srivastava, 1980, Narasimham and Chacko, 1988). Despite the increasing damage inflicted by *R. iceryoides* to horticultural crops in invaded areas, none of these promising primary parasitoids have been used for classical biological control of *R. iceryoides*.

The introduction of biological control agents to manage invasive pests have been practiced for over 100 years and remains a long-term sustainable solution for exotic mealybug pests, especially *R. iceryoides* (Kairo et al., 2000, Inter-American Institute for Cooperation on Agriculture (IICA), 2002, Moore, 2004, Roltsch et al., 2006, Garcia-Valente et al., 2009, Gilrein, 2014). However, for it to be successful, the biocontrol agent must be carefully selected to ensure that they are capable of surviving and thriving in the climatic environment where control is anticipated (Robertson et al., 2008). This is further supported by Hoelmer and Kirk (2005), who confirmed that biocontrol agents obtained from regions with comparable climatic settings are more likely to achieve effective control. Climate suitability is of paramount importance because climatic mismatch amid the area of origin and that of introduction is one of many reasons why biocontrol agents do not establish, or do not form viable populations (Wapshere, 1983, Wapshere, 1993, Dennill and Gordon, 1990, McClay and Hughes, 1995, Stewart et al., 1996, Good et al., 1997, Byrne et al., 2002, Hoelmer and Kirk, 2005).

Meta-analysis studies on natural enemy failures have demonstrated that approximately 35% of biological control agent introductions have been unsuccessful because of climate related factors (Van Driesche et al., 2008, Hoddle et al., 2015, Sheppard et al., 2019). The most important factors reported to limit the establishment, spread, and impact of natural enemies have been presumed to be related to extreme temperatures, rainfall, humidity, predation, hyperparasitism by native fauna and photoperiod (Van Driesche et al., 2008, Daane et al., 2012, Tanga et al., 2013a, Tanga et al., 2015a, Tanga et al., 2015b; Heimpel and Mills, 2017; Schulz et al., 2019, Tanga et al., 2019). Goolsby et al. (2005) further demonstrated that majority of failures of introduced biological control agents to establish have been frequently accredited to climatic incompatibility between area-of-origin and areas-of-establishment. As such, climatic matching tools have been used to predict climatically suitable areas in the invaded range of the pest before introduction of effective natural enemies (Byrne et al., 2002, Senaratne et al., 2006, Robertson et al., 2008). According to Sutherst, 2003, Hoelmer and Kirk, 2005, promising natural enemies should be obtained from regions (i.e., aboriginal home of the pest) with climatic settings that are closely related to the environment (i.e., invaded range of the pest) into which they are intended to be introduced. This is further confirmed by other studies which emphases the importance of these predictions to strengthen the probability of biocontrol agents' establishment and colonization in the introduced range of the invasive pest (Welk et al., 2002, Scott et al., 2002, Peterson and Shaw, 2003, Cammell and Knight, 1992, Gevrey and Worner, 2006, Kiritani, 2006, Tuda et al., 2006, Guo et al., 2006, Hance et al., 2007).

Given the narrow range of *R. iceryoides* in its aboriginal home, India, and the limited area of eco-climatic suitability under which the pest thrives in Asia, it is important to establish which segment of this range is climatically indistinguishable to the regions in Asia (Williams, 1989, Williams, 2004) and Africa (Tanga et al., 2015a) that are currently invaded by *R. iceryoides*. This approach has been strongly supported by previous studies, whereby modelling tools have been used to carefully select areas in the native home of the pest for search of co-evolved biocontrol agents (Goolsby et al., 2005, Dhileepan et al., 2006, Senaratne et al., 2006). Firstly, suitable habitats in the native range of the pest (India) were identified using presence records from the invaded range in Africa and Asia. The aim was to facilitate the task of narrowing down the search area for effective natural enemies' exploration that are well adapted to the climate of the invaded countries, thereby reducing climatic incompatibility. Secondly, extensive field surveys were carried out in areas predicted by the models to be climatically suitable for the establishment of *R. iceryoides*. The distributional range of *R. iceryoides*, its host plant relationships and potentially associated coevolved natural enemies were established throughout the selected ecological range. Thirdly, the presence records of the identified natural enemies, particularly the parasitoids of *R. iceryoides* in the native range was used to predict habitat suitability in the invaded range (Africa and Asia), based on a set of bioclimatic predictor variables (Peterson and Vieglais, 2001). The novelty in the present study is that it compares between two climatic matching approaches for tracking promising natural enemies in their native range and estimates their potential to thrive in invaded areas of their host *R. iceryoides*, which is information that is rare in literature.

2. Materials and methods

2.1. Obtaining presence records of the occurrence of *R. iceryoides*

Presence records of *R. iceryoides* were collected from different sources published in literature (Williams, 1989) and from independent surveys carried out across different mango production areas in Kenya and Tanzania. The recorded occurrence data with coordinates were verified and validated using Google Maps (www.google.com/maps) to avoid the use of doubtful coordinates. All the coordinates from the invaded range were double-checked with the help of QGIS 3.10.6 software (https://qgis.org/en/site/), before being used to generate a map as shown in Fig. 1.

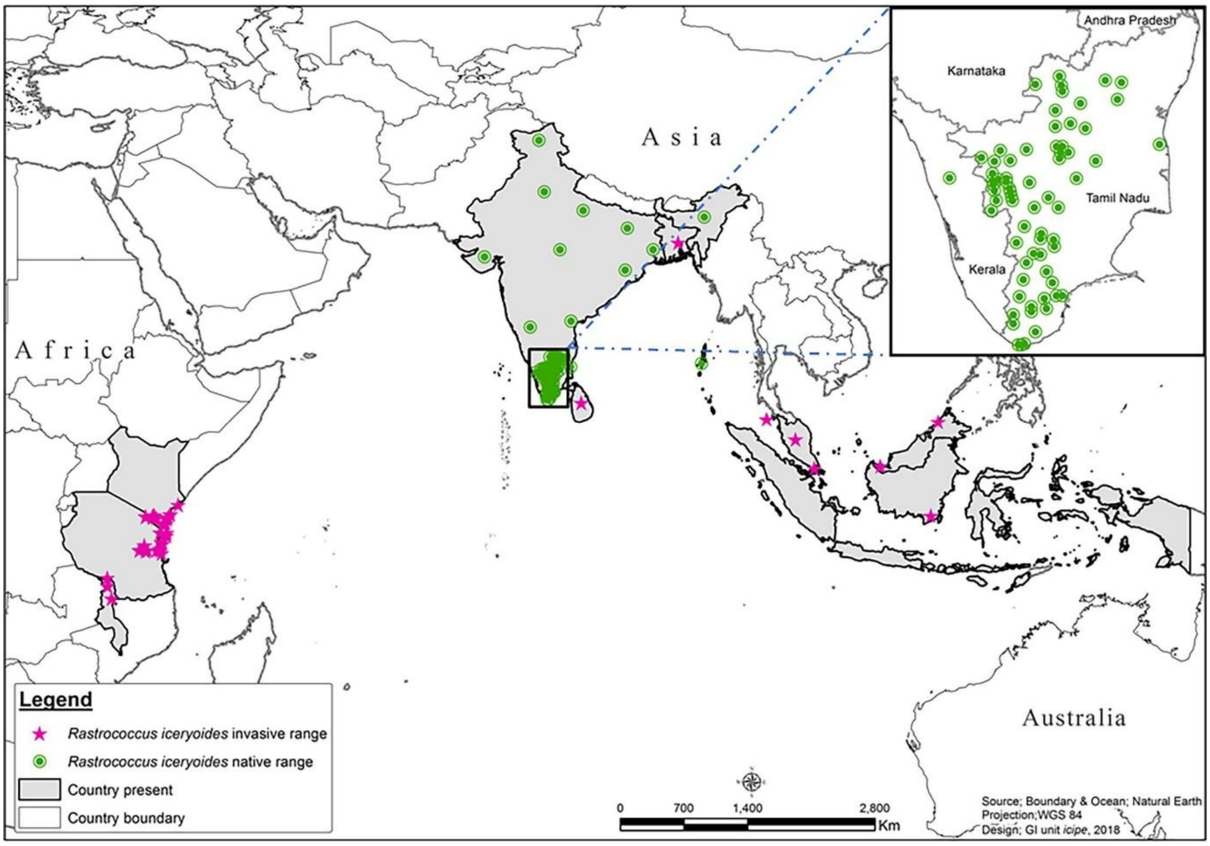

Fig. 1. Map showing the present occurrence records of *R. iceryoides* in Africa and Asia. Green dots represent the distribution record in the native range of the pest. Pink dots represent the invasive range. Distribution points in the black rectangular box indicate locations where foreign exploration for efficient co-evolved biological control agents was undertaken.

2.2. Bioclimatic variables used to generate the potential distribution models

Occurrence records together with bioclimatic variables obtained from the WorldClim Global Climate Database version 1.4 (http://www.worldclim.org/) were used in combination (Hijmans et al., 2005). These bioclimatic variables have been derived from long-term (1960 – 1990) monthly dataset averaged over 30-years (1960 – 1990), and are assumed to reflect the climate suitability for the growth and development of different organisms (Hijmans et al. 2005). The bioclimatic data spatial resolution for this study was 30 arc-seconds (around 1 km). The prediction of potential distribution of the pest under future climate scenarios simulations, downscaled global climatic models (GCMs) HadGEM2-ES data at a resolution of 30 arc-seconds sourced from the WorldClim Global Climate Database 1.4 (http://www.worldclim.org/) was used. Based on Representative Concentration Pathways Scenarios, the Fifth Assessment Report (RCPs-AR5) (IPCC, 2013) future year 2050 (mean over 2041–2060) were taken into consideration. Dataset used contained grids of rainfall, temperatures and bioclimatic summary variables obtained, which provided a snapshot of the annual trends, limited environmental factors and seasonality. Future climatic simulations using bioclimatic data to predict future scenarios and given the non-availability of vegetation data, vegetation and topography information were assumed to remain unchangeable over the projected period. On the other hand, minimization of multicollinearity among the predictor variables (Merow et al., 2013), over and underfitting of climate suitability maps of the invasive *R. iceryoides* (U.S. Geological Survey (USGS), 2004, Kuhn, 2008), prompted us to carry out a Pearson’s correlation test and the variance inflation factor (VIF) across all the

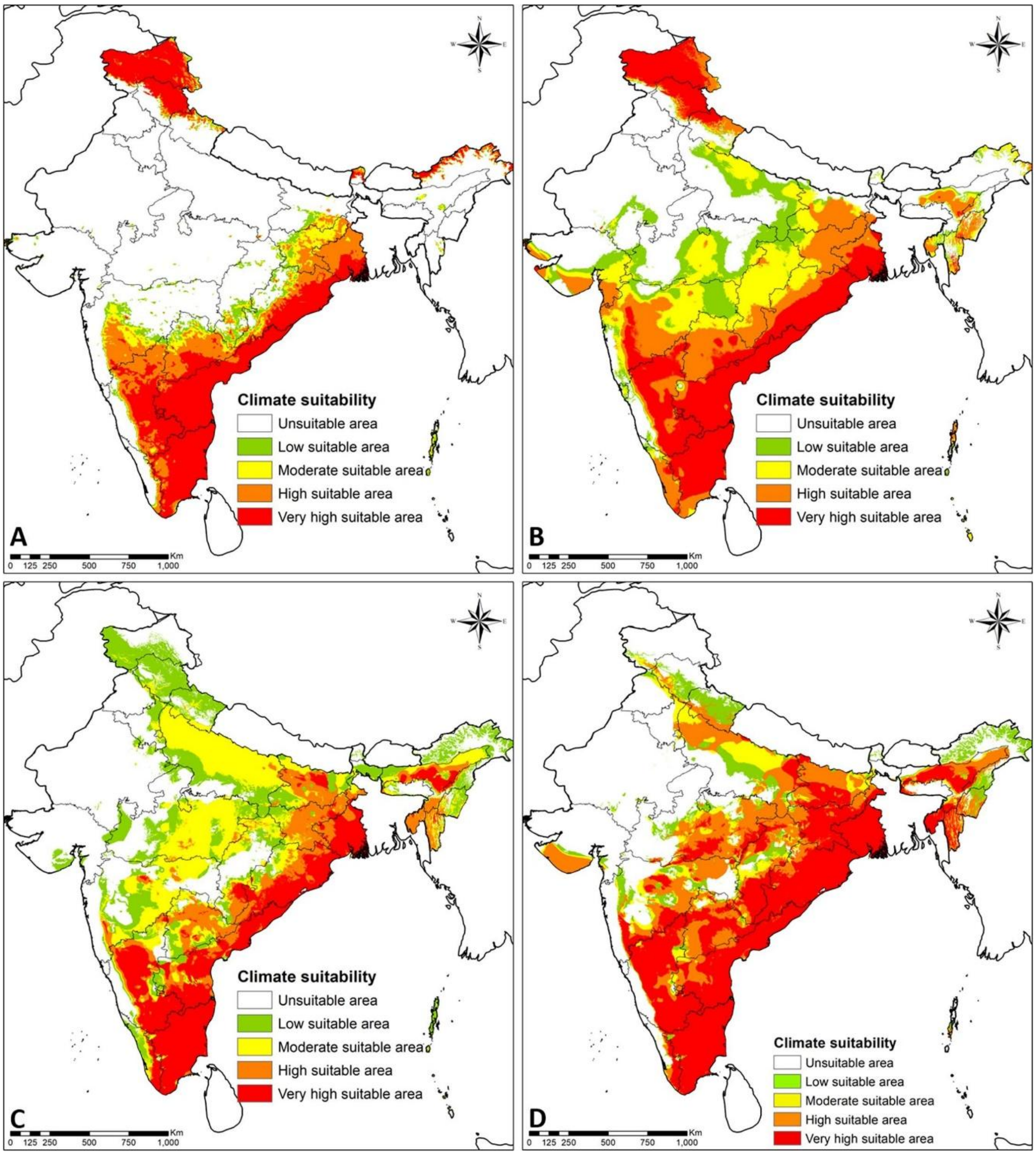

Fig. 2. Areas predicted using data from the invaded range of *R. iceryoides* to establish optimal climatically suitable areas for foreign exploration of efficient co-evolved biological control agents in its native range, India using MaxEnt [current climatic scenario (2 A) and future climatic scenario (2B)] - and GARP [current climatic scenario (2C) and future climatic scenario (2 D) models.

bioclimatic variables (Marquardt, 1970). Pairwise Pearson correlation coefficient, considered at a threshold of $r > 0.7$ (Dormann et al., 2013), while a VIF greater than 10 served as an indicator of collinearity. Thus, only 7 bioclimatic variables were finally selected after running the collinearity test: BIO-2 (mean diurnal range), BIO-4 (Temperature Seasonality), BIO-10 (Mean Temperature of Warmest Quarter), BIO-14 (Precipitation of Driest Month), BIO-15 (Precipitation Seasonality (Coefficient of Variation)), BIO-18 (precipitation of the warmest quarter) and BIO-19 (Precipitation of Coldest Quarter). The seven bioclimatic variables described above were used to model the climate suitability of *R. iceryoides* under current and future climate scenarios in India (Fig. 2) using the occurrence records from the invaded range of *R. iceryoides*.

2.3. Modelling approaches and performance evaluation

Based on previous studies reported by Elith et al., 2006, Phillips et al., 2006 two machine learning algorithms were used: Maximum Entropy Modelling (MaxEnt) and the evolutionary-computing approach Genetic Algorithm for Ruleset Production (GARP). Maxent and GARP were selected for this study due to their powerful ability to develop ecological niche models using presence only species data. An in-depth study conducted by Elith et al., 2006, Hernandez et al., 2006 indicate that both algorithms perform better in predicting species distribution compared to other methods. Several studies (Pearson et al., 2007, Qin et al., 2015, Ray et al., 2018, Townsend et al., 2007) have applied the two ecological niche models (ENMs) to predict the habitat suitability of various species including invasive species. The utilization of the two algorithms in the study assisted in assessing the variability in the predictions. Thus, the two model algorithms compliments each other in terms of commission and omission error due to the underlying assumptions and complexity of the individual algorithms (Elith et al., 2006).

We used 70% of the presence data to train the models based on the sample size as well as its popularity as a rule of thumb for most of the ecological niche models (Yang et al., 2013; Richard et al., 2018; Kimathi et al., 2020; Mudereri et al., 2020) and 30% for model validation. The MaxEnt prediction performance for the validations (30% of the data set) was evaluated by area under the curve (AUC) (Phillips et al., 2006). The value of AUC ranged from 0 to 1, where 1 was an indicator a perfect ability to discriminate between the omission areas with records and overlap of the areas occupied. The results generated by the models represented an area with climate change conditions comparable to that of *R. iceryoides* known distributional range. The values between 0 and 1 was also an indication of regions without or with the most highly suitable habitats. Several studies have demonstrated that this method is good when the performance of models are evaluated because it remains completely independent of the occurrence compared to the frequently used kappa dataset (Manel et al., 2002, McPherson et al., 2004, Liu et al., 2005). According to Elith et al., 2006, Manel et al., 2002, Liu et al., 2005 the AUC can be a measure for assessing the independent models at a given cut-off temperature threshold. Based on the decline or increase of the AUC, the permutation importance was calculated, when the respective environmental bioclimatic variables are altered.

2.4. Establishment of temperature thresholds particularly for zones predicted to harbour *R. iceryoides*

Using Maximum Entropy algorithm, the threshold for reliably selecting areas suitable for establishment and colonization by *R. iceryoides* or unsuitable for the pest survival was based on the values recorded for the Minimum Training Presence (MTP). Based on GARP algorithm, 70% probability of presence of the species was the threshold adopted. Considering this threshold value, ecological niche preference was generated and converted from probability maps to species distribution maps. All the maps were presented using simple Plate Carrée (WGS 84) prediction. This forecast is an equidistant prediction, which was carefully selected as it is an appropriate fitting for area-wide surveys to ensure that we achieve a balance in the areas distorted and the outline.

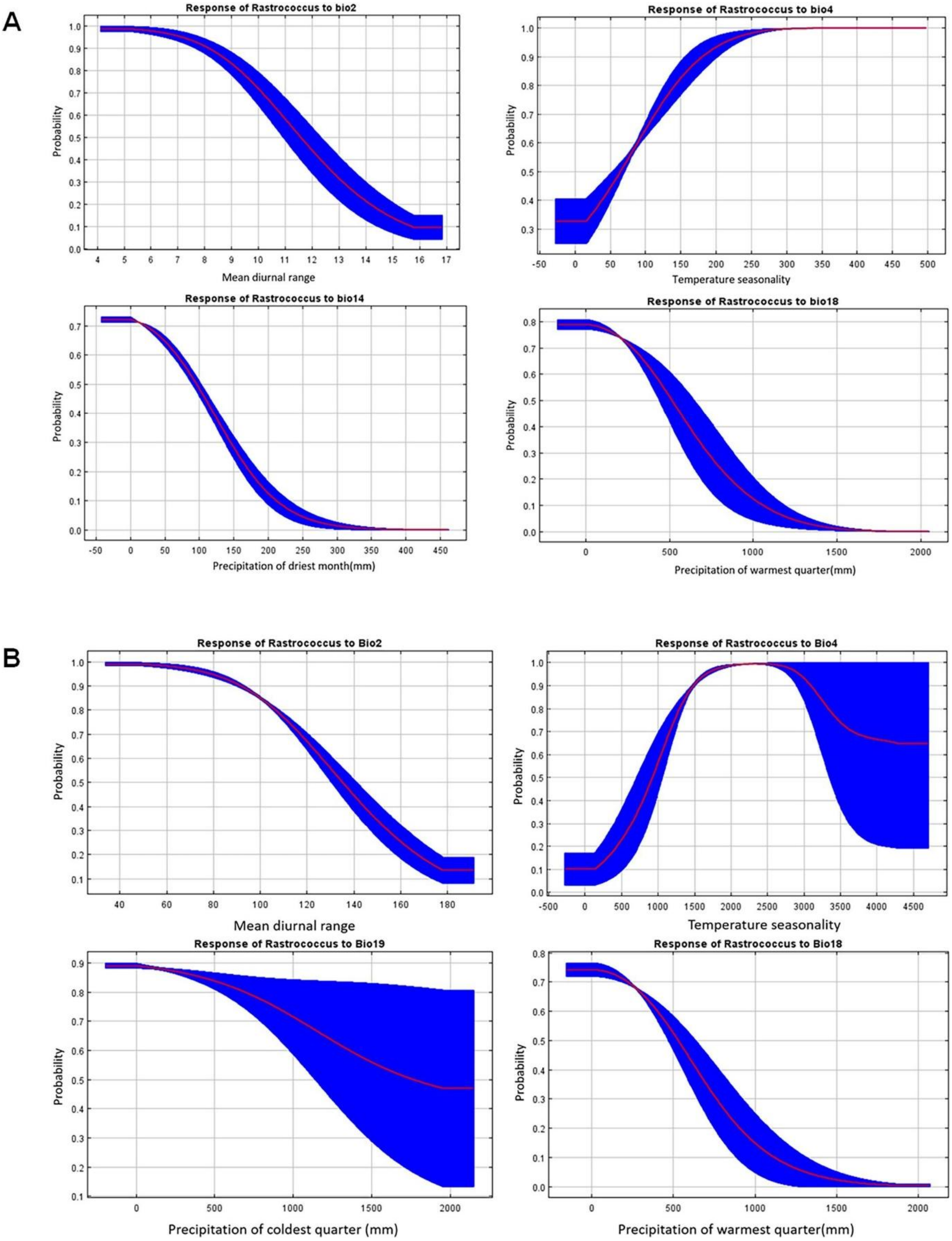

Fig. 3. Average response curves of the main predictor variables of the distribution model of *R. iceryoides* generated by the MaxEnt algorithm under current (A) [mean diurnal range (Bio - 2), temperature seasonality (Bio - 4), precipitation of driest months (Bio - 14) and precipitation of warmest quarter (Bio-18)] and future (B) [mean diurnal range (Bio - 2), temperature seasonality (Bio - 4), precipitation of warmest quarter (Bio-18) and precipitation of coldest quarter (Bio - 19)] used to estimate the probability of occurrence of *R. iceryoides*. The red lines show the average of probability values from 1000 iterations using randomized input, and the blue lines show the standard deviations.

2.5. Evaluation and validation of the models

This study generated 130 occurrence records for *R. iceryoides*, which were used for the calibration and evaluation of the models according to the methods described by Pearson et al. (2007), using the jackknife approach. This approach allows for the model to be calibrated based on the n-1 records and verified using one record. A repetition of this process was carried out until the existing records were exhausted for testing. The final decision on the appropriate threshold is then utilized to change the continuous values (0–1) from predicted model into a comprehensive map that depicts the "presence" and "absence" of the species (Pearson et al., 2007). The lowest predicted value observed to be closely associated with the set of presence records was selected to represents the 'lowest presence threshold' (LPT; Pearson et al., 2007). This was a more conservative approach, because it was able to identify grid cells, which were at least suitable as those representing the current distribution record of the species (Pearson et al., 2007).

Field surveys were undertaken to validate the suitability of many predicted locations, which were later compared with the suitability values generated by the models. We ensured that over 80% of the sites predicted were visited and confirmed to be suitable (Fig. 3). Also, three locations predicted to be unsuitable were visited to ascertain the actual absence of the species. The sites visited were separated by at least a minimum of 1 km distance from each other. The suitability map produced from the model was used to carefully locate the sites that were inspection. The habitat suitability map created from the models were loaded to a Trimble Juno® 5 series GPS (https://geospatial.trimble.com/products-and-solutions/juno-5) to effortlessly and correctly circumnavigate to areas predicted to be highly suitable during the survey. This approach significantly assists to minimize the time and cost involved in the exploration for new associated effective parasitoids in the aboriginal home of the invasive mealybug pest.

2.6. Host plant survey and levels of damage

Host plant survey was carried in the State of Tamil Nadu (Fig. 1), which represents one of the most important state where mango production is highly rated in terms of quality and quantity for commercialization (Tharanathan et al., 2006, Mehta and George, 2003). The state also has over 385 fruit processing facilities (Raj, 2008).

Using the results generated by the predictive models, a thorough survey was conducted across the state of Tamil Nadu using the methods described by Tanga et al. (2015a). Sampling was carried out in selected major mango orchards with plot size ranging between 0.5 and 5 ha. In each orchard a transect was set up and sampling points along each transect was measured from the most northerly point of the transect. At each of the sampling points along each transect, twenty mango plants were selected using random bearing at fixed distances before commencing the sampling. For plants that were 1–5 m tall, sampling was performed at approximately 1–2 m from the ground while for plants that were 5–10 m tall, sampling was performed at approximately 1–3.2 m above the ground. Hedge clippers attached to wooden poles were used to access sampling units that were 2 m above the ground. On each host plant, the sampling units consisted of 80 leaves, 20 twigs (~10 cm length) and 5 fruits selected at random within a surface area of 1 m^2 for mealybug counts. To avoid taking mealybugs only from one section of the plant, the order in which plant parts were examined around each plant (bottom to top and vice versa) was reversed accordingly. During the survey, care was taken to make sure that no plant was sampled twice within the same location.

Occasionally, unbiased choice of sample locations along footpaths and jeep trails in major mango production zones were sampled after 8 km of drive. However, sampling along the road leading away from the sampled mango orchard was discontinued after several stops without *R. iceryoides* infestation (Bokonon-Ganta and Neuenschwander 1995). Furthermore, to generate a future comprehensive map on the distributional range of *R. iceryoides* in the state of Tamil Nadu, global positioning system (GPS) readings of all the locations sampled were recorded.

Sampling units of each host plant (leaves, twigs, and fruits) and mealybug species observed during the survey were kept separately in well ventilated plastic bags with tiny perforations. Samples were transported in cool boxes to the laboratory for further analysis. In the laboratory, head lenses were used to count all the mealybugs (2nd, 3rd and adult stages) per host plant portion and recorded. Stereomicroscope [Leica MZ 125 Microscope (Leica Microsystems Switzerland Limited)] were used when necessary during the process of counting. The severity of damage caused by the mealybugs was scored per locality and host plant species (leaves, twigs, and fruits) (Tobih et al., 2002, Tanga et al., 2015a). From the field-collected mealybugs, 10 – 15 adult mealybugs of each species were selected from each sampling location and slide-mounted following the method described by Watson and Kubiriba (2005). Taxonomic identifications were carried out at Tamil Nadu Agricultural University (TNAU), Department of Agricultural Entomology. The leaves and/or twigs and fruit from various plants that were pressed and bagged for further identified to species levels using the institutional keys of India trees, shrubs and Lianas. Further confirmation was carried out using the plant nomenclature as described by the International Plant Names Index database (IPNI, 2004) and Missouri Botanical Garden database (MBOT, 2006). Voucher specimens of each mealybug species and plant parts encountered in the field were deposited for future reference at TNAU.

2.7. Parasitoids of *Rastrococcus iceryoides*

Live and mummified mealybugs collected in brown paper bags with perforations were counted and carefully transferred into well aerated cages (45 cm length × 45- cm width × 50 cm height) in the laboratory. The set up was maintained at 70 ± 5% RH, photoperiod of 12:12 (L: D) h and ambient temperatures (26 ± 2 °C) (Tanga et al., 2015a). On the roof of each cage, streaks of 10% honey solution were applied to serve as food for emerging parasitoids. The experimental set up was checked thrice daily to collect data on emerged parasitoids. The emerged parasitoids were fed for 7 days until sexual maturity, when all the body colourations were fully attained. They were then killed by freezing at −20 °C and later preserved in 70% alcohol. Samples were then sent to Annamalai University for taxonomic identification and later confirmation at the Aligarh Muslim University, India. Voucher specimens were kept in the collections of Project Directorate of Biological Control (PDBC), Aligarh Muslim University (AMU) in Bangalore and Annamalai University, Faculty of Agriculture (Departments of Agricultural Entomology), Centre for Plant Protection Studies (CPPS), TNAU. The distributional range of the parasitoids in the state of Tamil Nadu was recorded using global positioning system (GPS) and the coordinates were later used to generate a comprehensive map (Fig. 1).

2.8. Predators of *Rastrococcus iceryoides*

During the survey, beat sheet method described by Wade et al., 2006, Tanga et al., 2015a were used for sampling predators of *R. iceryoides*. In each mango orchard, 5 branches of each tree sampled for mealybug infestation were hit using a 60 cm long heavy stick over a 1 m^2 white cloth screen to dislodge predators. This exercise was performed during the early hours of the morning (7:00 am – 12:00 noon) (Garcia et al., 1982, Knutson et al., 2008). Adult predators collected were carefully transferred into well-labelled glass jars containing 90% of ethyl alcohol for preservation. On the other hand, immature predators were further reared on *R. iceryoides* maintained on butternut fruits in cages (20 cm height × 25 cm length × 20 cm width) until adult emergence. Taxonomic identification of the predators were carried out at the Department of Entomology, TNAU, India.

2.9. Climatic suitable habitats of parasitoids in invaded range of *R. iceryoides*

Using the same approach described in 2.2 Bioclimatic variables used to generate the potential distribution models, 2.3 Modelling approaches and performance evaluation, 2.4 Establishment of temperature thresholds particularly for zones predicted to harbour above, the occurrence records of the parasitoids in India (Fig. 1) together with bioclimatic variables obtained from the WorldClim Global Climate Database 2.1 (http://www.worldclim.org/) were used in combination (Hijmans et al., 2005) to determine suitable habits for parasitoid establishment under current and future climatic scenarios in the invaded regions in Africa and Southern Asia. The climatic compatibility with the native range of *R. iceryoides* was established using 10 bioclimatic variables, which included, Bio-2 (mean diurnal range), Bio-1 (annual mean temperature), Bio-3 (isothermality), Bio-4 (temperature seasonality), Bio-6 (minimum temperature of coldest month), Bio-13 (precipitation of wettest month), Bio-14 (precipitation of driest month), Bio-15 [precipitation seasonality (coefficient of variation)] and Bio-18 (precipitation of the warmest quarter).

2.10. Data analysis

The infestation by *R. iceryoides* is presented as per sampling part of each host plant recorded. Percent parasitism of major parasitoid species were expressed based on the number of emerged biocontrol agents (parasitoid) divided by total number of *R. iceryoides* life stages recorded per host per locality. The data on *R. iceryoides* abundance and percent parasitism were evaluated and compared among the different host plant portion. Data was then subjected to *t*-test or one-way ANOVA using Proc *T*-Test or Proc GLM after being log-transformed. The relative abundance of *R. iceryoides* on various host species as well as between the different localities was compared. Percent parasitism data generated from the study were arcsine transformation to comply with homogeneity of variance and normality assumptions before being subjected to *t*-test or one-way ANOVA. All the analysis in this study were performed using R 2.13.1 software (R Development Core Team, 2015).

3. Results

3.1. Climatic suitability of *R. iceryoides* in India

Both models predicted areas that fitted the current distribution of *R. iceryoides* reasonably well in India. The models showed optimal performance; the mean AUC value for the GARP algorithm 0.95, while for MaxEnt it was 0.98, which indicate acceptable models. The projections of the potential distribution of *R. iceryoides* in both models under their respective thresholds were quite similar (Fig. 2A, B, C and D), indicating high reliability in the generated predictions.

However, the MaxEnt model (Fig. 2A) was somewhat more restrictive in predicting the potential area of suitability of *R. iceryoides* except in Tamil Nadu, Andhra Pradesh, Karnataka, Orissa and West Bengal, where its prediction of the potential distribution area was similar to that of GARP (2C) under current climatic scenario. Contrary to GARP, Jammu and Kashmir, and Himachal Pradesh were additional regions with the highest suitability in the model developed with the MaxEnt algorithm under current and future climate scenarios (Fig. 2A and B).

3.2. Environmental variables determining the distribution of *R. iceryoides*

Four environmental variables were selected as informative variables for the *R. iceryoides* model by the MaxEnt method under current (Fig. 3A) and future (Fig. 3B) climate scenarios. The MaxEnt model calculated the percentage contribution of each of these variables to the final model prediction (Table 1). Under current climate change, variable Bio 18 (Precipitation of warmest quarter) had the highest contribution to the prediction by MaxEnt followed by Bio 4 (Temperature seasonality), Bio 2 (Mean diurnal range) and Bio 14 (precipitation of driest month) (Table 1 and Fig. 3A). However, under future climate change, variable Bio 4 (Temperature seasonality), followed by Bio 18 (Precipitation of warmest quarter), Bio 2 (Mean diurnal range) and Bio 19 (precipitation of coldest quarter) were the most important variables with the highest contributions (Table 1 and Fig. 3B).

3.3. Infestation levels of *R. iceryoides* on associated host plants

The infestation levels on the various host plants were extremely low with only 5950 samples of *R. iceryoides* collected throughout the survey. However, ten (10) cultivated and wild host plants belonging to eight (8) different families were observed to be attacked by *R. iceryoides* (Table 2). The highest infestation levels were observed on *M. indica* (mango) in Kundal and Kanyakumari districts, while the lowest levels on mango were recorded in Erode district (Table 2). Guava (*P. guajava*) was the second most infested host plant, followed by *M. zapota* in Coimbatore.

Other mealybug species recorded on mango in negligible number included, *R. invadens* (William), Drosicha *mangiferae* (Green), *Icerya* aegyptiaca (Douglas), *Icerya seychellarum* (Westwood), *Planococcus citri* (Risso), *Ferrisia virgata* (Cockerell) and *Paracoccus marginetus* (Williams and Granara de Willink).

3.4. Percent parasitism of parasitoid species on various host plants

Throughout the survey, 3788 mummified *R. iceryoides* were recorded accounting for 63.7% parasitism. The highest number of mummified *R. iceryoides* (3167) were collected from mango representing 83.6% parasitism. In Othakadei, Madurai district, the percentage parasitism of *R. iceryoides* on mango was 88.4 and 91.3% on leaves and twigs, respectively. In Karur, the highest percent parasitism was recorded on guava leaves (20.6%) and twigs (16.7%). The percent parasitism recorded in each locality and host plant species is presented in Table 3.

From the mummified *R. iceryoides* collected, all the emerged parasitoid species belonged to the family Encyrtidae. These species included *Ericydnus paludatus* Haliday, *Praleurocerus viridis* Agarwal, *Anagyrus* chryos Noyes & Hayat, *Neoplatycerus tachikawai* Subba Rao, *Parechthrodryinus excelsus* Hayat, *Leptomastidea minyas* Noyes & Hayat, *Aenasius advena*

Table 1. Percent contribution (out of 10,000 iterations) of predictor variables used for modelling the ecological suitability of *Rastrococcus iceryoides* in its native range (India) under current and future conditions for exploration of biological control agents using presence data of the pest in the invaded range.

Abbreviation	Variables description	Units	Current		Future	
			% of contribution	**Permutation importance**	**% of contribution**	**Permutation importance**
BIO2	Mean diurnal range (Mean of monthly (max temp - min temp))	°C	20	11.6	14.3	12.4
BIO4	Temperature Seasonality (standard deviation*100)	–	24.3	17.9	46.2	53.1
BIO10	Mean Temperature of Warmest Quarter	°C	0	0	2.4	1
BIO14	Precipitation of Driest Month	mm	14.1	3.3	5	3.5
BIO15	Precipitation Seasonality (Coefficient of Variation)	–	8.6	10.7	7.3	18.1
BIO18	Precipitation of Warmest Quarter	mm	32.4	56.5	16.9	11.4
BIO19	Precipitation of Coldest Quarter	mm	0.6	0	8.1	0.5

Table 2. Distribution, host plants and infestation levels by *Rastrococcus iceryoides* in the state of Tamil Nadu, India.

District/Locality	Host plants	Plant family	Mean no. of mealybugs/leaf	Mean no. of mealybugs/twig	Mean no. of mealybugs/fruit	Statistics *T or F*	*df*	*P*
Coimbatore	***Mangifera indica* Linn.**	**Anacardiaceae**	3.70 ± 1.74	9.15 ± 4.43	–	0.2196	4	0.0262
	***Manilkara zapota* Linn.**	**Sapotaceae**	1.96 ± 1.05	3.90 ± 2.26	–	−0.6124	4	0.5403
	***Tectona grandis* Linn.**	**Verbenaceae**	0.68 ± 0.36	2.0 ± 1.12	–	0.5238	4	0.6004
	***Ficus benghalensis* Linn.**	**Moraceae**	2.03 ± 1.07	2.7 ± 1.34	–	−0.2299	4	0.2187
	***Gossypium hirsutum* Linn.**	**Malvaceae**	0.25 ± 0.16	0.30 ± 0.21	–	−0.9172	4	0.3590
	***Gossypium gossypioides* Ulbr.**	**Malvaceae**	0.38 ± 0.20	0.90 ± 0.50	–	1.1616	4	0.2454
	***Pongamia pinnata* Linn.**	**Fabaceae**	1.09 ± 0.59	1.85 ± 1.12	–	−0.5490	4	0.5830
	***Psidium guajava* Linn.**	**Myrtaceae**	1.69 ± 0.80	4.60 ± 2.17	–	−0.2861	4	0.7748
	***Cajanus cajan* (L) Millsp.**	**Fabaceae**	0.29 ± 0.22	0.70 ± 0.42	–	0.3568	4	0.7213
Salem								
Erummaiputti	***Mangifera indica* Linn.**	**Anacardiaceae**	2.78 ± 1.33	7.10 ± 3.23	–	−0.3571	4	0.7210
Dharmapuri								
Paiyur	***Mangifera indica* Linn.**	**Anacardiaceae**	3.21 ± 1.24	1.40 ± 0.98	–	−2.1632	4	0.0605
	***Ceiba pentandra* Linn.**	**Bombacaceae**	0.54 ± 0.27	0.60 ± 0.34	–	−1.4759	4	0.1400
Periyapatti	***Mangifera indica* Linn.**	**Anacardiaceae**	4.61 ± 1.96	5.75 ± 2.43	–	−1.1216	4	0.2620
	***Cajanus cajan* (L) Millsp.**	**Fabaceae**	0.86 ± 0.43	0.80 ± 0.52	–	−1.8371	4	0.0662

District/Locality	Host plants	Plant family	Mean no. of mealybugs/leaf	Mean no. of mealybugs/twig	Mean no. of mealybugs/fruit	Statistics *T or F*	*df*	*P*
Kariyamangakam	***Mangifera indica* Linn.**	**Anacardiaceae**	1.39 ± 0.63	3.25 ± 1.79	–	−0.5170	4	0.6052
Madurai								
Othakadei	***Mangifera indica* Linn.**	**Anacardiaceae**	1.08 ± 0.52	1.15 ± 0.52	–	−1.3038	4	0.1923
	***Ceiba pentandra* Linn.**	**Bombacaceae**	0.35 ± 0.20	0.35 ± 0.18	–	1.7530	4	0.0796
Valeyapatti	***Mangifera indica* Linn.**	**Anacardiaceae**	0.64 ± 0.36	0.75 ± 0.32	–	1.9347	4	0.0530
Virudhunagar								
Rajapalayam	***Mangifera indica* Linn.**	**Anacardiaceae**	0.81 ± 0.35	0.75 ± 0.44	–	−1.9246	4	0.0543
Theni								
Periyakulam	***Mangifera indica* Linn.**	**Anacardiaceae**	0.43 ± 0.29	0.95 ± 0.50	–	0.3721	4	0.7098
Kanyakumari								
Pechiparai	***Mangifera indica* Linn.**	**Anacardiaceae**	2.03 ± 0.80	22.35 ± 7.09	–	−1.6340	4	0.1022
Kundal	***Mangifera indica* Linn.**	**Anacardiaceae**	9.46 ± 2.99	45.4 ± 15.23	73.8 ± 50.11	2.7027	2,8	0.2589
Erode	***Mangifera indica* Linn.**	**Anacardiaceae**	0.13 ± 0.07	0.75 ± 0.56	–	0.1800	4	0.8571
	***Ceiba pentandra* Linn.**	**Bombacaceae**	0.58 ± 0.26	1.60 ± 0.73	–	−0.2873	4	0.7739
Cuddalore	***Manilkara zapota* Linn.**	**Sapotaceae**	0.50 ± 0.24	1.60 ± 0.76	–	0.3214	4	0.7479
Tirunelveli	***Mangifera indica* Linn.**	**Anacardiaceae**	0.29 ± 0.15	1.40 ± 0.74	–	0.4920	4	0.6228
Tiruvannamalai	***Gossypium hirsutum* Linn.**	**Malvaceae**	0.11 ± 0.07	1.0 ± 0.50	–	−0.3018	4	0.7628

District/Locality	Host plants	Plant family	Mean no. of mealybugs/leaf	Mean no. of mealybugs/twig	Mean no. of mealybugs/fruit	Statistics		
						T or F	*df*	*P*
Tuticorin	***Gossypium gossypioides* Ulbr.**	**Malvaceae**	0.01 ± 0.01	0.95 ± 0.48	–	−1.0607	4	0.2888
Karur	***Psidium guajava* Linn.**	**Myrtaceae**	0.43 ± 0.25	0.60 ± 0.42	–	−0.8839	4	0.3768
Dindigul	***Mangifera indica* Linn.**	**Anacardiaceae**	0.23 ± 0.10	1.35 ± 0.81	–	1.4473	4	0.1478
Namakkal	***Mangifera indica* Linn.**	**Anacardiaceae**	0.24 ± 0.12	0.65 ± 0.35	–	0.4871	4	0.6262

Plants parts samples based on 80 leaves, 20 twigs of 10 cm length and 5 fruits; - = plant part were either not infested and omitted from analysis or not available during sampling.

Table 3. Combined percentage parasitism based on the number of mummified *Rastrococcus iceryoides* in the state of Tamil Nadu, India.

		Percentage parasitism			Statistics		
District/Locality	**Host plants**	**Leaves**	**Twigs**	**Fruits**	***T or F***	***df***	***P***
Coimbatore	***Mangifera indica* Linn.**	73.99 (2 9 6)	74.86 (1 8 3)	–	−0.4518	4	0.6514
	***Manilkara zapota* Linn.**	40.76 (1 5 7)	43.59 (78)	–	0.2745	4	0.7837
	***Tectona grandis* Linn.**	55.56 (54)	55.0 (40)	–	−0.1235	4	0.9017
	***Ficus benghalensis* Linn.**	57.41 (1 6 2)	20.37 (54)	–	−2.3368	4	0.0195
	***Gossypium hirsutum* Linn.**	25.0 (20)	50.0 (6)	–	0.5401	4	0.0492
	***Gossypium gossypioides* Ulbr.**	30.0 (30)	44.44 (18)	–	−0.5843	4	0.5590
	***Pongamia pinnata* Linn.**	47.13 (87)	70.27 (37)	–	1.3858	4	0.0258
	***Psidium guajava* Linn.**	59.26 (1 3 5)	33.7 (92)	–	−1.3571	4	0.0447
	***Cajanus cajan* (L) Millsp.**	34.78 (23)	35.71 (14)	–	0.1768	4	0.8597
Salem							
Erummaiputti	***Mangifera indica* Linn.**	82.88 (2 2 2)	78.87 (1 4 2)	–	−0.7153	4	0.4744
Dharmapuri							
Paiyur	***Mangifera indica* Linn.**	77.04 (2 5 7)	89.29 (28)	–	2.0888	4	0.0367
	***Ceiba pentandra* Linn.**	34.88 (43)	41.67 (12)	–	0.1246	4	0.9009
Periyapatti	***Mangifera indica* Linn.**	81.3 (3 6 9)	85.22 (1 1 5)	–	0.5898	4	0.5553
	***Cajanus cajan* (L) Millsp.**	49.28 (69)	68.75 (16)	–	0.3737	4	0.0086
Kariyamangakam	***Mangifera indica* Linn.**	87.39 (1 1 1)	78.46 (65)	–	−0.2932	4	0.7694
Madurai							
Othakadei	***Mangifera indica* Linn.**	88.37 (86)	91.3 (23)	–	1.0746	4	0.2826
	***Ceiba pentandra* Linn.**	25.0 (28)	57.14 (7)	–	−1.1616	4	0.0285
Valeyapatti	***Mangifera indica* Linn.**	82.35 (51)	60.0 (15)	–	0.6464	4	0.5180
Virudhunagar							
Rajapalayam	***Mangifera indica* Linn.**	72.31 (65)	80.0 (15)	–	1.8403	4	0.0657
Theni							
Periyakulam	***Mangifera indica* Linn.**	82.35 (34)	84.21 (19)	–	−0.1246	4	0.9009

District/Locality	Host plants	Percentage parasitism			Statistics		
		Leaves	**Twigs**	**Fruits**	***T or F***	***df***	***P***
Kanyakumari							
Pechiparai	***Mangifera indica* Linn.**	12.41 (1 6 2)	35.54 (4 4 7)	–	−1.5218	4	0.0281
Kundal	***Mangifera indica* Linn.**	23.82 (7 5 7)	09.38 (9 0 8)	18.44 (3 6 9)	2.7836	2,8	0.0486
Erode	***Ceiba pentandra* Linn.**	41.3 (46)	34.38 (32)	–	−0.8643	4	0.3874
Cuddalore	***Manilkara zapota* Linn.**	37.5 (40)	53.13 (32)	–	1.2928	4	0.0501
Tuticorin	***Gossypium gossypioides* Ulbr.**	–	21.05 (19)	–	–	–	–
Karur	***Psidium guajava* Linn.**	20.59 (34)	16.67 (12)	–	−0.1852	4	0.8530

– = infested plant parts were either not infested or not available at the time of sampling. Numbers in parentheses represent the actual number of *R. iceryoides* collected per plant part during the survey.

Compere, *Aphycus sapporoensis* Compere & Annecke, *Agarwalencyrtus ajmerensis* Fatima & Shafee, *Anagyrus mirzia* Agarwal & Alam and *Carabunia bicoloripes* Hayat (Table 4). Among these species, *P. viridis, A. chryos* and *N. tachikawai* accounted for 53.2, 31.3 and 8.8% parasitism, respectively. The percent parasitism of each parasitoid species on the various host plant species was observed to vary considerably (Table 4).

Besides, the primary parasitoids described above, two (2) hyperparasitoids were also recovered from the mummified *R. iceryoides*. These hyperparasitoids included *Coccophagus* ceroplastae (Howard) (Hymenoptera: Aphelinidae) and *Coccidoctonus terebratus* (Hayat, Alam & Agarwal) (Hymenoptera: Encyrtidae) (Table 4). However, hyperparasitism was generally low and sporadic accounting for 12.8%.

Dipteran parasitoid, *Cryptochaetum iceryae* (Williston) (Diptera: Cryptochaetidae) was also recovered from mummified *I.* seychellarum in Coimbatore district accounting for 74.6% parasitism. Parasitoid species recovered from other mealybug pests included *Aenasius advena* Compere (Hymenoptera: Encyrtidae) from Planococcus citri (Risso) (Hemiptera: Pseudococcidae) and Ferrisia virgata Cockerell (Hemiptera: Pseudococcidae). Finally, two key parasitoid species recovered from *R. invadens* included *Gyranusoidea tebygi* Noyes and *Anagyrus mangicola* Noyes (Hymenoptera: Encyrtidae) in the districts of Madurai and Coimbatore. No parasitoid species were recorded from *D. mangiferae* and *I. aegyptiaca*.

3.5. Inventory of predators attacking *R. iceryoides*

Ten (10) predatory species belonging to 7 families were recorded. This included 1 species [*Spalgis epius* (Westwood)] from the family of Lycaenidae and 4 species (*Scymnus* coccivora Ayyar, *Chilocorus* nigritus Fabricius, *Hyperaspis maindroni* Sicard and *Cryptolaemus montrouzieri* Mulsant) from the family coccinelidae. *Chilocorus nigritus* was the most important, abundant and widespread species among the predators. The green (*Chrysopa* sp.) and brown (*Hemerobius* sp.) lacewing were also observed variously consuming *R. iceryoides*. Three dipteran species: hover fly-larvae (Syrphidae: Diptera), *Leucopis* sp. (Chamaemyiidae: Diptera) and *Cacoxenus perspicax* Knab (Drosophilidae: Diptera) were recorded rapaciously preying on *R. iceryoides*. However, among the dipterans, *C. perspicax* was the most predominant species widely encountered.

3.6. Ant species tending *R. iceryoides*

Five (5) species of ants were frequently observed tending *R. iceryoides*. These species included, *Camponotus* barbaricus Emery (Hymenoptera: Formicidae), *Camponotus* (*Myrmoserícus*) *rufipes* Fabricius (Hymenoptera: Formicidae), *Crematogaster* cerasi Fitch (Hymenoptera: Formicidae), *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae) and *Monomorium pharaonis* Linnaeus (Hymenoptera: Formicidae). Direct transportation of *R. iceryoides* was observed to be commonly practiced by two species, *O. longinoda* and *C. rufipes*. *Camponotus rufipes* proactively transport *R. iceryoides* to their underground nest, while *O. longinoda* transported them to their leafy next on tree branches. On the other hand, both *C. rufipes* and *O. longinoda* were frequently observed attacking predatory larvae of *S. epius*.

Table 4. Parasitoid complex associated with *Rastrococcus iceryoides* and percent parasitism recorded on the various host plants in the state of Tamil Nadu, India.

			Percentage parasitism			Statistics		
District/Locality	**Parasitoid species**	**Plant species**	**Leaves**	**Twigs**	**Fruits**	***T or F***	***df***	***P***
Coimbatore	***Praleurocerus viridis* Agarwal**	***Mangifera indica* Linn.**	26.69 (2 9 6)	27.32 (1 8 3)	–	−0.3660	4	0.7144
	***Anagyrus chryos* Noyes & Hayat**	***Mangifera indica* Linn.**	21.28 (2 9 6)	16.39 (1 8 3)	–	−1.3229	4	0.1859
	****_Coccophagus ceroplastae_ Howard**	***Mangifera indica* Linn.**	7.09 (2 9 6)	6.01 (1 8 3)	–	−0.2208	4	0.8253
	***Parechthrodryinus excelsus* Hayat**	***Mangifera indica* Linn.**	2.36 (2 9 6)	2.19 (1 8 3)	–	1.0849	4	0.2780
	***Ericydnus paludatus* Haliday**	***Mangifera indica* Linn.**	1.01 (2 9 6)	2.19 (1 8 3)	–	1.4187	4	0.1560
	***Neoplatycerus tachikawai* Subba Rao**	***Mangifera indica* Linn.**	2.7 (2 9 6)	3.28 (1 8 3)	–	1.0008	4	0.3169
	***Agarwalencyrtus ajmerensis* Fatima & Shafee**	***Mangifera indica* Linn.**	2.7 (2 9 6)	0	–	−1.6985	4	0.0494
	***Aenasius advena* Compere**	***Mangifera indica* Linn.**	0	4.37 (1 8 3)	–	2.2768	4	0.0228
	***Praleurocerus viridis* Agarwal**	***Manilkara zapota* Linn.**	26.11 (1 5 7)	26.92 (78)	–	1.1023	4	0.2703
	***Anagyrus chryos* Noyes & Hayat**	***Manilkara zapota* Linn.**	19.75 (1 5 7)	25.64 (78)	–	0.1225	4	0.9025
	****_Coccophagus ceroplastae_ Howard**	***Manilkara zapota* Linn.**	10.19 (1 5 7)	8.97 (78)	–	0.4229	4	0.6723
	***Parechthrodryinus excelsus* Hayat**	***Manilkara zapota* Linn.**	5.10 (1 5 7)	10.26 (78)	–	1.3703	4	0.1706
	***Neoplatycerus tachikawai* Subba Rao**	***Manilkara zapota* Linn.**	8.28 (1 5 7)	5.13 (78)	–	−0.2460	4	0.8057
	***Praleurocerus viridis* Agarwal**	***Tectona grandis* Linn.**	27.78 (54)	15.0 (78)	–	−0.4920	4	0.0558
	***Anagyrus chryos* Noyes & Hayat**	***Tectona grandis* Linn.**	20.37 (54)	25.0 (78)	–	0.1246	4	0.9009
	****_Coccophagus ceroplastae_ Howard**	***Tectona grandis* Linn.**	9.26 (54)	7.5 (78)	–	−0.6228	4	0.5334
	***Parechthrodryinus excelsus* Hayat**	***Tectona grandis* Linn.**	5.56 (54)	12.5 (78)	–	0.6708	4	0.5023
	***Ericydnus paludatus* Haliday**	***Tectona grandis* Linn.**	7.41 (54)	2.5 (78)	–	−0.5821	4	0.5605
	***Praleurocerus viridis* Agarwal**	***Ficus benghalensis* Linn.**	25.31 (1 6 2)	16.67 (54)	–	−0.2299	4	0.2187

District/Locality	Parasitoid species	Plant species	Percentage parasitism Leaves	Twigs	Fruits	Statistics T or F	df	P
	Anagyrus chryos **Noyes & Hayat**	***Ficus benghalensis*** **Linn.**	20.99 (1 6 2)	31.48 (54)	–	1.3472	4	0.1779
	*******Coccophagus ceroplastae*** **Howard**	***Ficus benghalensis*** **Linn.**	8.64 (1 6 2)	7.41 (54)	–	0.4229	4	0.6723
	Praleurocerus viridis **Agarwal**	***Psidium guajava*** **Linn.**	28.89 (1 3 5)	25.0 (92)	–	0.4346	4	0.6639
	Anagyrus chryos **Noyes & Hayat**	***Psidium guajava*** **Linn.**	16.30 (1 3 5)	20.65 (92)	–	0.1451	4	0.8847
	*******Coccophagus ceroplastae*** **Howard**	***Psidium guajava*** **Linn.**	11.11 (1 3 5)	9.78 (92)	–	−0.5143	4	0.6070
Salem								
Erummaiputti	***Praleurocerus viridis*** **Agarwal**	***Mangifera indica*** **Linn.**	20.27 (2 2 2)	20.42 (1 4 2)	–	−0.2861	4	0.7748
	Anagyrus chryos **Noyes & Hayat**	***Mangifera indica*** **Linn.**	15.77 (2 2 2)	19.01 (1 4 2)	–	1.4486	4	0.1474
	*******Coccophagus ceroplastae*** **Howard**	***Mangifera indica*** **Linn.**	2.70 (2 2 2)	2.11 (1 4 2)	–	−0.0814	4	0.9351
	*******Coccidoctonus terebratus*** **Hayat, Alam & Agarwal**	***Mangifera indica*** **Linn.**	17.12 (2 2 2)	17.61 (1 4 2)	–	−1.5000	4	0.1336
	Ericydnus paludatus **Haliday**	***Mangifera indica*** **Linn.**	2.70 (2 2 2)	2.11 (1 4 2)	–	−0.0814	4	0.9351
	Leptomastidea minyas **Noyes & Hayat**	***Mangifera indica*** **Linn.**	2.70 (2 2 2)	3.52 (1 4 2)	–	0.6222	4	0.5338
Dharmapuri								
Paiyur	***Praleurocerus viridis*** **Agarwal**	***Mangifera indica*** **Linn.**	15.18 (2 5 7)	21.43 (28)	–	0.0783	4	0.9388
	Anagyrus chryos **Noyes & Hayat**	***Mangifera indica*** **Linn.**	24.13 (2 5 7)	28.57 (28)	–	−0.5363	4	0.5918
	Anagyrus mirzia **Agarwal & Alam**	***Mangifera indica*** **Linn.**	3.89 (2 5 7)	0	–	−1.9291	4	0.0537
	*******Coccophagus ceroplastae*** **Howard**	***Mangifera indica*** **Linn.**	5.84 (2 5 7)	0	–	−1.6714	4	0.0016
	Praleurocerus viridis **Agarwal**	***Ceiba pentandra*** **Linn.**	18.60 (43)	16.67 (12)	–	−0.4025	4	0.6873

District/Locality	Parasitoid species	Plant species	Percentage parasitism			Statistics		
			Leaves	Twigs	Fruits	*T or F*	*df*	*P*
	Anagyrus chryos **Noyes & Hayat**	***Ceiba pentandra*** **Linn.**	20.93 (43)	16.67 (12)	–	−0.1246	4	0.9009
	*******Coccophagus ceroplastae*** **Howard**	***Ceiba pentandra*** **Linn.**	6.98 (43)	0	–	−1.1739	4	0.0008
Periyapatti	***Praleurocerus viridis*** **Agarwal**	***Mangifera indica*** **Linn.**	21.14 (3 6 9)	13.91 (1 1 5)	–	−1.3577	4	0.1746
	Anagyrus chryos **Noyes & Hayat**	***Mangifera indica*** **Linn.**	23.04 (3 6 9)	21.74 (1 1 5)	–	−0.0589	4	0.953
	*******Coccophagus ceroplastae*** **Howard**	***Mangifera indica*** **Linn.**	8.67 (3 6 9)	10.43 (1 1 5)	–	0.6505	4	0.5154
	Praleurocerus viridis **Agarwal**	***Cajanus cajan*** **(L) Millsp.**	11.59 (69)	6.25 (16)	–	−0.6708	4	0.5023
	Anagyrus chryos **Noyes & Hayat**	***Cajanus cajan*** **(L) Millsp.**	18.84 (69)	25.0 (16)	–	0.4229	4	0.6723
	*******Coccophagus ceroplastae*** **Howard**	***Cajanus cajan*** **(L) Millsp.**	8.70 (69)	6.25 (16)	–	−0.9391	4	0.3477
Kariyamangakam	***Praleurocerus viridis*** **Agarwal**	***Mangifera indica*** **Linn.**	17.12 (1 1 1)	24.62 (65)	–	0.3765	4	0.7066
	Anagyrus chryos **Noyes & Hayat**	***Mangifera indica*** **Linn.**	20.72 (1 1 1)	20.0 (65)	–	0.1474	4	0.8828
	*******Coccophagus ceroplastae*** **Howard**	***Mangifera indica*** **Linn.**	8.11 (1 1 1)	9.23 (65)	–	−0.6159	4	0.5380
Madurai								
Othakadei	***Praleurocerus viridis*** **Agarwal**	***Mangifera indica*** **Linn.**	24.42 (86)	13.04 (23)	–	−1.0104	4	0.0123
	Anagyrus chryos **Noyes & Hayat**	***Mangifera indica*** **Linn.**	24.42 (86)	21.74 (23)	–	−0.1641	4	0.8696
	*******Coccophagus ceroplastae*** **Howard**	***Mangifera indica*** **Linn.**	6.98 (86)	13.04 (23)	–	0.1811	4	0.8563
	Praleurocerus viridis **Agarwal**	***Ceiba pentandra*** **Linn.**	10.71 (28)	42.86 (7)	–	−0.4613	4	0.0046
	Anagyrus chryos **Noyes & Hayat**	***Ceiba pentandra*** **Linn.**	39.29 (28)	28.57 (7)	–	1.1983	4	0.2308
	*******Coccophagus ceroplastae*** **Howard**	***Ceiba pentandra*** **Linn.**	10.71 (28)	0	–	1.3229	4	0.0001
Valeyapatti	***Praleurocerus viridis*** **Agarwal**	***Mangifera indica*** **Linn.**	27.45 (51)	13.33 (15)	–	1.2478	4	0.0121
	Anagyrus chryos **Noyes & Hayat**	***Mangifera indica*** **Linn.**	31.37 (51)	20 (15)	–	1.5884	4	0.1122

District/Locality	Parasitoid species	Plant species	Percentage parasitism Leaves	Twigs	Fruits	Statistics T or F	df	P
	***Coccophagus ceroplastae* Howard**	***Mangifera indica* Linn.**	9.80 (51)	13.33 (15)	–	0.0995	4	0.9207
Virudhunagar								
Rajapalayam	***Praleurocerus viridis* Agarwal**	***Mangifera indica* Linn.**	16.92 (65)	33.33 (15)	–	0.3300	4	0.0211
	***Anagyrus chryos* Noyes & Hayat**	***Mangifera indica* Linn.**	23 (65)	20 (15)	–	−0.5413	4	0.5883
	***Coccophagus ceroplastae* Howard**	***Mangifera indica* Linn.**	9.23 (65)	13.33 (15)	–	0.1114	4	0.9113
	***Ericydnus paludatus* Haliday**	***Mangifera indica* Linn.**	4.62 (65)	0	–	−1.4427	4	0.0319
Theni								
Periyakulam	***Praleurocerus viridis* Agarwal**	***Mangifera indica* Linn.**	41.18 (34)	42.11 (19)	–	0.1303	4	0.8963
	***Aenasius advena* Compere**	***Mangifera indica* Linn.**	11.74 (34)	10.53 (19)	–	0.2697	4	0.7874
Kanyakumari								
Pechiparai	***Praleurocerus viridis* Agarwal**	***Mangifera indica* Linn.**	12.93 (1 6 2)	10.16 (4 4 7)	–	0.9131	4	0.3612
	***Anagyrus chryos* Noyes & Hayat**	***Mangifera indica* Linn.**	5.90 (1 6 2)	8.72 (4 4 7)	–	−0.1409	4	0.2539
	***Aphycus sapporoensis* Compere & Annecke**	***Mangifera indica* Linn.**	2.35 (1 6 2)	1.23 (4 4 7)	–	0.2311	4	0.3661
	***Coccophagus ceroplastae* Howard**	***Mangifera indica* Linn.**	3.26 (1 6 2)	5.29 (4 4 7)	–	−0.6900	4	0.4902
	***Leptomastidea minyas* Noyes & Hayat**	***Mangifera indica* Linn.**	1.09 (1 6 2)	2.79 (4 4 7)	–	0.5620	4	0.5741
Kundal	***Praleurocerus viridis* Agarwal**	***Mangifera indica* Linn.**	6.95 (7 5 7)	1.92 (9 0 8)	8.28 (3 6 9)	2.7977	2,8	0.0469
	***Anagyrus chryos* Noyes & Hayat**	***Mangifera indica* Linn.**	4.62 (7 5 7)	3.10 (9 0 8)	4.16 (3 6 9)	4.9536	2,8	0.0840
	***Coccophagus ceroplastae* Howard**	***Mangifera indica* Linn.**	5.14 (7 5 7)	2.59 (9 0 8)	2.13 (3 6 9)	22.7534	2,8	< 0.0001
	***Leptomastidea minyas* Noyes & Hayat**	***Mangifera indica* Linn.**	1.06 (7 5 7)	0.33 (9 0 8)	0	1.3729	2,8	0.5034
	***Carabunia bicoloripes* Hayat**	***Mangifera indica* Linn.**	0.79 (7 5 7)	0.33 (9 0 8)	0	0.7290	2,8	0.6946

- = infested plant parts were either not infested or not available at the time of sampling. Numbers in parentheses represent the actual number of mealybugs collected per plant part during the survey. ** = Hyperparasitoids emerged from the mummified *R. iceryoides*.

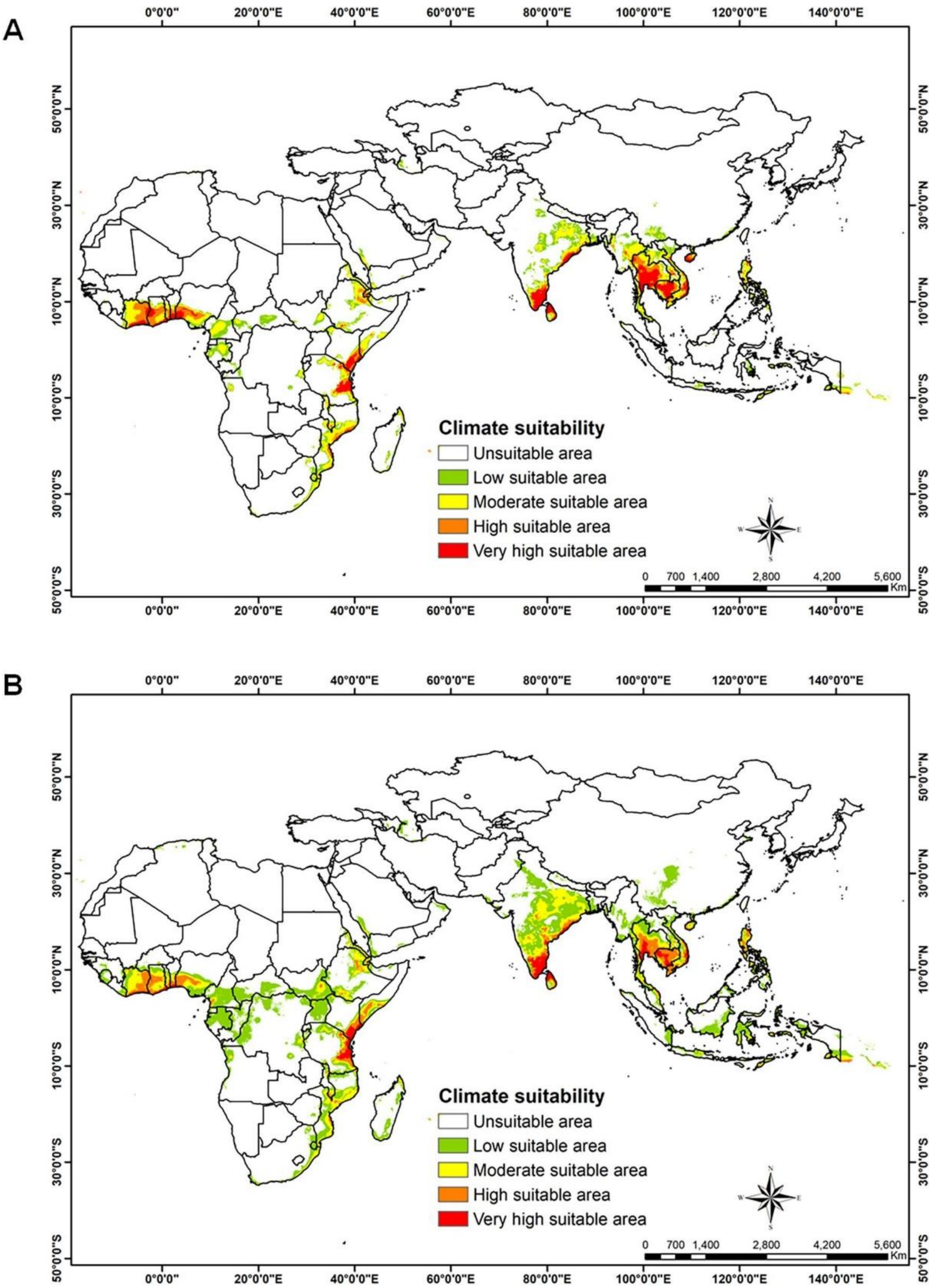

Fig. 4. Climatic compatibility and optimal habitat suitability in Africa and Asia for the establishment of promising potential biological control agents (i.e., parasitoids) generated by the MaxEnt algorithm under current (A) and future (B) climatic scenarios.

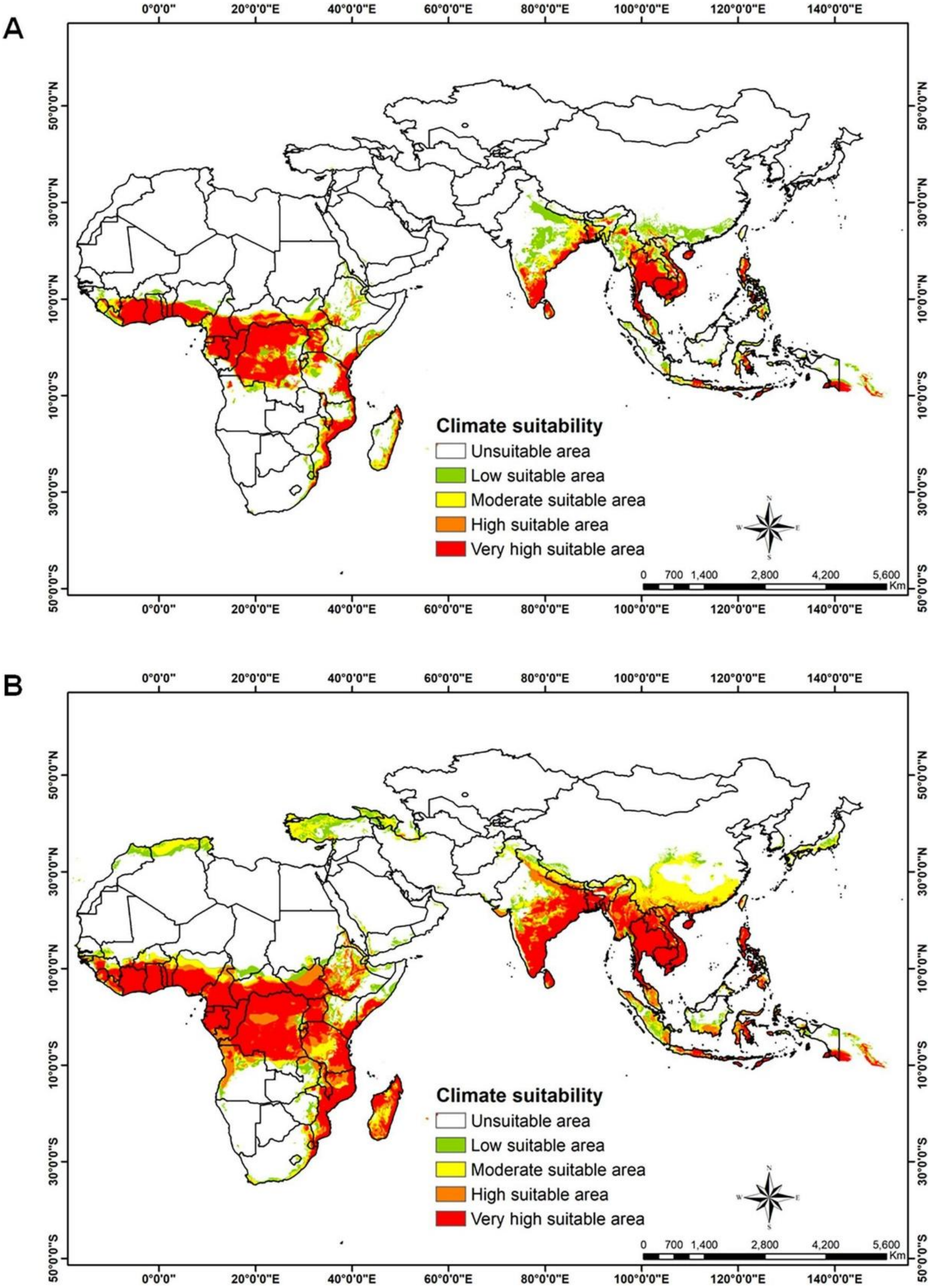

Fig. 5. Climatic compatibility and optimal habitat suitability in Africa and Asia for the establishment of promising potential biological control agents generated by the GARP algorithm under current (A) and future (B) climatic scenarios.

Table 5. Percent contribution (out of 10,000 iterations) of predictor variables used for modelling the climatic compatibility of the invaded range in Africa and Asia for the establishment of the biological control agents of *Rastrococcus iceryoides* under current and future conditions.

Abbreviation	Variables description	Units	Current		Future	
			% of contribution	Permutation importance	% of contribution	Permutation importance
BIO1	Annual Mean Temperature	°C	3.9	0	2.3	0
BIO2	Mean diurnal range (Mean of monthly (max temp - min temp))	°C	3.7	6.1	4.8	9.1
BIO3	Isothermality (BIO2/BIO7) (*100)	°C	11.5	1	9.5	1.4
BIO4	Temperature Seasonality (standard deviation*100)	°C	11.9	59.8	8.5	68.9
BIO6	Minimum Temperature of coldest month	°C	33.2	1.9	30.3	0.3
BIO12	Annual Precipitation	mm	2.1	0.5	1.7	0.2
BIO13	Precipitation of Wettest Month	mm	4.6	2.8	7.3	2.4
BIO14	Precipitation of Driest Month	mm	6.4	8.7	0.9	2.2
BIO15	Precipitation Seasonality (Coefficient of Variation)	mm	3.7	1.4	6.2	1.9
BIO17	Precipitation of Driest Quarter	mm	13.4	4.9	18.9	7.7

3.7. Potential habitat suitability for establishment and colonization by promising parasitoids in invaded regions in Africa and Asia

In Africa, the optimal potential areas for the establishment and colonization of promising parasitoids as predicted by the MaxEnt algorithm extend the length of the coast in invaded regions like Kenya and Tanzania, which is similar under current (Fig. 4A) and future (Fig. 4B) climate scenarios, but differed from the GARP algorithm (Fig. 5A and B for current and future climate scenarios, respectively). However, in Africa GARP algorithm showed higher suitability in *R. iceryoides* invaded areas farther removed from the coastal belts, especially under future climate, particularly in Kenya, Tanzania, and Malawi. To date, there are no records of *R. iceryoides* in West, South, and Central Africa. However, our models (GARP) indicated that high environmental suitability of parasitoid species may exists in some regions of West Africa (Côte d'Ivoire, Ghana, Togo, Liberia, Benin, Nigeria), Central Africa (Cameroon, Central African Republic, Gabon, Democratic Republic of the Congo, Equatorial Guinea, and Congo), East Africa (part of Somalia, Ethiopia, Uganda, South Sudan) and Southern Africa (Madagascar and Mozambique).

In Asia, areas predicted by GARP and MaxEnt to be highly suitable for parasitoids establishment included India, Sri Lanka, Thailand, and Cambodia. Additional, highly suitable habitats predicted by GARP included Myanmar, Laos, Philippines, Malaysia, Indonesia, Hainan Island and Vietnam. Generally, in Africa and Asia, areas predicted by MaxEnt were more restricted compared to GARP, both under current and future climatic scenarios.

Bioclimatic variables such as Bio 6 (Minimum temperature of coldest month), Bio 17 (Precipitation of driest quarter), Bio 4 (Temperature seasonality) and Bio 3 (Isothermality) contributed the most to the final model (Table 5).

4. Discussion

The aim of our study was to detect climatically suitable areas in the native home of *R. iceryoides* using MaxEnt and GARP algorithms, and bioclimatic variables of the sites where the species has already invaded. This was to underpin specific source regions in the native range of *R. iceryoides* in India for foreign exploration for closely associated natural enemies, pest native distributional range and host-plant relationship. Thereafter, we demonstrated climatic compatibility between area-of-origin (India) and areas-of-establishment (Africa and Asia) to predict climatically suitable areas in the invaded range of the pest for potential introduction of effective natural enemies (Byrne et al., 2002, Senaratne et al., 2006, Robertson et al., 2008). Based on the economic threats posed by invasive mealybug species on agriculture worldwide, surveys for co-evolved natural enemies from the aboriginal home of the pest to control them in invaded areas remains the best options to pesticide use for suppression of pest populations with little or no damage to both humans, environment, and biodiversity (Eiswerth, 2010, DeBach and Schlinger, 1964). Biological control has been considered an environmentally friendly alternative tactic to be used in integrated pest management strategies for the control of invasive mealybug pests (Franco et al., 2009). Contrarily, the success of biological control programme against invasive mealybug pests could be impaired by either the absence of efficient co-evolved natural enemies and/or climatic incompatibility between the native range and the area where the biological control agents will be introduced (Robertson et al., 2008). Noteworthy, we utilized different climate matching approaches to estimate the potential of promising parasitoids to thrive and establish permanent self-sustaining populations that will disperse and track the pest's distribution in invaded areas. Furthermore, assuming that the geo-referencing of some records may not be reliable, the MaxEnt and GARP algorithms excluded 5% of the sites with outlying environmental conditions from the train dataset to increase the model confidence (Giannini et al. 2012).

Rastrococcus iceryoides was the major mango mealybug in Tamil Nadu state, India. Though, *R. iceryoides* was widespread in the mango growing areas, they were of no ecomomic importance. It appears that the existence of a complex of natural enemies identified in the current studies, the population of *R. iceryoides* was adequately suppress and under excellent control. Our findings agrees to that reported by Tandon and Lal, 1978, Narasimham and Chacko, 1988 in India. Among the complex of parasitoid communities, *P. viridis* and *A. chryos* were the most abundant and widespread primary parasitoid species of *R. iceryoides*. Parasitoid species were highly specific to their associated host *R. iceryoides*, which is consistent with the reports by Narasimham and Chacko, 1988, Mani and Krishnamoorthy, 1998 and Mani et al. (2011), who demonstrated that these parasitoids shared evolutionary history with *R. iceryoides*. Due to the outstanding co-evolved relationship, the parasitoids have develop and adapted enhanced searching behavior, foraging efficiency and high parasitism rates of *R. iceryoides* (Narasimham and Chacko, 1988, Mani and Krishnamoorthy, 1998). This is in accordance with the report by Sagarra et al. (2000), who confirmed that the effectiveness of many parasitoids to sufficiently control populations of mealybug pest are largely depended on their ability to employ countermeasures to overcome the host immune response. Therefore, understanding the ability of the parasitoid to overcome host defense strategies has been considered the most relevant factor for the success of the parasitoids used in biological control programs (Blumberg and van Driesche, 2001).

Therefore, *P. viridis* and *A. chryos* can be considered as efficient and promising bio-control agents against *R. iceryoides* in invaded regions because of their coevolutionary history. Remarkably, despite the economic importance of *P. viridis* and *A. chryos* in adequately suppressing *R. iceryoides* in its native home, these parasitoids have never been used in any classical biological control programs in affected regions in Africa or other parts of Asia beside India. *Praleurocerus viridis* and *A. chryos* coexist in India, complementing each other in regions infested with *R. iceryoides*. On all the host plant species sampled, the highest percent parasitism by *P. viridis* and *A. chryos* were frequently observed on *mangifera indica* (mango), followed by *C. pentandra, P. guajava* and *T. grandis*. This information on the dynamics of *R. iceryoides* parasitism on various host plants is very useful and serves as a prerequisite for local conservation and augmentation programs of these parasitoids. The other parasitoids played a minor role and had patchy distribution with very low parasitism rates. The huge records of both new and old parasitoid/*R. iceryoides* associations might be the key facts responsible for the excellent control of the pest, translating to its minor pest status throughout India (Narasimham and Chacko, 1988, Mani and Krishnamoorthy, 1998; Mani et al. 2011).

According to the models, all the non-invaded areas predicted to be highly suitable for parasitoids establishment should be prioritized as potentially new areas for possible invasions with the view to formulating pre-emptive preventive management strategies such as surveillance and monitoring, early detection, and rapid response for targeted localized suppression. Although, *R. iceryoides* has invaded areas in Africa and Asia, with great potential to expand its distributional, if all the environmental barriers are breached (Richardson and van Wilgen, 2004), no analysis of their future risk and spread has yet been undertaken However, many of the areas predicted to be potentially suitable are new, implying that *R. iceryoides* is likely to expand its distributional range further in these regions. Therefore, this study marks the first attempt in the two continents. Compared to MaxEnt, GARP algorithm demonstrated higher predictions for suitability in areas farther removed from the coastal belts with broader latitudinal limits under current and future climate in the tropics. The huge pockets of population outbreaks frequently observed in Kenya, Malawi, and Tanzania (Tanga, 2012), might be new nuclei for expansion. Furthermore, the climatic suitability of East and West Africa, and their proximity to Central Africa underlines further threats of invasion. The GARP model also predicted that the large part of Mozambique is highly vulnerable to future invasion by *R. iceryoides*. Also, the proximity of Madagascar to the Indian Subcontinent, which is the native home of *R. iceryoides* further compound the high risk of invasion. Contrarily, the MaxEnt model showed restricted areas of suitability for parasitoid establishment in Central Africa under current and future climatic conditions but this does not imply that *R. iceryoides* can be introduced without any risk of invasion.

The areas projected to be climatically suitable for the establishment of the parasitoids in Asia and Africa conform well to the published distributional range of *R. iceryoides*. New areas predicted to be climatically suitable for the establishment of the identified parasitoids in Asia included Myanmar, Laos, Thailand, Cambodia, Vietnam, part of China, and Philippines and Sri Lanka. However, GARP predicted much higher suitability further inland from the coastlines, while MaxEnt indicated suitability in isolated pockets scattered around the coastlines. All the areas predicted to be highly suitable for parasitoid establishment in India such as Assam, Bihar, Andaman and Nicobar Islands, Delhi, Jammu and Kashmir, Gujarat, Madhya Pradesh, Kerala, West Bengal and Uttar Pradesh, are known to harbour populations of *R. iceryoides* (Williams, 1989, Noyes and Hayat, 1994, Halder et al., 2019). The accuracy of the models can be attributed to the utilization of complete data set on the distributional range of the parasitoids (Wharton and Kriticos, 2004, Soberon and Peterson, 2005) to avoid predictive errors due to the presence of possible natural barriers (Davis et al., 1998, Kriticos and Randall, 2001).

The climatic matching models identified extralimital destinations that could be colonized by the parasitoids based on similarity to climates in the pest species' native range (Robertson et al., 2008). Our models were only able to assess one of the major challenges that natural enemies must overcome, that is the likelihood of the species to survive in their new areas of introduction. The major shortcoming of the present study is that we did not explored the entire array of challenges reported by Richardson and van Wilgen (2004). However, we ensured that majority of the bioclimatic variables presumed to limit the establishment and spread of the parasitoids were taken into consideration (Stiling, 1993, Syrett et al., 2000, Van Driesche et al., 2008, Daane et al., 2012). The high climatic matching indices observed in the present studies does not guarantee establishment and spread of the parasitoids, as such our results should be construed with care. This is consistent with the report by Goolsby et al. (2005), who demonstrated in several instances that climatic matching indices of 80% might still result in total failure of parasitoid establishment. This can be attributed to factors other than climate that could affect establishment, though suitable biological control agents with good climatic tolerance are identified (Goolsby et al. 2005). Van Klinken et al. (2003) listed some of the mechanisms that could prevent the establishment of climatically well-matched natural enemies, which include the lack of genetic diversity, attacks by generalist predators, impoverished habitat or insufficient numbers released. What is remarkable about the current study is that most of the regions highlighted as highly suitable by MaxEnt and GARP models have been invaded by *R. iceryoides*, giving more predictive trustworthiness to future biological control programs.

During the survey in India, *Gyranusoidea tebygi* Noyes was recorded as the main primary parasitoid parasitizing *R. invadens*. *Rastrococcus invadens* is also known to be native to South East Asia, particularly India but was accidentally introduced probably on infested plant materials into some West and Central Africa countries in 1982, where it caused severe damage on horticultural crops (Agounké et al., 1982). However, it was brought under control using *G. tebygi* and *Anagyrus* mangicola Noyes imported from India (Bokonon-Ganta and Neuenschwander, 1995; Noyes and Hayat, 1994). Given that our models strongly highlighted all the areas where *G. tebygi* and *A. mangicola* were introduced to control *R. invadens* (Bokonon-Ganta and Neuenschwander, 1995; Noyes and Hayat, 1994), this reassurance future studies that classical biological control of *R. iceryoides* using *P. viridis* and *A. chryos* would have greater probability of success due to climatic compatibility between area-of-origin and areas-of-establishment (Goolsby et al., 2005). Optimal climate suitability for parasitoid establishment was mostly predicted around the coastal zones with warmer temperatures and relatively high humidity, which will be conducive for successfully parasitoid establishment (Meyerdirk et al., 2004).

This study provides useful information to guide decision-makers in the assessment of site-specific risks of invasion and spread of *R. iceryoides* with a view to developing appropriate surveillance, phytosanitary measures, and management strategies. However, efforts are presently on the way to explore opportunities to import *P. viridis* and *A. chryos* that are highly specific and widely associated with *R. iceryoides* from their putative aboriginal home of India for classical biological control programs in East Africa and Asia.

5. Conclusion

Classical biological control remains the most important component of integrated pest management programs against *R. iceryoides*. Given that *R. iceryoides* is native to India, its populations is under excellent control from the locally available natural enemies. The models predicted potentially suitable areas for parasitoid introduction in areas where *R. iceryoides* is not (yet) present, but due to quarantine concerns, these findings would help to guide biosecurity agencies in decision-making and serve as an early warning tool to safeguard against *R. iceryoides* invasion into unaffected areas. Although, the predictive models might serve as a novel tool to support classical biological control program targeting *R. iceryoides* in invaded areas, the key to any successful future control program would largely depend on further research on the effectiveness of *P. viridis* and *A. chryos* and their impact on other key mealybug species in invaded areas in Africa such as *Pseudococcus longispinus* (Targioni-Tozzetti), *Planococcus citri* (Risso), *Ferrisia virgata* (Cockerell), *Phenococcus solenensis* (Tinsley), *Nipaecoccus nipae* (Maskell) and *Planococcus kenyae* (Le Pelley), which share many host plants with *R. iceryoides*. To this end, laboratory experiments should be carried out to determine the host-stage preference, acceptability for oviposition, and physiological suitability of the six mealybug host species mentioned above.

Although, *P. viridis* and *A. chryos* have been credited with outstanding successes of biological control of *R. iceryoides*, augmentation of parasitoid populations should also be considered to boost their efficiency in India. In the same way, the role of indigenous parasitoids such as *Anagyrus* pseudococci Girault in Kenya and Tanzania that are helping to suppress *R. iceryoides* to a limited extent should be enhanced by augmentative releases. This calls for the involvement of the private sector in mass rearing of these parasitoids identified for mass releases in affected areas. The conservation of parasitoids, whether introduced or indigenous, is a fundamental pillar in ensuring the success of biological control programmes.

It is, therefore, essential to make mango growers in Africa and Asia more aware of how to conserve these parasitoids by using more eco-friendly management approaches rather than expensive blanket cover sprays of insecticide. Additionally, growers should be encouraged to practice habitat management that provides refuges and food sources for parasitoids in the areas surrounding orchards and gardens. Finally, the future benefits of introducing co-evolved parasitoids from India into Africa or other parts of Asia, particularly for biological control of *R. iceryoides* should not be overlooked.

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Declaration of Competing Interest

The authors declare no conflict of interest.

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