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Potential distribution and monitoring the invasive species "The little fire ant" *(Wasmannia auropunctata*)

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Potential distribution and monitoring the invasive species "The little fire ant" *(Wasmannia auropunctata)*

Research Thesis

In Partial Fulfilment of The
Requirements for the Degree of
Master of Science in Environmental Quality Sciences

Roy Federman

Submitted to the Senate of
the Technion - Israel Institute of Technology

Tevet, 5771 Haifa December 2010

Acknowledgements

The research thesis was done under the supervision of Prof. Yohay Carmel in the Faculty of Civil and Environmental Engineering at the Technion Institute. The generous financial help of the Faculty of Civil and Environmental Engineering at the Technion Institute is gratefully acknowledged.

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Abstract

The Little Fire Ant (*Wasmannia auropunctata*) is an invasive species that originates in South and Central America and it is among the 100 most damaging invasive species as defined by the IUCN. Over the past century, this species invaded many areas around the world, including Israel. The monitoring method used to identify newly infested sites in Israel has not been evaluated for efficiency and lacks defined conditions for execution. The main objectives of this study are to predict *W. auropunctata* potential distribution at the global and local (Israeli) scales and to improve the monitoring method of this species. *W. auropunctata's* potential distribution was predicted using a model for species distribution called MAXENT. Model input data included species location records within the native range and climatic variables. The model output is a map which assigns a value for potential establishment for each pixel relative to other pixels within the model extent. Invasive records were used to evaluate the performance of the models. Climate variables were obtained from online datasets. These datasets do not account for water input due to irrigation. I corrected this gap by adjusting precipitation data to express actual water input in these areas. This correction improved the performance of the global and local models, demonstrating the importance of water input in determining the distribution of this species. Improvement in the global model prediction occurred in five different geographical regions; a result which demonstrates the importance of irrigation correction for various geographical and climatic regions. Globally, areas of high establishment potential were distributed mainly within the equatorial climate zone. The local model predicted high establishment potential in the transition between semi-arid and Mediterranean climate zones as well as in irrigated lands within the Mediterranean zone. The global and local models were compared for the area of Israel, and showed high agreement between them, even though they were based on different datasets at different scales. Within Israel, currently the species does not utilize the full range of its potential niche and is expected to further spread to suitable habitats, mainly to irrigated lands. This study also sought to improve monitoring within Israel by defining the optimal survey methodology in this region. Current methods, which include bait placement and direct searching, were tested using field observations and experiments. The following parameters were tested: bait density, microclimate conditions at occupied bait locations and optimal weather conditions for

performing surveys. In addition, I compared the efficiency of the bait and direct search methods. Direct searching was found as the recommended monitoring method for sites with known infestation, supplemented by baits placed in locations that humans can not effectively observe. Baits were found to be more effective in shaded sites. Surveys are most effective when performed on summer mornings. For discovering new infestations, I recommend direct searches in combination with baits placed at 1m intervals. By identifying areas of high *W. auropunctata* establishment potential and improving current monitoring methodologies, this study allows managers to more effectively monitor and prevent the spread of this invasive species.

List of Abbreviations

- **Ann-prec:** Annual precipitation
- **Ann-temp:** Annual mean temperature
- **AUC**: Area Under the Curve
- **CV**: Coefficient of variation
- **ENFA**: Ecological Niche Factor Analysis
- **Evap:** Evapotranspiration
- **GARP:** Genetic algorithm
- **GAM:** Generalized additive models
- **GLM:** Generalized linear models
- **IMEP:** Israel Ministry of Environmental Protection
- **IUCN:** International Union for Conservation of Nature
- **MAXENT:** Maximum Entropy
- **Max-Warm:** Maximum temperature of warmest month
- **MD**: Mahalanobis distance
- **Min-cold:** Minimum temperature of coldest month
- **Prec-CV:** Precipitation Coefficient of variation
- **Prec-Dry:** Precipitation of driest month
- **P-E:** Annual precipitation minus annual evaporation
- **Prec-wet:** Precipitation of wettest month
- **ROC**: Receiver Operating Characteristic
- **SDM:** Species distribution model
- **Temp-range:** Temperature annual range
- ***W. auropunctata*****:** *Wasmannia auropunctata*, The Little Fire Ant.

Background

Invasive species

An invasive species is a species which was transported accidentally or intentionally by human activity to a location where it has not previously occurred naturally, distant from its home territory (Castri et al. 1990, Williamson 1996). Sandland *et al*. (1999) extend this definition by stating that invasive species become established in a new territory and cause a threat to the native biological diversity. Other expressions used in the scientific literature for non harmful invasive species are: introduced species, non native species, exogenous species and alien species (Sandland et al. 1999), but these expressions are also used for invasive species which cause a threat to biological diversity (Castri et al. 1990, Williamson 1996, Simberloff 2004, Pimentel et al. 2005).

The origins of invasion biology as a sub-discipline in ecology can be traced 52 years ago to the book: "The Ecology of Invasions by Animals and Plants" (Elton 1958), but even earlier authors including Darwin had dealt with this issue (Garci´a-Berthou 2010). In the last two decades biological invasion became a main research topic in ecology. Since the early 90's there is an exponential growth in scientific articles (Puth and Post 2005), and books related to invasions (Simberloff 2004), as well as citations of Elton's book (Ricciardi and MacIsaac 2008).

Invasive species are a global problem, negatively affecting agriculture, forestry, fisheries, human health and natural ecosystems (Sandland et al. 1999, Baskin 2002, Simberloff 2004). Estimates of cumulative losses in the United States resulting from harmful invasive species reached almost $120 billion per year (Pimentel et al. 2005). In the context of biodiversity, invasive species are regarded as one of the greatest threats, second only to habitat destruction (Simberloff 2004). In a global biodiversity scenario for the year 2100, invasive species was found as the 4th out of the five most important determinants of changes in global biodiversity. However, in the Mediterranean biome, species invasions together with land use change are considered the strongest drivers of future decline in biodiversity (Sala et al. 2000). Parker et al. (1999) measure the impact of invasive species at five hierarchical ecology levels: (1) effects on individuals, (2) genetic effects (3) population dynamic effects (4) community effects, and (5) effects on ecosystem processes. Effects on individuals include reduced growth or reproduction and changes in individual organisms' morphology or change in behavioral due to new predators or competitors. Genetic impacts can either be indirect, as a result of altered patterns of natural selection within native populations, or direct, through hybridization. Population dynamic effects following species invasion can be changes in abundance, distribution and demography. These changes may result from competition with invasive species or may be mediated through shared pathogens or parasites. Community effects are usually framed in terms of species richness and reduction in biodiversity. Effects on ecosystem processes include impacts on resource pools and supply rates. These effects may change the physical habitat in ways that drastically change ecosystem functioning (Parker et al. 1999).

Invasive ants

Ants play diverse ecological functions in terrestrial ecosystems: they act as leading predators of other insects and small invertebrates, as herbivores, granivores and scavengers. Ants also serve as premier soil turners and nutrient redistribution. These functions are implemented by a variety of ant species (Holldobler and Wilson 1990). Ants are among the most widespread and damaging introduced species (Tsutsui and Suarez 2003). Many invasive ant species reduce the presence and diversity of local ant species, while competing with and praying on other invertebrates and vertebrates (Holway et al. 2002). There are five ant species in the list of the 100 world worst invasive species, defined by the IUCN (International Union for Conservation of Nature): Argentine ant (*Linepithema humile)*, Big-headed ant (*Pheidole megacephala*), Crazy ant (*Anoplolepis gracilipes*), Red Imported Fire ant (*Solenopsis invicta)* and The little Fire ant (*Wasmannia auropunctata*) (Lowe et al. 2000). Examples of their negative impacts are the shift in composition of the plant community following invasion of *Linepithema humile* to South African shrublands (Christian 2001), reduction in abundance and richness of native ants and other invertebrates following *Pheidole megacephala* presence in Australia (Hoffmann et al. 1999), a rapid, catastrophic shift in the rain forest ecosystem of a tropical oceanic island following the invasion by *Anoplolepis gracilipes* (O'Dowd et al. 2003), reduction of abundance, diversity, and species richness of native ants in south USA following invasion of *Solenopsis invicta* (Porter and Savignano 1990) and the harmful affect of *W. auropunctata* on population abundances, species richness, and community structure of local ant species and other ground arthropods in Israel (Vonshak et al. 2010).

The little fire ant

Description

W. auropunctata is a small ant, characterized by monomorphic workers of ~1.5 mm in length. The workers colour is golden brown with the gaster (part of the abdomen) often darker. The queens are ~4.5 mm long and darker than the workers (Spencer 1941, Wetterer and Porter 2003). The males are about as long as the queens, but with a more slender body. The colony of *W. auropunctata* is polydomous (consist of many nests) and polygynous (many queens in one nest) (Holldobler and Wilson 1990, Ulloa-Chacon and Cherix 1990). Intra-specific aggression between colonies was not found in sites of invasion including New Caledonia (Errard et al. 2005)**,** the Galapagos (Clark et al. 1982) and Israel (Vonshak et al. 2010), but high intra-specific aggression was found in the non-invasive Brazilian populations (Errard et al. 2005). The natural dispersal method of the species is largely or entirely by budding, where queens accompanied by workers walk to a new nest location nearby (Holldobler and Wilson 1990).

Habitat and Feeding

W. auropunctata is a generalist in its choice of habitats (Ulloa-Chacon and Cherix 1990). It occurs in a range of habitats from urban settlements (Delabie et al. 1995), plantations (Medeiros et al. 1995), anthropogenic sites such as fishponds and cemeteries (Vonshak et al. 2010) through dry forests (Causton et al. 2005), degraded and restored subtropical forest (Bestelmeyer and Wiens 1996) and dense native rainforest (Le-Breton et al. 2003). It can occur in habitats that are wet or dry, shaded or open (Deyrup et al. 2000).

W. auropunctata is also a generalist in its choice of food. It was recorded feeding on honeydew from insects, dead insects and other invertebrates, fruit juices and oils (Spencer 1941) and plant parts (Clark et al. 1982). Honeydew was found as a more important food source than other items (Spencer 1941, Clark et al. 1982).

Negative impacts

W. auropunctata has been listed as one of the 100 most damaging invasive species by the IUCN (Lowe et al. 2000), due to its impact on biological diversity and human activities. The majority of reports describing negative impacts caused by *W. auropunctata* are for introduced locations. At some of these locations there is a documented negative impact on the local ant species diversity following invasion. In a native forest in Gabon fewer native ant species were present in areas infested with *W. auropunctata* (Walker 2006). In New Caledonian rainforest, the abundance and richness of the native ant species was consistently lower in the invaded zones (Le-Breton et al. 2003). In Israel, *W. auropunctata* had a remarkable negative impact on abundance, species richness, and community composition of the local ant species (Vonshak et al. 2010). In contrast, in lowland rain forests in its native range, *W auropunctata* does not have devastating effects on local ant communities (Tennant 1994). *W. auropunctata* has a negative impact on other invertebrates, such as the reduction of population densities of arachnids and flying and arboreal insects in the Galapagos (Lubin 1984), and negative impact on arachnids abundance, richness and community structure in Israel (Vonshak et al. 2010). Negative impacts on other trophic levels were described in New Caledonia where lizard species were threatened by *W. auropunctata* presence (Jourdan et al. 2001) and on the Galapagos where *W. auropunctata* ate the hatchlings of tortoises and attacked the eyes of the adult tortoises (Wetterer 2009). In addition, photographic evidence suggests that *W. auropunctata* may have damaged wild mammal eyes in Gabon (Walsh et al. 2004).

W. auropunctata has a negative impact on humans as a result of its painful stings. Few stings can cause a passing discomfort to a pain and itching that lasts three days, while dozen stings can cause serious effects like pallor and shakiness (Spencer 1941). In some areas it was difficult to convince labourers to work in groves or fields where these ants were abundant (Spencer 1941, Smith 1965). *W. auropunctata* is also a problem in households since it contaminates foods, is attracted to dirty clothing and infests beds (Spencer 1941). This species also enhances Homoptera populations (aphids, white flies, scales), which sap plants of nutrients and increase the occurrence of plant diseases (Spencer 1941, Souza et al. 1998). Homoptera excrete honeydew which serves as an essential food source for the ants while the ants protect these insects from natural enemies (Ulloa-Chacon and Cherix 1990).

Distribution

W. auropunctata is a native species in central and South America (Wetterer and Porter 2003, Harris et al. 2005). During the past century, exotic populations of this species invaded other tropical and subtropical areas around the world (Table 1). *W. auropunctata* was recorded also in temperate climate greenhouses in England, and Canada (Wetterer and Porter 2003). Outdoor occurrence records of the species are presented (Fig.1).

Locale	Year
Gabon	1914
Florida	1924
Bermuda	1925
Galapagos	1935?
Bahamas	1951
Cameroon	1959
New Caledonia	1972
Solomon Islands	1974
Wallis and Futuna	1981
Vanuatu	1998
Hawaii	1999
Santa Cruz Islands	1999
Israel	2005
Australia	2006

Table 1. Earliest known records of *W. auropunctata* in invaded localities (modified after Wetterer and Porter 2003).

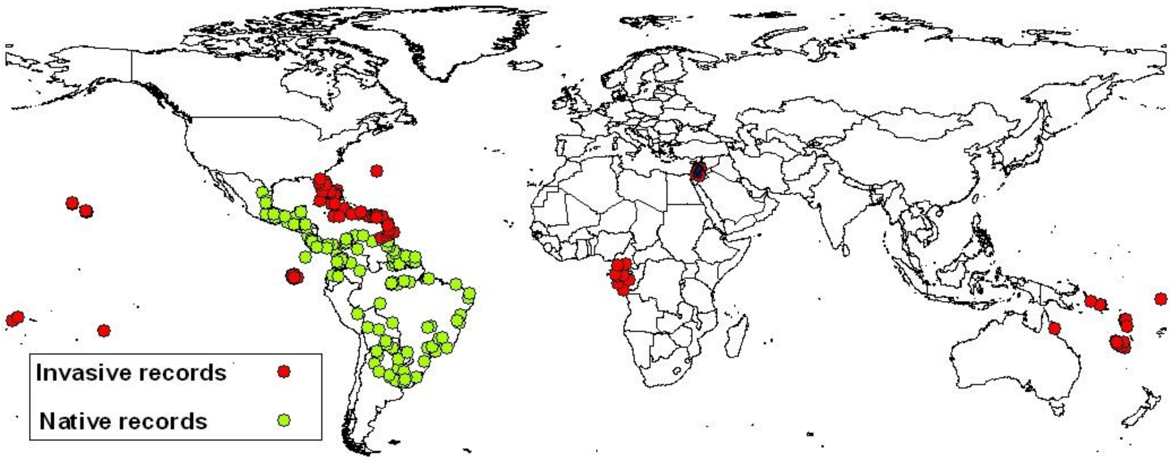

Fig. 1. Global distribution of *W. auropunctata* (modified after Harris et al. 2005). Green points denote native locations, red points denote introduced locations.

W. auropunctata was first identified in Israel at the end of 2005 and probably arrived in Israel in ca. 1998 (Vonshak et al. 2010). Since the discovery of *W. auropunctata* in Israel, nests of this species were found in 89 Israeli rural locations and in a single natural reserve (near the Jordan River) (Fig 2.). The assumed vector for invasion to Israel is logs imported to a wood factory in the Jordan Valley region (Israel Ministry of Environmental Protection (IMEP) (2010). The Israeli population reflects a single introduction of one queen and one male genotypes (Vonshak et al. 2009). The means of spread within Israel are by flowerpots, seedling, earth, wood, chips for mulching, logs for heating, etc. (IMEP, 2010).

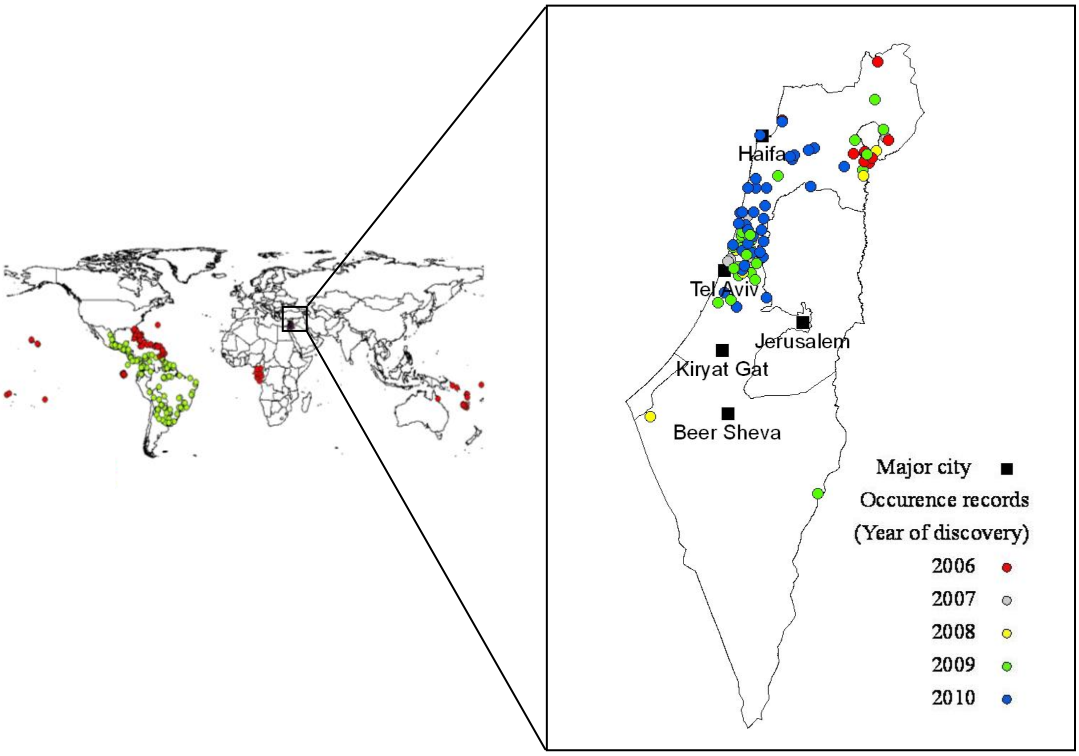

Fig. 2. Left: Global map showing Israel location. Right: Occurrence locations of *W. auropunctata* and the year of discovering of each location on a map of Israel (After IMEP 2010).

This study is composed of two parts, each of them deals with different aspects of the *W. auropunctata* invasion. The first part deals with the potential distribution of *W. auropunctata*, both globally and in Israel, using a computerized model. The second part deals with the monitoring method of the species using field observations and experiments. The two parts are described separately and each part is composed of introduction, methods and discussion. A Summary that combines the conclusions of the two parts concludes this report.

Modelling potential distribution

Introduction

Species distribution models (SDMs)

The understanding of species distribution is an important ecological challenge, related to biogeography, conservation biology, evolution, and climate change (Guisan and Thuiller 2005, Pearson 2007). In recent years, a wide variety of modelling techniques have been developed to predict species distribution (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith et al. 2006, Pearson 2007). These models are generally categorized as empirical models (Guisan and Zimmermann 2000) and known as "Species Distribution Models" (SDMs) (Guisan and Thuiller 2005), "Habitat Distribution Models" (Guisan and Zimmermann 2000), "Climate-Matching envelope", "Ecological Niche-based Models" or other related names (Roura-Pascual and Suarez 2008). SDMs originated in the mid-1970s and proliferated in the early 1980s. Since the early 1990s, developments in computer and statistical sciences resulted in increased number of publications in this field (Guisan and Thuiller 2005). The use of these models recently received additional attention as a result of global change and the corresponding need to predict species range shifts, potential distribution of invasive species, potential spread of disease and the fate of endangered species. Other common uses of SDMs include guiding field surveys to find populations of known species, describing the actual species range from survey data, supporting conservation prioritization and assessing the impacts of land cover change on species distributions (Guisan and Thuiller 2005, Pearson 2007, Jeschke and Strayer 2008).

SDMs rely on the ecological concept of the ecological niche. This concept was initially proposed by Grinnell (1917) who defined the niche as the range of ecological conditions within which a species can maintain populations (potential niche). The concept was developed by Hutchinson (1957) who added the influence of biotic competition and predation (realized niche) and later by Mac- Arthur (1972) that made the niche concept more quantitative (Peterson, 2003). According to this view, "ecological niches delineate the set of conditions under which species can maintain populations in the long term without immigration of individuals" (Peterson 2003).

SDMs use numerical methods to combine observations of species occurrence with environmental variables, in order to identify environmental conditions within which species populations can be maintained (Pearson 2007). Model output is a forecast map of potential species distribution in the defined regions (Guisan and Zimmermann 2000, Anderson et al. 2003, Peterson 2003, Guisan and Thuiller 2005).

Choice of parameters and model type

Environmental variables

Environmental variables can exert direct or indirect effects on species distribution. These variables can express limiting factors controlling species eco-physiology, disturbances of the environmental system or resources that can be assimilated by organisms (e.g. energy and water) (Guisan and Thuiller 2005). Variables expressing limiting factors for species eco-physiology are commonly used in SDMs although physiological tolerances are not always known and the modelling process disregards it (Jeschke and Strayer 2008). The common variables used in SDMs relate to climate, topography, soil and land cover. Such data are increasingly accessible electronically. A commonly used data source is 'WorldClim'- an online database of high resolution climate data at a global scale (Hijmans et al. 2005).

Model selection is an important step in which the most influential explanatory variables and the number of variables used are chosen. A common principle for model selection is that simplicity should be favoured in terms of the number of explanatory variables (Occam's razor principle). There are two competing criteria for model selection, simplicity and goodness of fit. Goodness of fit is a measurement of how well the explanatory variables fit a set of observations. Higher value of goodness of fit indicates that the explanatory variables fit the observations well, but also fit possible errors or 'noise' in the observations data. Accordingly, the use of many variables is expected to improve the goodness of fit, but could cause ‘overfitting’- accidental discrepancies that do not represent the broader regularity. Simplicity acts as a counterbalance to such overfitting, since few meaningful variables usually represent the main regularity (Baker 2004). A common numerical method to account for the trade-off between simplicity and goodness of fit is the Akaike Information Criterion (AIC) (Akaike 1973). This index takes into account both the goodness of fit and the number of parameters used, by imposing a penalty for increasing the number of parameters.

Simplicity is also essential in order to avoid multicolinearity (high correlations between predictors). Multicolinearity can be fixed by either combining predictor variables or by removing one variable when two variables are highly correlated (Guisan and Thuiller 2005). Removing a variable due to high correlation is widely used in SDMs (Ficetola et al. 2007, Tsoar et al. 2007, Ward 2007, Kumar et al. 2009). The final number of predictors used in SDMs varies from 3 variables (Tsoar et al. 2007, Kadoya et al. 2009) through 6 variables (Roura-Pascual et al. 2009), 20 variables (Giovanelli et al. 2008) to 39 variables (Kumar et al. 2009).

Climate variables are widely used in SDMs since climate is assumed to be a major driving factor of species distribution (Thuiller et al. 2005). Other variables such as soil and vegetation cover are much more difficult to obtain and are usually generated at very coarse resolution (Guisan and Zimmermann 2000). Combination of precipitation and temperature effectively represents correlates of physiological tolerance (Tsoar et al. 2007). Precipitation minus evaporation represents soil moisture (Dirmeyer et al. 2009), a variable that is not available at large scales. Specifically for ants, temperature usually controls the metabolism and activity of ant colonies. Extremes hot temperatures can kill adults or whole colonies (Harris et al. 2005 and references within). On the other hand cooler temperatures may slow oviposition rates and may limit ant activity (Korzukhin et al. 2001). No experimental data on climatic preferences were found for *W. auropunctata*.

Species data

Species distribution data may be either records of localities where the species has been observed (Presence-only) or records of presence and absence of the species at sampled localities (Presence-absence). Different modelling approaches have been developed to deal with these two data types (Pearson 2007). Presence-absence data are usually obtained from surveys, and provide more information about the species niche than presence-only data. The collection efforts for presence-absence data are much greater and thus such data are usually not available at large scales. In addition, common mistakes in classification of absence data occur due to difficulties to detect the species although it is present. Other type of error can occur due to historical reasons for species absence although the habitat is suitable (Hirzel et al. 2002). Contrary, presence-only data consist of less wrong classifications and are available at large scales. A possible bias in presence-only data can occur due to unplanned sampling in which data are collected in easily accessible locations (Graham et al. 2004). Although Presence-absence data provide more information about the species niche, recent comprehensive comparison of modeling methods found that models with presence-only data were sufficiently accurate for modeling species distributions (Elith et al. 2006, Kumar et al. 2009).

Types of models

There is a variety of model types to predict species distribution. The models differ in the data used (presence-only or presence-absence), in their analytical methods, and in the form of their output. The most common output is a continuous prediction which assigns values ranging from 0 to 1 (or 0 to 100) to each map pixel. The meaning of the values can be a suitability value relatively to other pixels or a probability for species presence.

Methods based on presence-only data belong to two broad groups based on the type of data they use: methods that use only presence records and methods that use, in addition to species presence records, background environmental data (pseudo-absence data) (Pearson 2007). The first group of methods includes models such as BIOCLIM and DOMAIN. BIOCLIM characterizes sites located within a rectilinear ‘envelope’ in the environmental space, defined by the most extreme records of the species on each environmental variable. DOMAIN uses point-to-point similarity metric in order to assess suitability to each potential site based on its proximity in the environmental space to the most similar occurrence location (Tsoar et al. 2007 and references therein). The second group can potentially be implemented to any presence-absence algorithm using pseudo-absence data instead of real absence data (Pearson 2007). Examples of models in this group are ENFA (Ecological Niche Factor Analysis) and MAXENT (Maximum Entropy). ENFA produce species suitability prediction based on calculation of how the variable mean and variance in species locations differs from the variable mean and variance in the entire habitat (Hirzel et al. 2002). Maxent estimates the potential distribution of species based on machine learning approach (Phillips et al. 2006) (see detailed description in Methods). There are additional presence-only based methods and some of them have been implemented in user-friendly software (Table 2).

Model/software name	Method	Species data type	Reference
BIOCLIM	Envelope model	Presence-only	(Busby 1991)
DOMAIN	Gower metric	Presence-only	(Carpenter et al. 1993)
BIOMAPPER	Ecological niche factor analysis	Presence and background	(Hirzel et al. 2002)
MAXENT	Maximun Entropy	Presence and background	(Phillips et al. 2006)
GARP	Genetic algorithm	Pseudo-Absence	(Stockwell and Peters 1999)
Implemented in R	Generalized linear models (GLM) Generalized additive models (GAM)	Pseudo-Absence (or Presence-Absence)	(Elith et al. 2006)
OPEN MODELLER	Multiple methods	Depends on method implemented	

Table 2. Models based on presence-only methods (Elith et al. 2006, Pearson 2007)**.**

Several studies compared the performance of different SDM methods (Elith et al. 2006, Phillips et al. 2006, Tsoar et al. 2007, Kumar et al. 2009). These comparative studies did not reveal a single method that consistently outperforms other model techniques (Jeschke and Strayer 2008), but some techniques tend to be better than others. In comparison of six different methods a superiority of GARP and MD (Mahalanobis distance) was found over all other models and a low performance of Bioclim and ENFA was found (Tsoar et al. 2007). In a single-comparison study MAXENT outperformed GARP (Phillips et al. 2006). MAXENT also provided the most accurate predictions, followed by 2 types of regression, and by GARP in comparison of SDMs for a freshwater diatom (Kumar et al. 2009). In the most comprehensive comparison of 16 presence-only methods, 3 groups of performance were identified. The group that performed relatively poorly included methods that use only presence data (BIOCLIM, DOMAIN). The second group with intermediate performance included GLM and GAM models. The highest performing group included boosted decision trees, multivariate adaptive regression splines, generalised dissimilarity modelling and MAXENT (Elith et al. 2006). Among these models only MAXENT has been implemented in user-friendly software. Following these findings, MAXENT was chosen for this research.

Model validation

The meaning of validation is not always clear in the context of simulation models. According to Rykiel (1996), validation is a demonstration that a model possesses a satisfactory range of accuracy within its domain of applicability, consistent with the intended application of the model. Accordingly, a valid model does not express absolute truth but it does indicate that it is acceptable for use. SDM validation may be done in several approaches (Jeschke and Strayer 2008): 1. 're-substitution': model predictions are compared to the same data used to fit the model 2. 'data splitting': the data are split into a training set used to fit the model and a validation set used to evaluate the model. 3. 'independent validation': the model is compared to a spatially or temporally independent data set from a different region or different time period. Independent validation is the preferable approach (Fielding and Bell 1997, Elith et al. 2006, Jeschke and Strayer 2008) and was used as a main method in this research.

Common methods of Data splitting are Jackknife and bootstrapping. Both methods use repeated model runs, each time with a different set of data left aside and evaluated against model predictions for the respective locations. The results are summed or averaged to a single measurement of model performance. The most commonly used methods fitted to the mentioned approaches are Cohen’s kappa and Receiver Operating Characteristic (ROC) with its Area Under the Curve (AUC) (Jeschke and Strayer 2008). Both methods use Presence-absence (or pseudo absence) data and are based on a confusion matrix. A confusion matrix records the frequencies of each of the four possible types of prediction outcome from analysis of test data (table 3).

	Recorded present	Recorded absent
Predicted present	**True Positive (a)**	**False positive (b)**
Predicted absent	**False negative (c)**	**True negative (d)**

Table 3. A confusion matrix structure.

Indexes for model validation based on the confusion matrix require a binary prediction. To generate a binary prediction from a model that gives continuous output, it is necessary to set a threshold value above which the prediction is classified as ‘present’ (Pearson 2007). The kappa index is calculated based on a single threshold and its values range between 0–1, where 0 is no agreement and 1 is a complete agreement with model results. The kappa index is easy to calculate but the choice of a single threshold affects the index value. Contrary, ROC AUC is a threshold-independent index that describes the relationship between true positive and false positive data, both calculated across the entire range of possible thresholds (See Methods for detailed description).

Anthropogenic variable in SDMs

A possible false negative error of SDMs can occur due to urban habitation or greenhouses holding the appropriate range of temperatures and precipitation (Roura-Pascual and Suarez 2008 and references therein). Such urban influence is probably the main reason for most of the under-prediction results in SDM based study of 96 invasive plant taxa (Thuiller et al. 2005). Another example is the preference of the invasive bird Common Myna (*Acridotheres tristis*) to anthropogenic habitats, typically large areas of irrigated grass (Holzapfel et al. 2006). Despite the above mentioned influence of anthropogenic habitats on invasive species distribution, only few SDM based researches considered this influence. An exception is a study which used "human footprint variable" in addition to climate variables to model the global distribution of the American bullfrog (*Rana catesbeiana*). The human footprint variable was defined as a combination of population density, land transformation, human access, and presence of infrastructures. It was found to positively influence species occurrence (Ficetola et al. 2007).

Limitations and challenges

SDMs rely on three main assumptions: 1. biotic interactions are less important in determining species distributions or are constant over space and time 2. the genetic and phenotypic composition of species is constant over space and time 3. a state of equilibrium exist between the environment and the observed species presence data (Guisan and Zimmermann 2000, Jeschke and Strayer 2008 and references therein). These assumptions ignore a number of biological principles and are thought to constitute the main limitations of SDMs. The main principles that are being ignored are the inter-specific biotic interactions, evolutionary change, source–sink dynamics and non-equilibrium state between species and their environment (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Jeschke and Strayer 2008). Other limitations and challenges of SDMs include the improvement of accuracy and resolution of input maps, taking into account the influence of historical factors on the current distribution of species, improving sampling design for collecting data and revealing details about the spatial distribution of prediction uncertainties (Guisan and Zimmermann 2000). Despite these limitations "It is generally unwise to prejudge models based on their assumptions; instead, their usefulness should be evaluated by means of performance tests against empirical data" (Jeschke and Strayer 2008).

SDMs for invasive species

There are various uses of SDMs in ecology: finding new populations in field surveys, identifying suitable sites for reintroduction of a species, identifying potential areas for disease outbreaks, examining temporal changes in species niche and predicting sites where a species is most likely to become invasive (Pearson 2007). Predicting potential distribution of invasive species involves an extension of the basic niche concept- invasive species will be able to establish populations only in areas that match climatic conditions to which they are limited in their native distributional areas. This approach holds "excellent predictive ability" and has seen application to a broad diversity of species invasions (Peterson 2003). Some concepts should be emphasized when using SDMs for invasive species: 1. The SDMs limitation of not accounting for biotic interactions is less of a problem for invasive species, since they are usually not restricted by this factor (Peterson 2003) 2. under-prediction is more important than over-prediction and thus should be minimized (Ward 2007) 3. many invasive species are not in equilibrium with the environment in the invaded range, and thus should preferably be modelled using their distribution in the native range (Peterson 2003).

Limitations of SDMs for invasive species

Some limitations should be considered when modelling the potential distribution of invasive species. False negative error could occur since species records in the native range do not always represent the complete niche of the modelled species (Thuiller et al. 2005). Another source for false negative error is the fact that environmental data resolution usually does not represent local environmental heterogeneity (e.g. an invader could persist in a region drier than its home range by its restriction to local wet sites) (Mack 1996). Similarly, false negative error could occur due to phenotypic plasticity and/or rapid evolutionary changes in tolerance, which can cause establishment of the species outside its current environmental conditions (Roura-Pascual and Suarez 2008). Sources of false positive errors can be the influence of competition, predation or pathogens in the invaded range (Mack 1996) although invasive species may be less restricted by biotic interactions.

SDMs for invasive ants

Ant distribution is influenced significantly by climatic variables, mainly temperature, precipitation and humidity (Ward 2007). Accordingly, the climate condition within invasion sites of many exotic ant species, approximately matches the conditions in their native habitats (Holway et al. 2002). Despite the influence of climate on the survival and distribution of ants and the environmental and economic damages they cause, only few attempts were made to model the potential distribution of invasive ant species (Dettmers and Bart 1999). Examples of such models include: the potential distribution of six invasive ant species in New Zealand (Ward 2007), the red imported fire ant, (*Solenopsis invicta*) in Texas (Pimm and Bartell 1980), the Argentine ant (*Linepithema humile*) at global scale (Roura-Pascual 2004), and the potential distribution of *Linepithema humile* in the Iberian Peninsula (Roura-Pascual et al. 2009).

***W. auropunctata* potential distribution**

The southern-most record of *W. auropunctata* outdoors populations (out of temperate greenhouses) is in Argentina (32º40'S) (Wetterer and Porter 2003) and the northern-most record is in Israel (33º13'N) (Vonshak et al. 2010). There are vast areas of the world between these two limits where *W. auropunctata* may be able to invade. A prediction of the future distribution of *W. auropunctata* could be performed by a SDM (Wetterer and Porter 2003). Despite this research potential, only one model-based research for the invasive risk of *W. auropunctata* was found in the scientific literature. The research modelled the potential distribution of the species in New Zealand based on climatic variables, though it has not invaded this country to this day (Harris et al. 2005). The new invasion of *W. auropunctata* into Mediterranean climate, which is drier than its native range, arose the hypothesis that water availability could be key to the spread in this region (Vonshak et al. 2010). Water availability in natural habitats is mainly influenced by precipitation, while within anthropogenic habitats it is mainly influenced by irrigation. Accordingly, variables expressing irrigation should be considered in addition to precipitation variables, when modelling the potential distribution of *W. auropunctata* and other species. I hypothesize that modification of precipitation variables to express real water input will improve the distribution prediction of *W. auropunctata* within irrigated lands.

Objectives

The main objective of this part is to predict *W. auropunctata* potential future distribution. The detailed objectives are:

1. To examine the influence of climatic variables on the native species distribution

2. To create a forecast map of the potential species distributions globally and in Israel scale.

3. To examine the influence of climatic variables on the potential distribution within Israel.

4. To examine a distribution prediction that includes modification of precipitation variables to represent proximity of real water input in irrigated lands.

Methods

Species distribution Model for *W. auropunctata*

I used a habitat suitability model based on presence-only data to predict the potential distribution of *W. auropunctata* at different scales. The habitat suitability model type that was used is "maximum entropy" model (MAXENT Version 3.3.1) (Phillips et al. 2006, Phillips and Dudı´k 2008). MAXENT is a machine learning method that estimates the potential distribution of species based on species occurrence records and a set of environmental variables in a set of grid cells (X). The method refers to species records ($x_1 \ldots x_m$) as localities independently selected from X, according to an unknown probability distribution π. The model produces a probability distribution estimation $\hat{\pi}$ which assigns a non-negative conditional probability for species establishment in each site x.

Common statistical methods, such as logistic regression estimate P(y=1|x), (i.e. the probability of species presence (y=1) given the environmental conditions in the site x). MAXENT, on the other hand, estimates P(x|y=1), where x represent a site rather than environmental conditions. This estimation expresses the probability of the observer to choose a site x, given that the species is present in the site. These probabilities of all the pixel sites in X sum to one (Phillips et al. 2006, Phillips and Dudı´k 2008). Without any information of species occurrence, every site x gets the same probability, i.e. a uniform distribution among X (Elith et al. 2010). The probability estimation, however, respects a set of constraints derived from the environmental variables in the occurrence data locations. Subject to this set of constraints, MAXENT finds the probability distribution of maximum entropy, (i.e. the most spread out, or closest to uniform) (Phillips et al. 2006). The constraints are expressed in terms of simple functions of the environmental variables, called features (f). The feature types implemented by Maxent software are: Linear, Quadratic, Product, Threshold and Hinge. A linear feature is equal to the environmental variable and it imposes the constraint on $\hat{\pi}$ that the mean of the environmental variable, should be close to its mean on the sample localities (See clarifying example in appendix 1.). A quadratic feature equals the variable square and it imposes the constraint on $\hat{\pi}$ that the variance of the environmental variable should be close to its observed value on the sample localities and thus it expresses the species' tolerance for variation from its optimal conditions. A product feature equals product of pairs of variables and it imposes the constraint that the covariance of two variables should be close to its observed value on the sample localities and thus expresses interactions between predictor variables. The Threshold feature imposes the following constraint: the proportion of $\hat{\pi}$ that has values for above the threshold should be close to the observed proportion (threshold is defined automatically by the program) (Phillips et al. 2006). A hinge feature is like a linear feature, but it is constant below a threshold (Phillips et al. 2006, Phillips and Dudı´k 2008). I used the default program option ("Auto features") which uses all feature types. Subject to the mentioned constraints MAXENT finds the probability distribution of maximum entropy. The maximum entropy distribution belongs to the family of Gibbs distributions. Gibbs distributions are exponential distributions derived from the set of features $f1 \ldots fn$ and parameterized by the features coefficients λ1…λn. The Gibbs distribution are defined by: $q_\lambda(x) = \exp(\lambda_1 \cdot f_1(x) + \lambda_2 \cdot f_2(x) + ...\lambda_n f_n(x))/Z$, where Z is a normalization constant ensuring that probabilities $q_\lambda(x)$ sum to one over the study area. The distribution of maximum entropy is the Gibbs distribution $q_\lambda(x)$ that maximizes the probability of the sites where the species was observed (m). To find this distribution, MAXENT performs number of iterations, each of which increases the probabilities of ‘m’. The probability is displayed in terms of 'gain', which is the log of the number of grid cells ‘m’ minus the average of the negative probabilities of the ‘m’ locations. The iterative procedure start from a uniform probability distribution, for which λ= (0,…,0), then repeatedly make adjustments to one or more of the weights λj. The gain starts at zero (uniform probability), and increases as the program increases the probabilities of ‘m’. The gain increases iteration by iteration, until the change falls below a defined gain threshold, or until maximum iterations have been performed. I used a default value of 0.00001 gains change and five hundred iterations.

To define the contribution of the environmental variables, each gain-increase following adjustment of the weights in λj is credited to the corresponding predictor variable. In case of a negative change, a subtraction from the contribution of the corresponding variable was performed. The overall ‘credits’ are used to define the relative contribution of the environmental variables. The λ values of the final model are also used for projection of the model to other sites. The establishment potential at a projection region depends on the feature of each pixel in this region and on its corresponding coefficient λj (Phillips et al. 2006, Phillips and Dudı´k 2008).

Species data

Presence-only data for *W. auropunctata* was obtained from two online databases: Landcare Research (Harris and Rees. 2004 and updates) and Global Biodiversity Information Facilities (GBIF), providing species global records. Records located in Israel were obtained from direct observations and research data (Vonshak et al. 2010). Records from Israel were reduced to one record per infested settlement to prevent a bias of many records in small geographical range. Each record contained information of country, location description, latitude-longitude and information source. Final dataset was composed of 183 records from the native range and 135 global invasive records (Fig 1). 40 out of the 135 invasive records were from Israel (Fig 2).

Environmental variables

'Bioclimatic' variables were obtained from the WorldClim dataset (Hijmans et al. 2005). These variables were derived from the monthly temperature and rainfall values in order to generate biologically meaningful variables. The bioclimatic variables represent annual trends, seasonality and extreme or limiting environmental factors. From the bioclimatic variables, I chose 8 variables that could potentially effect *W. auropunctata*'s distribution: Maximum temperature of warmest month (Max-Warm), Minimum temperature of coldest month (Min-cold), Annual Mean Temperature (Ann-temp), Temperature Annual Range (Temp-range), Precipitation of driest month (Prec-Dry), precipitation of wettest month (Prec-wet), Annual Precipitation (Ann-prec) and Precipitation coefficient of variation (Prec-CV). Yearly reference evapotranspiration variable (Evap) was obtained from FAO database (Hoogeveen 2004) and together with Ann-prec used to calculate another variable: Precipitation minus Evaporation (P-E), which represents the difference between yearly precipitation and evapotranspiration. P-E is used in water balance models (Seager et al. 2007) and represents soil moisture (Dirmeyer et al. 2009). The spatial resolution of evapotranspiration is 10 arc minutes (18.6 x 18.6 km at the equator); all other variables were used in a spatial resolution of 10 arc minutes for the global scale model and in a 30 arc-seconds (0.93 x 0.93 km at the equator) for the local scale model.

Variable selection

Correlation coefficients between each pair of climatic variables (N=10) was calculated and for high correlation (>0.8, pearson correlation, significance at the 0.05 level), one of the variables was eliminated from the model. Values for the correlation examination were taken from records from the species native range; records which were used to build the models. To decide which of the two variables will be eliminated in case of high correlation, I examined the differences between the native niche and the variable ranges of the whole area of Israel (see niche comparison). A variable with large part of its range in Israel being out of the variables native niche, could potentially limit the species distribution in Israel. This type of variables was preferably not eliminated from the model. In addition I considered biological factors that could be relevant for limiting the species distribution.

Scale of the Models

A model for *W. auropunctata* potential distribution was run at two scales: Global and local. I chose Israel as a case study for the local scale model. The environmental data for the local model were at finer resolution (30 arc-seconds) and thus the resultant map of potential distribution was at finer resolution too. The potential distribution of the global scale model was examined for the whole globe and for specific areas of interest. Both models were based on records from the species native range (training records) and environmental (training) layers of this range (Fig. 3). I assumed that invasive records do not reflect equilibrium with climate conditions and thus I did not use them to build the model. The models were run over the native range and projected to evaluate the environmental suitability of each grid cell at global and local (Israel) scales. Global and Israel invasive records were used to evaluate the performance of global and local models, respectively. Extrapolation of suitability prediction was not used for projected regions characterized by variable ranges which are out of the native extent (Fig 3.). The establishment potential of these regions was not estimated and I defined it as 'no prediction'.

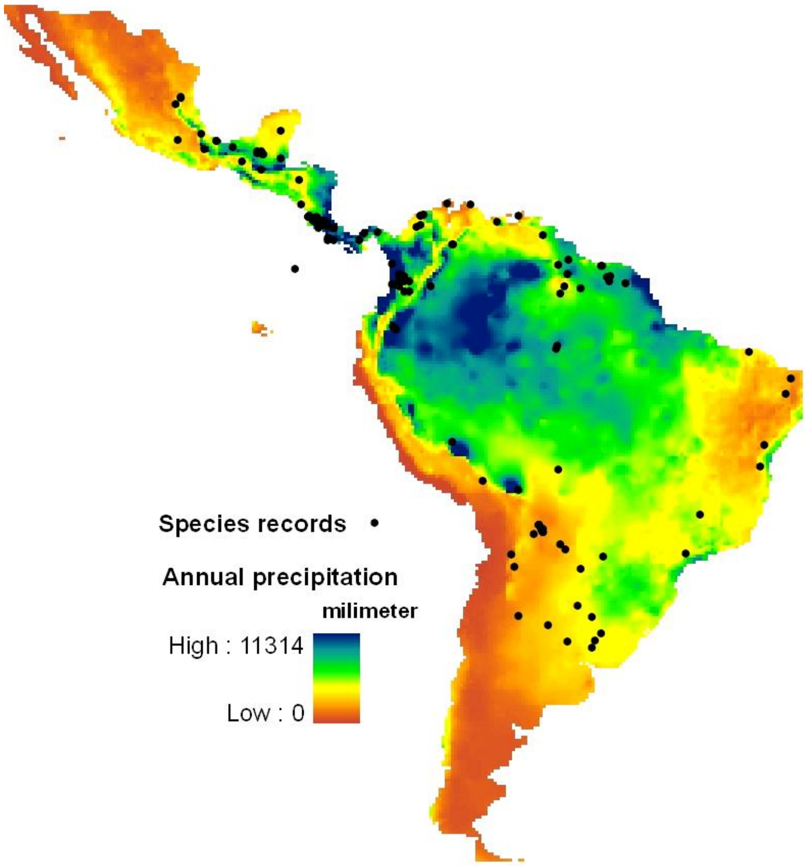

Fig. 3. Annual precipitation map of *W. auropunctata*'s native range and distribution records which were observed in non irrigated lands.

Correcting for irrigated habitats

Precipitation data in online databases represent natural water input as measured in climate stations and interpolated to other regions. Actual water input in irrigated lands is different from its representation in these databases. In order to account for this gap, precipitation in irrigated lands was modified to approximate actual water input. For our purpose, irrigated land includes irrigated agriculture as well as urban gardens. It was further assumed that urban gardens can be located anywhere within urban land, thus, every urban land was considered irrigated. In addition, the model was based only on native records from non-irrigated areas (Fig. 3). Records located in irrigated land were not used for model training in order to reduce bias caused by inaccurate water input in the species occurrence locations. For this purpose, land use in each record location was determined as natural /urban /irrigated agriculture, based on habitat description (when available), visual examination of satellite images from Google Earth program and on land covers GIS layer at a resolution of 5 arc-minutes (Velthuizen et al. 2007). The land cover map was used to classify records located in agricultural areas, while Google Earth satellite images were used to classify records located in urban habitats. The satellite images composed of a finer resolution data compared to the land cover layer. Despite this advantage, irrigated agriculture land was not classified using satellite images, since there is no confidence of irrigation status when examining these images.

Map of global irrigated lands was created using urban and irrigated agricultural lands of the FAO land covers type layer (Velthuizen et al. 2007). Israel irrigated lands map was created by the union of urban area layer acquired from the Israel Ministry of Environmental protection and annual irrigated agriculture (irrigated orchards) layer acquired from Israel's Central Bureau of Statistics. The irrigated lands are indicated more accurately in the local (Israel) layer than in the global layer.

Databases of climate include precipitation as the only representation of habitat water input. In order to represent actual water input within irrigated lands, four precipitation data layers were corrected at global and local (Israel) scales: Ann-prec, Prec-Dry, Prec-CV and P-E. To represent proximity of real water input within irrigated lands, each precipitation variable was modified based on different rationale:

- Annual precipitation (Ann-Prec): to represent actual water input in irrigated lands, annual irrigation should be added to annual precipitation. Irrigation quantities depend on crop-specific water need, which is defined as the amount of water needed to meet the water loss through evapotranspiration (Brouwer and Heibloem 1986). Based on this general principle, annual precipitation was corrected only in irrigated lands where reference evapotranspiration values were higher than annual precipitation. The difference between evapotranspiration and annual precipitation in the target irrigated pixels represents water loss through evapotranspiration and therefore could serve as a general estimator of irrigation. Adding this irrigation estimator to the natural precipitation yields evapotranspiration values. To represent water input of irrigated lands I assigned annual precipitation in these pixels to the values of evapotranspiration.
- Precipitation of the driest month (Prec-Dry): the correction method of annual precipitation could not be used to correct Prec-Dry in irrigated areas because of the lack of available online data of driest month evapotranspiration. Accordingly, I used monthly average of corrected annual precipitation minus natural precipitation values

of the driest month as an approximation for the water input in the driest month in irrigated lands.

- Precipitation coefficient of variation (Prec-CV): actual CV of water input in irrigated land over a year is smaller than the CV of natural precipitation. Exact CV of water input of irrigated lands was not available at a global or local scale. It was assumed that water input due to irrigation in the dry months is similar to water input due to precipitation in the wet months. Accordingly, the CV value of water input within irrigated land was set to zero.
- Precipitation minus evaporation (P-E): corrected values in irrigated lands were calculated using corrected annual precipitation values minus evapotranspiration values. This calculation yields zero values in the irrigated lands where reference evapotranspiration values were higher than annual precipitation

Following the correction of precipitations variables in irrigated habitats the following models were run: global projection without irrigated habitats data corrections, global projection with irrigated habitats data corrections, local projection without irrigated habitats data corrections and local projection with irrigated habitats data corrections.

Niche comparison

The range of variable values in ant records within its native region was compared to the range of values in invasive records from Israel, for all variables. For this purpose, the range of values for each variable in the native records was plotted against the respective range in records from Israel. In addition, the variable range of the whole area of Israel was plotted for each variable. The range of precipitation in Israeli records was re-examined following irrigation correction. These procedures were performed in ArcGis 9.

Model validation

The evaluation method I used for model performance is the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC). Using ROC curve is a recommended method that was used extensively in comparison studies of SDMs (Elith et al. 2006, Hernandez et al. 2006, Marmion et al. 2009). This method provides a single measure of overall accuracy that is not dependent upon a particular threshold (Fielding and Bell 1997, Pearce and Ferrier 2000, Pearson 2007). A threshold-independent method is less sensitive to errors originating from unsuitable threshold choice.

A ROC curve describes the relationship between the proportion of observed presences correctly predicted (Sensitivity) and the proportion of observed absences incorrectly predicted (1 – Specificity), both calculated across the range of possible thresholds. Sensitivity and 1 – specificity for a specific threshold can be calculated from a confusion matrix where 1 - Specificity is calculated as 1-[d/(d+b)] and sensitivity is calculated as a/(a+c) where a,b,c,d are calculated from the confusion matrix (Table 3). Placing the calculated values for many thresholds on a graph of sensitivity and 1–specificity creates the ROC curve.

To calculate the specificity component of a ROC curve, absence data is needed whereas this research is built only on presence data. Accordingly I used Phillips et al. (2006) method to create ROC curve which distinguishes presence from random, rather than presence from absence. This test is applied by using randomly selected 'pseudo-absence' records instead of observed absences. 'pseudo-absence' records are background pixels chosen uniformly at random from the study area. Following Phillips and Dudik, (2008), I used 10,000 'pseudo-absence' pixels.

AUC index was calculated for each ROC plot. AUC summarizes predictive performance across the full range of thresholds by measuring the total area defined by the ROC curve and axes (Pearce and Ferrier 2000, Pearson 2007). AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination and a score of 0.5 implies discrimination that is no better than random. Thus, an AUC value of 0.8 means a probability of 0.8 that a record selected at random from the set of presences will have a predicted value greater than a record selected at random from the set of absences (Fielding and Bell 1997) or from the set of 'pseudo-absence' records in this research. There is a simplified scale to interpret AUC values: 0.5–0.7 poor discrimination ability 0.7–0.9 reasonable discrimination ability 0.9–1 very good discrimination ability (Pearce and Ferrier 2000).

Initial model validation was executed based on the native occurrence records within non irrigated lands. These records were randomly split to calibration and test datasets. The model was built based on the calibration data and the test data was used only to evaluate model performance. Following guidelines provided by Huberty (1994) I used the common ratio of 70% of the data for calibration and 30% for test dataset. ROC curves and AUC values were calculated without and with irrigation correction for both calibration and test dataset. Calculation was performed using MAXENT software. The data division to calibration and test dataset was used only for the initial model validation and the next model runs were based on all the native occurrence records in non irrigated lands within the native range. Additional validation of the native range model was based on species records in irrigated lands within the native range. Records used for validation were different from those used for model building ('data splitting'). Prediction values of these records were compared with prediction values of 10,000 random pixels.

A set of global invasive records was used for validation of the global model (Fig 1). A set of records located in Israel was use for the validation of the local model (Fig 2). In addition, the global invasive records were divided into five geographical regions and model performance was examined for each group of records. The geographical regions are: Israel (40 records), Oceania and pacific islands (33 records), Florida (30 records), Caribbean (25 records) and West Africa (7 records). AUC values were calculated for models without irrigation correction as well as with irrigation correction. ROC and AUC calculation were produced in "ROC_AUC" program (Schroder 2004).

Effects of variables on species native distribution

Indication for the relative importance of variables in determining species native distribution was based on the iterative algorithm used to build the model. In each iteration of the training algorithm, the increase in gain was added to the contribution of the corresponding variable. In case of a negative change, a subtraction from the contribution of the corresponding variable was performed.

Another indication for the relative importance of the variables in determining species distribution was based on a comparison of gain values of multiple model-runs. Each model was composed of the original models variables leaving-out one variable (exclusion model). This comparison, called 'Jackknife test', expresses the unique information each variable provides. In addition, a comparison was made between gains retrieved from models composed of single variables. The full complement of variables was run as a baseline for the comparisons.

To examine variable influence on species native distribution, a histogram of variable values at native records was built for each variable. Since data may be influenced by non-systematic sampling these histograms provide indication rather than robust conclusion.

Map output format

Maxent software provides three types of map output formats: Raw, Cumulative and Logistic. The raw output is composed of the probability assigned to each cell. Since these probabilities must sum to 1, each probability is typically extremely small and thus raw values are not convenient to work with. The Logistic format transforms the raw data into logistic function that should represent probability of species presence conditional on environment (Phillips and Dudı´k 2008). However, preliminary results showed different probabilities in the Israeli model and in Israel extent of the global model. These results indicating that the Logisitic format could not be interpreted as probability of presence. Therefore I used the cumulative format which assigns value to a pixel from the probabilities of the pixel and all other pixels with equal or lower probabilities, multiply by 100 to give a percentage. Cumulative format is not necessarily proportional to probability of presence and pixel values indicate establishment suitability relative to other pixels. The cumulative format is calculated based on the native range extent and projected into the invasive extents (Israel and global), therefore pixel values in the projected extents do not necessarily range from 0 to 100. Logarithmic colour scale was used in the maps in order to emphasize the risk of species establishment.

Scales Comparison

The local model uses climate variables and land-use data at finer resolution than the global model. For the purpose of comparing local and global scales, the map of the local model and the map of Israel extent within the global model were compared. For comparison, the resolution of the resulting local map was degraded to match the resolution of the global map. Spearman rank correlation coefficient was used to evaluate the correlation between local and global maps. This index may be applied to non-normally distributed data. The data used for the analysis are 100 random pixels selected from Israel extent of both model maps. To present a visual examination of the similarity level between the maps, both map values were normalized to range from 0-100.

Results

Variable selection

Examination of variable values in the species records within the native range revealed four pairs of variables with correlation values higher than 0.8 (Table 4). All other pairs of variables had correlation values lower than 0.8 (Appendix 2.)

Variables	Correlation
Ann-prec : Prec-wet	0.906
Ann-prec : Prec-dry	0.821
Min-cold - Temp-range	-0.837
Min-cold : Ann-temp	0.808

Table 4. Pearson correlation coefficients for pairs of variables of the native range localities of *W. auropunctata* located in non-irrigated lands. Only pairs with significant correlation values (>0.8, P<0.001) are presented.

Following variables correlation, three variables were eliminated from the model: Annual precipitation (Ann-prec), Annual temperature (Ann-temp) and Temperature annual range (Temp-range). Variable elimination was based on differences between the native niche and the variables ranges of the whole area of Israel. It was preferred not to eliminate from the model those variables that large parts of their range in Israel are outside of the range of variable values of the native niche. These variables are Prec-wet, Min-cold (Fig. 5 c,d), Temp-range and Ann-temp. Temp-range and Ann-temp were eliminate instead of Min-cold since minimum temperatures could be important in restricting biological processes in ant species (Korzukhin et al. 2001). Most of the variable range of Ann-prec that was eliminated from the model is found within the native niche.

The remaining seven variables were used for the potential distribution model: Maximum temperature of warmest month (Max-warm), Minimum temperature of coldest month (Min-cold), Precipitation of driest month (Prec-dry), precipitation of wettest month (Prec-wet), Precipitation Seasonality (Prec-CV), Annual reference evaporation rate (Evap) and Annual precipitation minus Annual evaporation rate (P-E). The same set of variables was used for the global model in order to enable a comparison between a local model of Israel and a global scale model with the same variables.

Effects of variables on species native distribution

Niche comparison and variables distribution of the native records

Histograms of model variables of the native records are presented in Figures 4 and 5. Data in the histograms may be influenced by non-systematic sampling. Evap histogram shows increase in frequency within the range of 870-1250 mm/year and gradual decrease from 1500 mm/year to 2000 mm/year. The range of records from Israel is within the native niche, but ca. half of the range of the whole Israel extent is larger than the maximum value of the native niche (Fig 4A). The histogram of Prec-CV indicates a suitable range for establishment between CV values of 5-120. Records from Israel as well as the whole Israel range are located within the upper edge of this range (Fig 4B). Records from Israel with irrigation correction have a Prec-CV value of zero, below the minimum of the native niche. The histogram of P-E shows general increase in frequency from -1400 mm/year to 400 mm/year and general decrease from 400 mm/year to 6000 mm/year. Records from Israel are within the lower edge of the native niche, but large part of the whole Israel range is below the minimum value of the native niche (Fig 4C). Records from Israel with irrigation correction have a P-E value of zero.

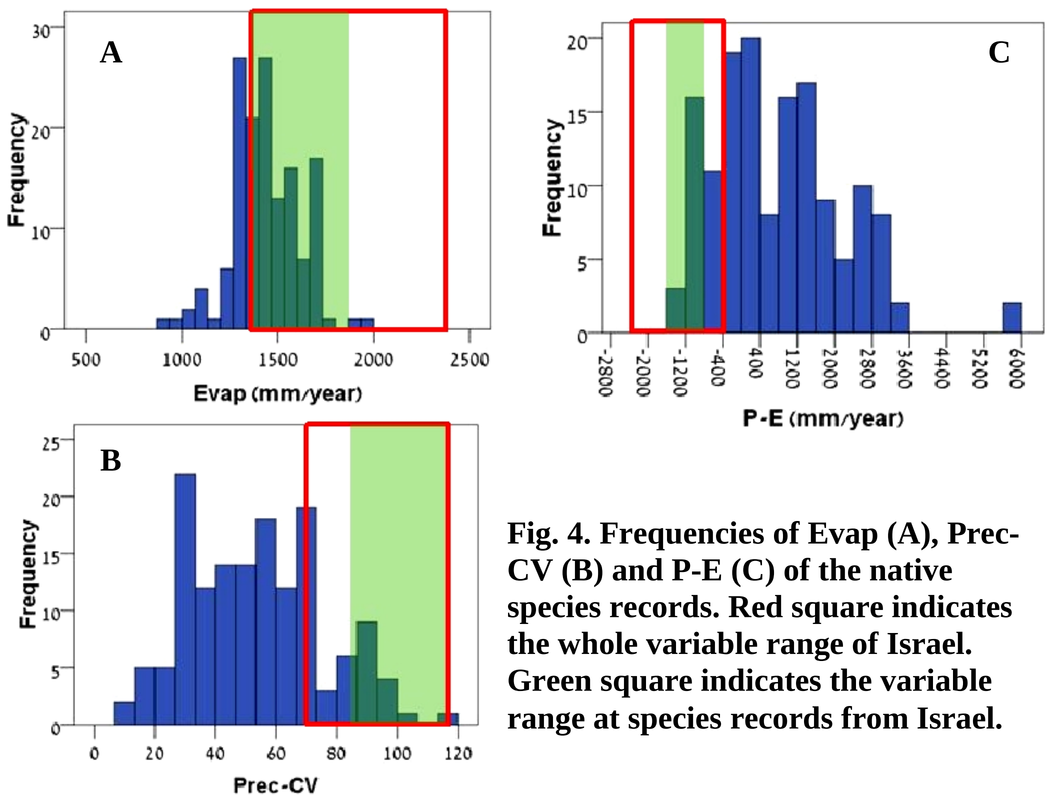

Fig. 4. Frequencies of Evap (A), Prec-CV (B) and P-E (C) of the native species records. Red square indicates the whole variable range of Israel. Green square indicates the variable range at species records from Israel.

The histogram of Max-temp indicates a suitable range for establishment between 21°c-37°c. The most frequent temperatures with species records are 30°c-34°c. The range of records from Israel is within the upper edge of the native niche, but the maximum value of the whole Israel extent is larger than the maximum value of the native niche (Fig 5A). The histogram of Min-temp shows a general increase in records frequency from the minimum value of 2°c-23°c. The range of records from Israel is within the lower edge of the native niche where records are less frequent. Large part of the whole range of Israel is below the minimum value of the native niche (Fig 5B). The Prec-wet histogram shows that most of the records are located in the range of 50-600 mm/month and few records located in the range of 600-900 mm/month. The minimum values of the whole Israel range and the records from Israel are below the minimum value of the native niche (Fig 5C). Prec-dry histogram shows frequency decrease from '0' mm/month to 375 mm/month. In Israel all values of Prec-dry are '0' mm/month (Fig 5D). With irrigation correction, records from Israel are within the native niche range and ranged from 45 mm/month to 156 mm/month.

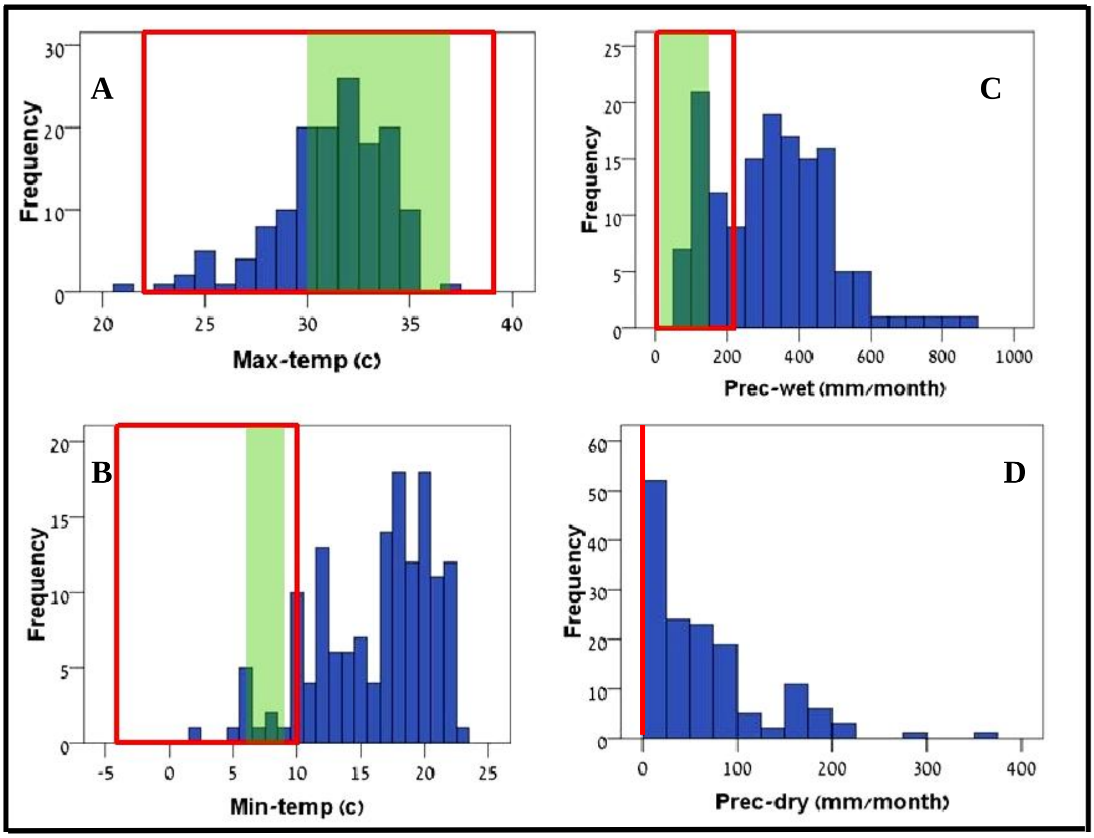

Fig. 5. Frequencies of Max-temp (A), Min-temp (B) Prec-wet (C) and Prec-dry (D) of the native species records. Red square indicates the whole variable range of Israel. Green square indicates the variable range at species records from Israel.

Importance of variables in determining species native distribution

The relative importance of the variables in determining the native distribution was assessed using three methods: iterative algorithm of the MAXENT model (model building), gain values derived from multiple model-runs (exclusion models) and single variable models. 'Model building' and single variable models show similar hierarchy of variable importance; a hierarchy which differ from the one revealed by the ‘exclusion models’. The most important variable based on model building and single variable models is Prec-wet. The least important is Max-warm. The most important variable based on exclusion models is Evap and the least important is Prec-wet. All procedures found Min-cold and P-E as second or third most importance variables (Fig. 6).

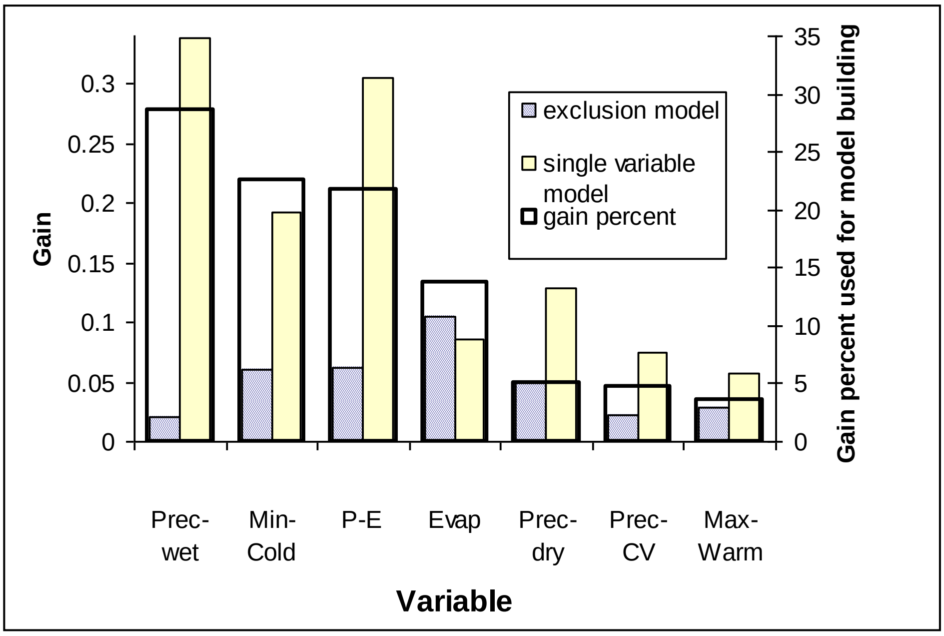

Fig. 6. Contributions of the variables based on ‘model building’ (black columns), exclusion models (blue striped columns) and single variable models (yellow columns).

Modeling results

Initial model was run based on calibration and test data of records in non-irrigated lands within the native range. AUC values were calculated without and with irrigation correction. AUC value of the calibration data was higher for the irrigation corrected model than for the non corrected model. AUC of the test data was the same for the corrected and uncorrected models (Table 5). The data division to calibration and test dataset was used only for the initial model validation and the next models were based on all the native occurrence records located in non-irrigated lands within the native range. Occurrence records within the native range which were located in irrigated lands were not used to build the model and were better predicted in the corrected model than in the non-corrected model (Table 5).

Global model

The global model map of the potential distribution of *W. auropunctata* with irrigation correction shows high establishment potential in the tropic and sub-tropic regions of America, Africa and Asia. Low establishment potential was found in the arid and temperate climate zones of the globe. Regions with no prediction are located at the northern regions of the north hemisphere, Sahara Desert, Arabian Desert and desert regions in Australia (Fig. 7). These regions are characterized by climate variables that are out of the training range.

At a global scale, very small visual differences were found between the model without and with irrigation correction. However, clear differences were found between two regions of the global scale models: north India, which had no records of *W. auropunctata* (Fig. 9) and Israel, which had species records (Fig. 10). Other regions with invasive records showed visual similarity between the non-corrected and corrected model maps, but the corrected global model predicted species records better than the non-corrected model (Table 5 and Fig. 8).

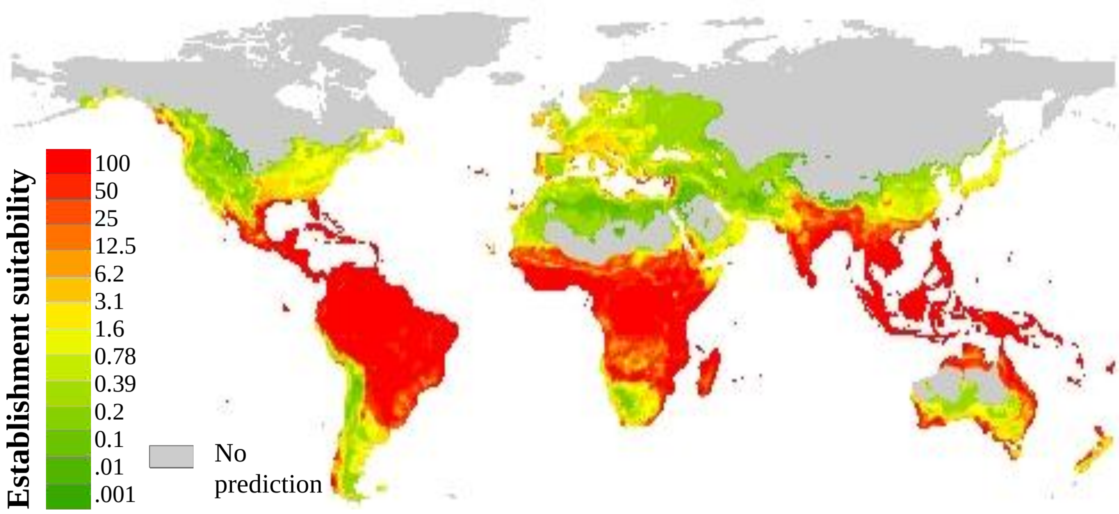

Fig. 7. Global model map with irrigation correction. Warm colours indicate high establishment suitability values, cold colours indicate low values. Gray indicates areas with no prediction (variables are out of the training range). Colour scale is logarithmic.

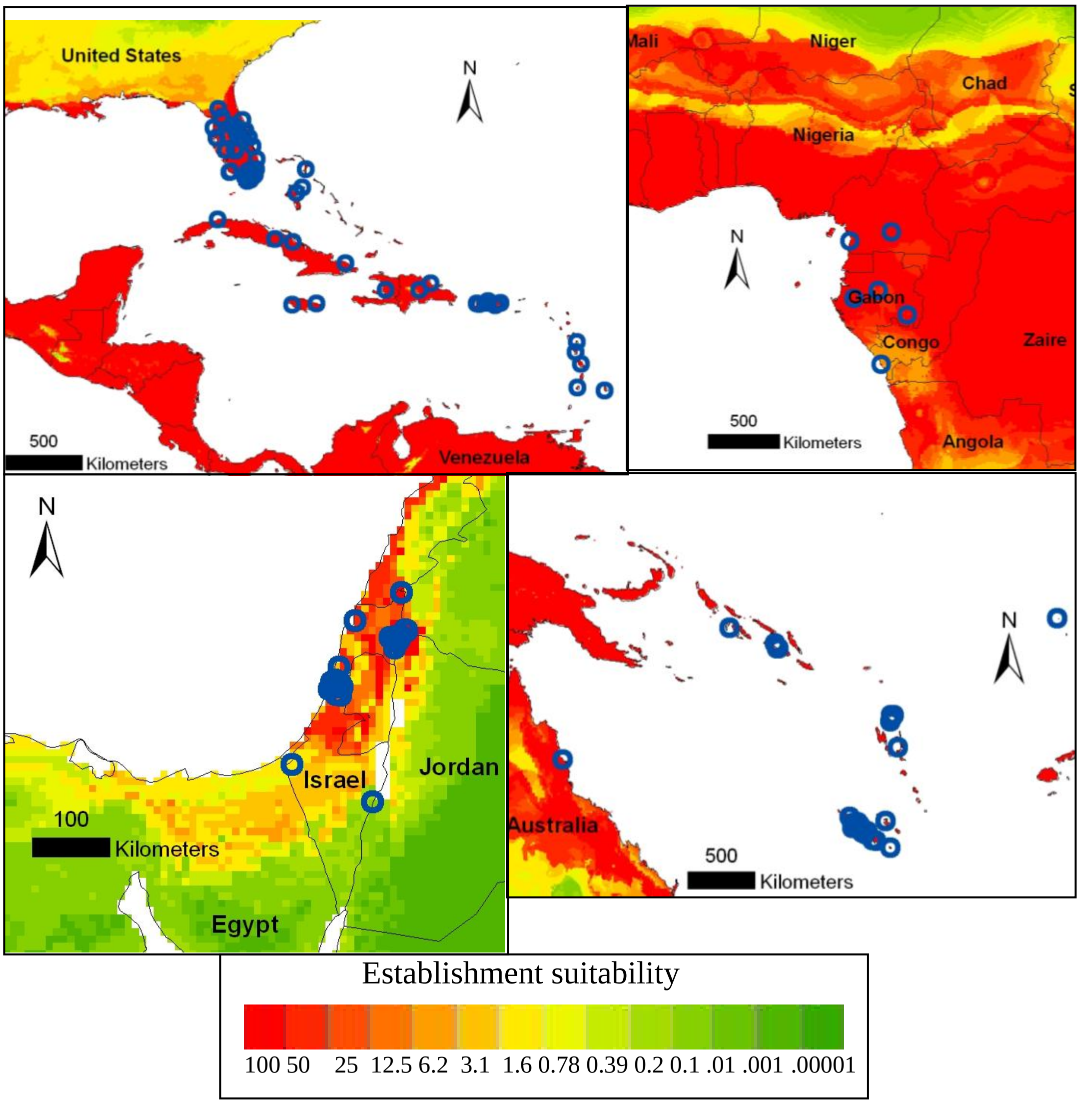

Fig. 8. Global model with land use correction. Maps of regions with known *W. auropunctata* records. Blue circles indicate the locations of species records.

		Without correction	With correction	Change	N
Native	Calibration data	0.871	0.883	+0.012	94
	Test data	0.801	0.801	0	40
	Irrigated	0.674	0.730	+0.056	49
Global	Oceania and pacific	0.542	0.556	+0.014	33
	West Africa	0.639	0.690	+0.051	7
	Caribbean	0.748	0.810	+0.062	25
	Florida	0.717	0.852	+0.135	30
	Israel	0.628	0.83	+0.202	40
	All	0.875	0.899	+0.024	135
Local	**Israel**	0.718	0.831	+0.113	40

Table 5. AUC values of native, global and local models without irrigation correction and with irrigation correction.

Examination of north India region of the global model without and with irrigation correction shows that the region south to Nepal border (the Gangetic Plain of Uttar Paradesh state) have higher species establishment risk with irrigated lands correction than without it. Sporadic patches of higher establishment risk after irrigated land correction were found in central India (Fig 9). No occurrence records of *W. auropunctata* are known in India to this date.

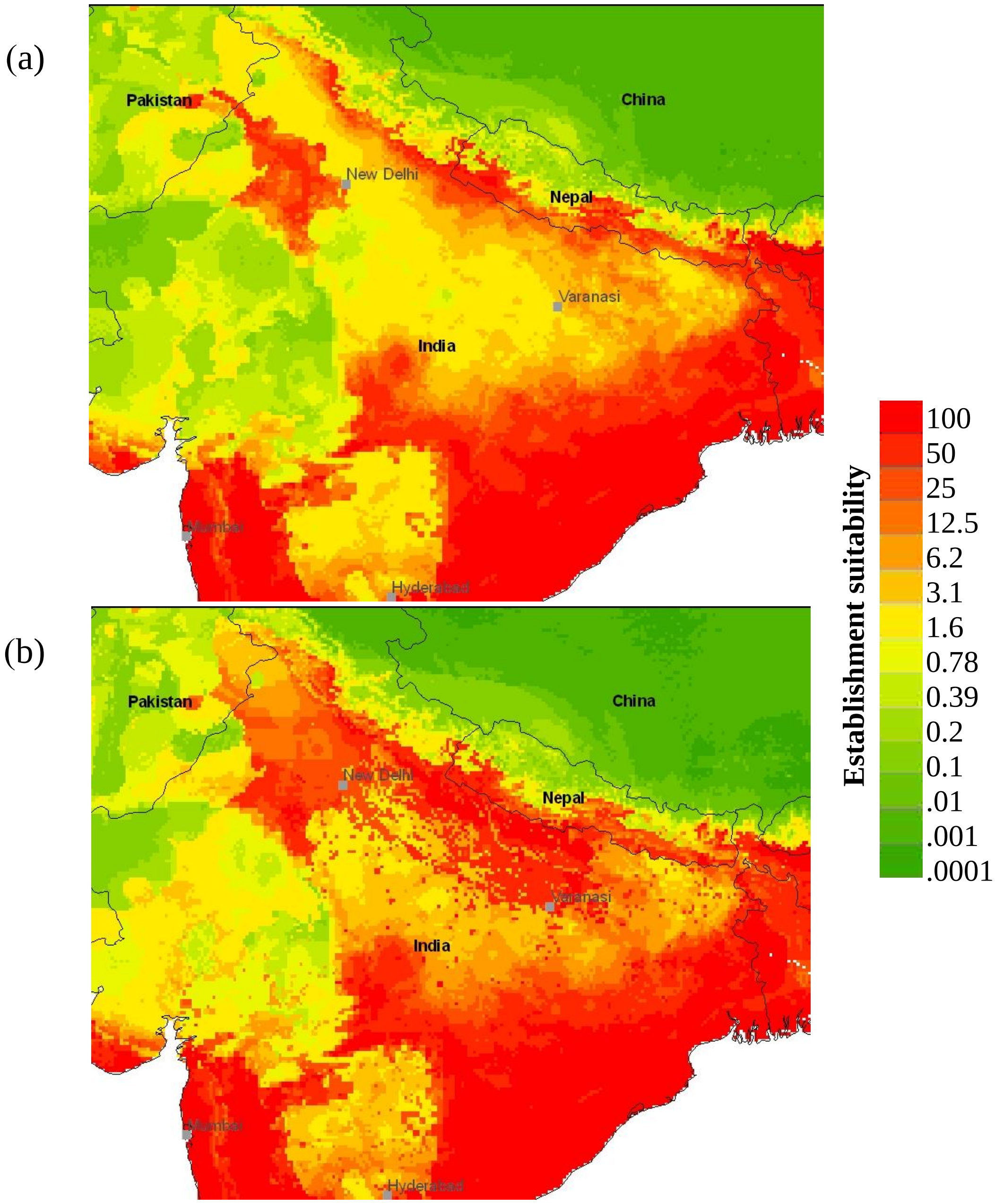

Fig. 9. Map of north India taken from the global model without irrigation correction (a) and with irrigation correction (b). Colour scale is logarithmic.

Local model

Clear differences were found between the local models for Israel without and with irrigation correction. These differences may be noticed in the two high resolution maps of this region, each representing a model (Fig. 10). The main regions with high establishment potential (red colors) were the same in both models. However, the model with irrigation correction showed additional regions characterized by high establishment potential. These regions were mainly urban and agricultural irrigated lands located north to Kiryat-gat latitude. In the non-corrected model, species records located north to this latitude were predicted as low establishment potential (Fig. 11a) while the corrected model predicted these records as high establishment potential (Fig. 11b).

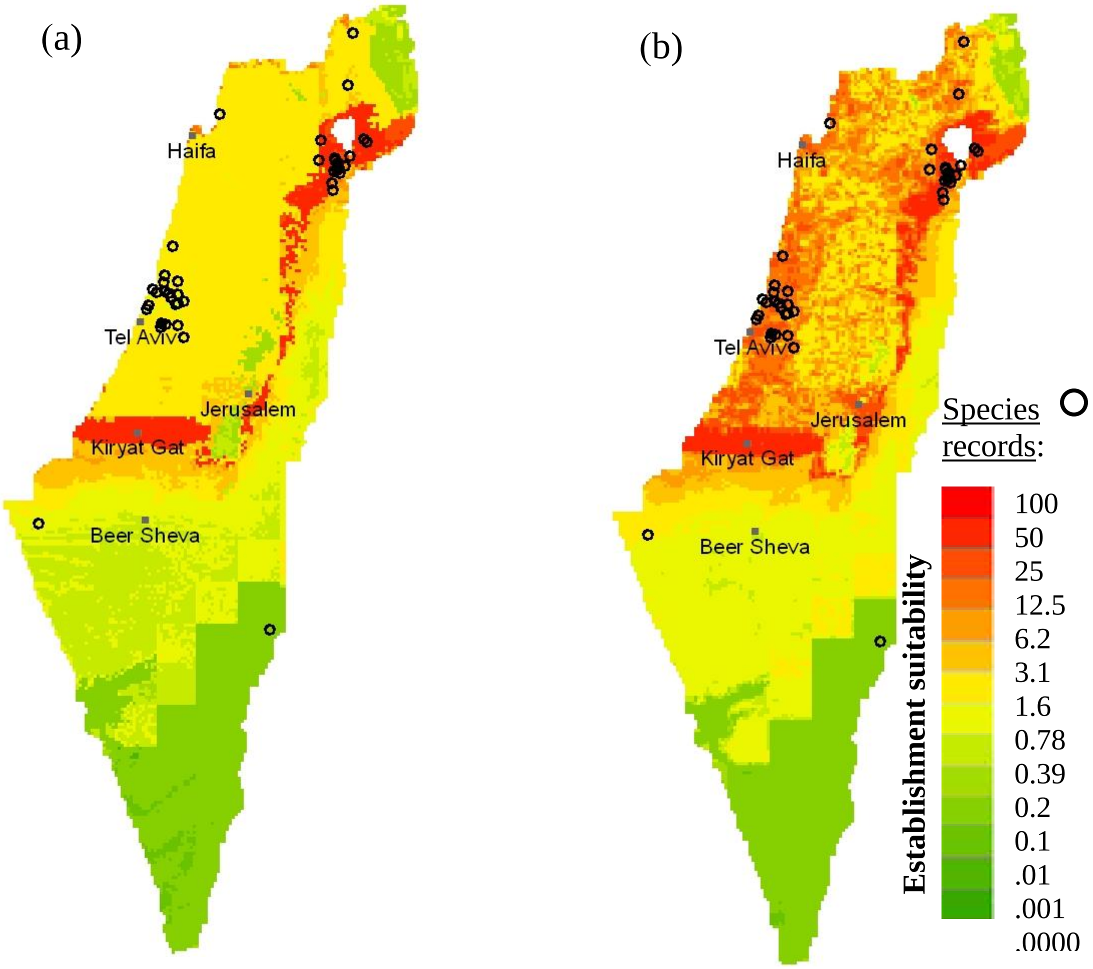

Fig. 10. Local model without irrigation correction (a) and with irrigation correction (b). Colour scale is logarithmic.

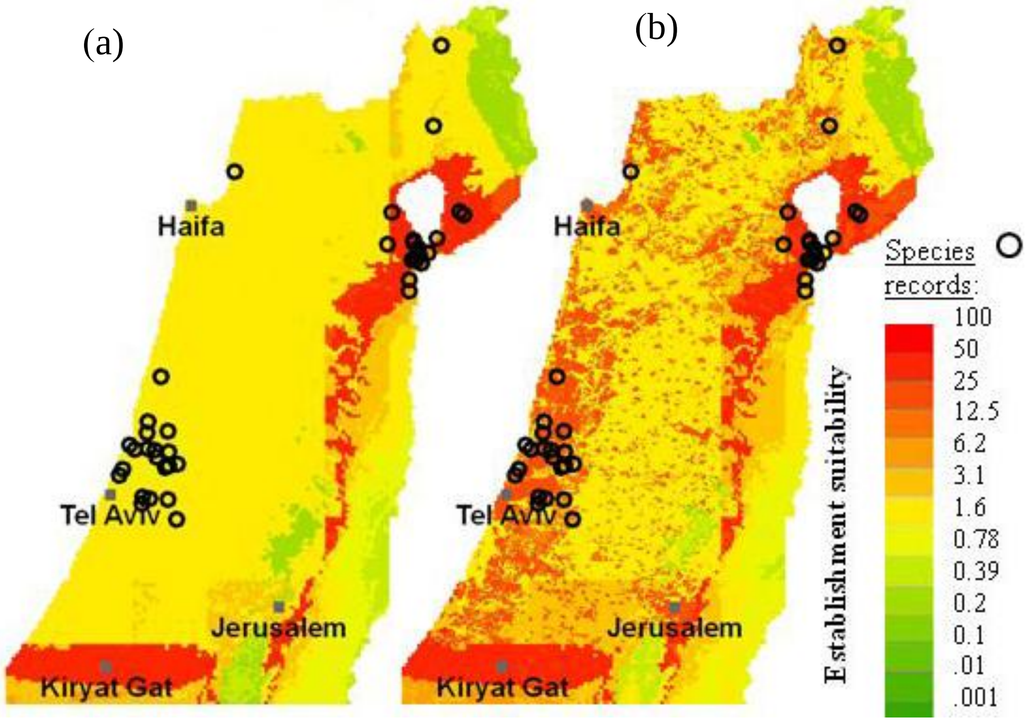

Fig. 11. The north part of the local model without irrigation correction (a) and with irrigation correction (b). Colour scale is logarithmic.

ROC curves of the local model with and without irrigation correction (Fig 12) indicates better performance of the corrected model of Israel compared to the non-corrected model of this extent (Table 5).

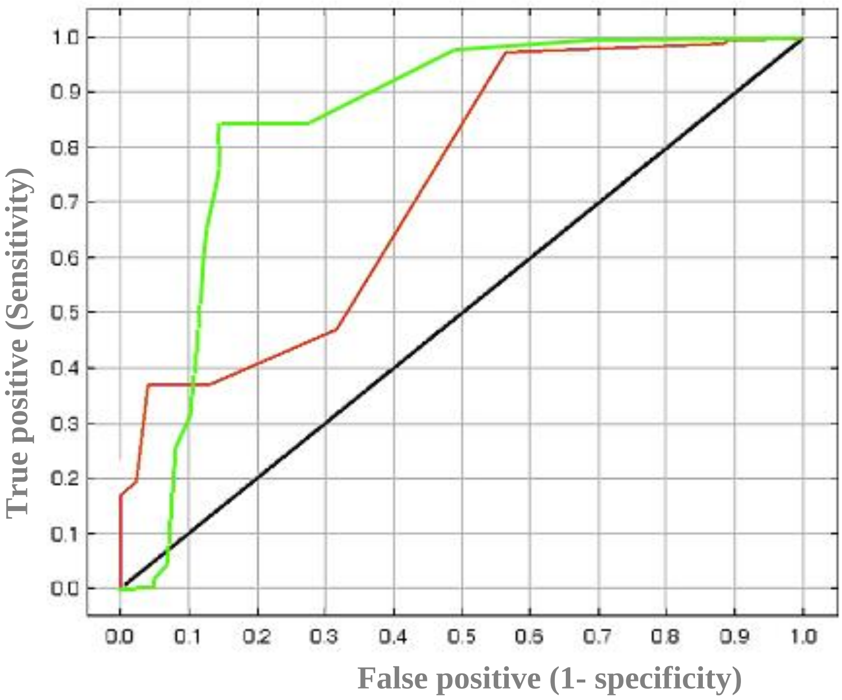

Fig. 12. ROC curves of the local model records. Red line: non corrected model, Green: corrected model. Black line indicates random prediction.

Scale comparison

The global, coarse resolution model was compared with the local, fine resolution model for the area of Israel. The spatial resolution of the resulting local map was degraded to match the resolution of the global map. The resulting maps had similar trends (Fig. 13). Spearman rank correlation coefficient between global and local models was significant both without irrigation correction (r=0.834, p<0.001) and with irrigation corrected (r=0.821, P<0.001).

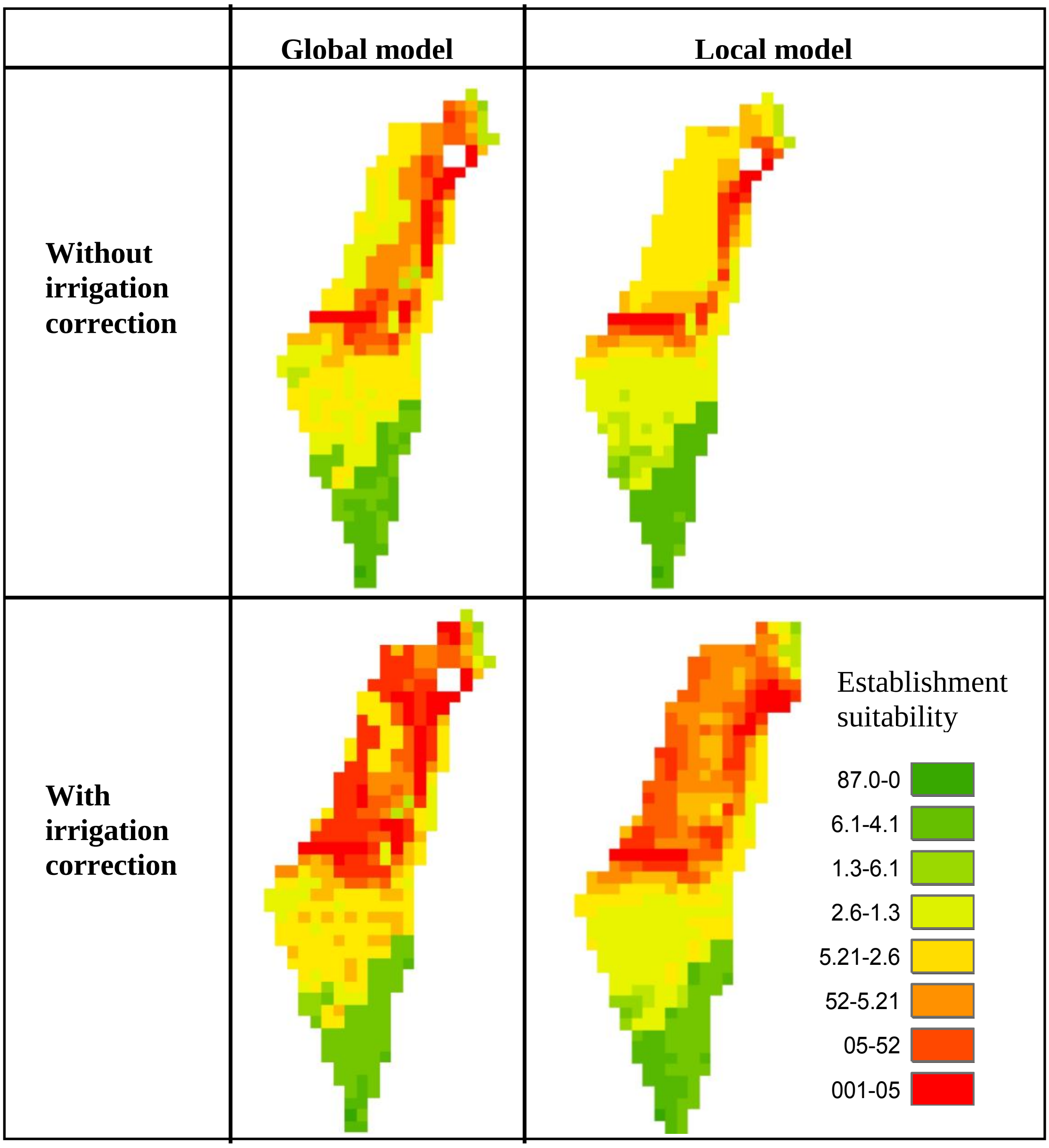

Fig. 13. Resulting maps of Israel extent taken from the global model without irrigation correction and with correction and local model results (degraded resolution) without irrigation correction and with irrigation correction.

Discussion and conclusions

Variable selection

To model the potential distribution of *W. auropunctata* I chose a set of seven climatic variables describing temperature, precipitation and evaporation. Variables describing precipitation and temperature were chosen since their combination effectively correlates with physiological tolerance (Tsoar et al. 2007). Evaporation-related variables were added since precipitation minus evaporation approximates soil moisture (Dirmeyer et al. 2009), which could affect *W. auropunctata* since its main habitat is in the top-soil. Other soil-related variables such as top-soil temperature and true soil moisture, sampled at different seasons and times of the day could be important factors affecting *W. auropunctata* distribution. Unfortunately, these data were not available at large spatial scales. Other variables such as geology, soil type, vegetation cover and vegetation type are not considered to be important variables affecting *W. auropunctata* distribution, since this generalist species is tolerant of wide ranges in these factors (Ulloa-Chacon and Cherix 1990).

The use of seven environmental variables in this study is within the range of the number of variables found to be used in SDMs studies found in the scientific literature (between 3 (Tsoar et al. 2007, Kadoya et al. 2009) and 39 (Kumar et al. 2009)). Common methods for model selection which determine the number of variables, such as AIC (Akaike Information Criterion) that function well in many SDM studies are not appropriate for this research due to a mismatch in selection goals. AIC could be effective for predicting *W. auropunctata* distribution in the native range, but the main goal of this study was to predict the species distribution in a non-native ranges. Methods which only take into account the conditions within the native habitat are limited in their utility to deal with model projection. This limitation is due to a possible difference in the hierarchy of variable importance between the native range and the invaded range. For example, a marginally important variable within the native range may restrict the distribution of a species within the invaded range. This study found Max-warm as the least important predictor within the native range (Fig. 6). However, in certain regions of Israel, high temperatures are higher than the maximum temperature of the native range (Fig. 5). High temperatures in these regions may limit species distribution. Accordingly, Max-warm should be included in the local model despite its restricted influence on the native range.

Variable selection was mainly deliberated according to the Israel model. The same variables were used for the global and local (Israel) models in order to perform scale comparison analysis (see scale comparison in the discussion).

Niche comparison

Plotting the variable range of native records, invasive records and the potential niche of the site of invasion provides insights into the species predicted distribution and invasion traits. In this study most of the records from Israel were restricted to the edge of the native niche range (Figs. 4-5). Plotting the potential niche of the whole Israel area shows that the variable range of records in Israel composes only a small part of the native niches available within Israel. These results indicate that the species is utilizing a small range of its potential niche in Israel. Accordingly, *W. auropunctata* is expected to further spread and establish new habitats with environmental conditions in Israel overlapping those of the native niche. This analysis does not take into account the spatial aspects which are represented in the potential distribution map. This map represents the geographic limitations for species distribution by combination of the limitation of all the environmental variables used to build the model.

Our findings, that Israeli occurrence records overlap with only a small part of the native niche plot, support the notion that invasive records should not be used to build SDMs. Using the Israeli records to build the model would not match a state of equilibrium between the environment and the observed species presence data, a main assumption of SDMs (Guisan and Zimmermann 2000, Jeschke and Strayer 2008).

Plotting the variable range of invasive records relative to the native niche is an effective method to reveal the variables that its range of invasive records deviant from the native niche. In this study, Prec-wet values of records from Israel shows lower minimum than the minimum Prec-wet of the native niche (Fig. 5). This deviant could be an indication of irrigation in Israel during the wettest month and accordingly, irrigation correction may be needed for this variable. In addition, other possible reasons for invasive records located out of the native niche may be: 1. the native area does not represent the whole potential species distribution due to geographical limitations (e.g. the native area is a small island) or biological limitations (e.g. the native distribution is limited by biotic interactions that are not exist in the invaded site) 2. niche shift in the invaded range due to evolutionary processes 3. the native niche records do not completely represent the real occupied niche due to biased sampling 4. the variables used to build the model do not properly represent the whole species niche. The first reason of geographic limitation is not relevant to the case of *W. auropunctata* since its native habitat is wide and represents wide range of climatic variables. However, 'biotic limitations in the native range' may be a possible explanation for invasive records located out of the native niche, since no biotic limitations has been described in the invasive range. Niche shift could also provide an explanation for invasive records located out of the native niche. Although *W. auropunctata* has been present in Israel for only a short period in evolutionary perspective (~15 years), the 'founder effect' may cause a genetic change and niche shift in the species population in Israel. The 'founder effect' occurs when a small group splinters-off from the original population and form a new population with different genetic composition. A single introduction of one queen and one male genotypes to Israel (Vonshak et al. 2009) is further supporting this possible explanation. Incomplete representation of the niche may also explain that invasive records of *W. auropunctata* are located out of its native niche. This may be a possible explanation as the records in the native range were not collected in planned surveys.

Variables that do not properly represent the whole species niche may reduce model performance and constitute a possible explanation for invasive records located out of the native niche. A model without irrigation correction may not accurately represent climate conditions and thus may cause deviant between invasive range and native niche. The irrigation correction in this study solves the deviant mentioned above and is discussed further in this study (see irrigation correction section).

Effects of variables on species native distribution

This study examined the influence of climate variables on species distribution only within the native range. As opposed to the native range which assumed to represent equilibrium between the environment and the observed species records, this state of equilibrium does not exist in the invaded areas. The presence of the species in the invaded areas is likely the result of stochastic, unpredictable human activities such as transportation and trade.

The relative influence of variables on the species native distribution is determined by the iterative algorithm used by MAXENT ('Model building'). Gain values of multiple model-run were used as another indication for the relative importance of the variables (‘exclusion models’ and ‘single variables models’). Hierarchy of variables importance revealed by 'Model building' and ‘single variable models’ were similar, while ‘exclusion models’ showed different hierarchy.

The methods for ranking variables importance are influenced by variables correlations. Accordingly, the revealed variables hierarchies of the three methods should be interpreted with caution. Correlations between variables could have different affects on species distribution. For example, negative correlation between precipitation and temperature is expected to restrict species more than positive correlation between these variables. On the other hand, the correlation between temperature and altitude expected to have no affect on species distribution.

Two issues arise when trying to determine the influence of variable correlations on species distribution in this study: correlations between the variables form a complex correlation matrix (Appendix 2) and the influence of variable correlations on *W. auropunctata* distribution is not yet known. Following the complex and uncertain influence of variable correlation on species distribution, the choice for ranking methods was based on biological principles. These methods are ‘model building’ and ‘single variable models’.

The most important variable in determining *W. auropunctata* native distribution is precipitation of the wettest month (Fig. 6). This variable indicates water input in the wet season, an important factor in non-irrigated sites. This factor affects the top soil moisture, which is the main habitat of *W. auropunctata*. The second and the third most important variables are minimum temperature of the coldest month (Min-temp) and precipitation minus evaporation (P-E). Min-temp is an important factor restricting biological processes in ant species (Korzukhin et al. 2001), and may be relevant especially for tropical ants such as *W. auropunctata*. P-E represents the moisture of the top soil (Dirmeyer et al. 2009) which is the main habitat of *W. auropunctata*.

To examine variable influence on species distribution, a histogram of variable values of native records was built for each variable (Fig 4-5). These histograms provide indication rather than robust conclusion about variable influence on species distribution, since data may be influenced by non-systematic sampling. The histograms show that the species is common in sites where there is no precipitation in the driest month. This finding provides evidence for its ability to survive a dry month. On the other hand, there are no records from sites with less than 77 mm precipitation during the wettest month. This finding indicates that the species requires high precipitation during the wet season for surviving the dry season. The maximum value of Max-temp with a species record is 37°c and the minimum value of Min-temp with a species record is 2°c. These values are indications for the species temperature tolerance. Lab experiments are required to determine this temperature tolerance more accurately. The histogram of precipitation minus evaporation shows records sites with negative values, an indication for sites with water run-off or irrigated sites that was not distinguished by this study (Fig 4-5).

Prediction maps of potential distribution

The global prediction map was found to overlap closely with a map of global climate regions (Fig 14). Areas of high species establishment potential overlapped with equatorial climate zone and with parts of the warm temperate region with hot or warm summers and high humidity. These predictions match the model inputs, which were mainly within tropical locations and partly within warm humid locations. Regions with no prediction are located at polar and desert climate zones. Climate variables at these regions are out of the model training range, i.e. out of the variables range of South and Central America. There are number of possible approaches to examine species potential establishment in regions with variables which are out of the model training range. One approach is to treat variables outside the training range as if they were at the edge of their training range (‘clamping’). Another approach is to zero out predictions of these regions. In this research I chose the most conservative approach of assigning no prediction value to regions characterized by variables which are out of the model training range.

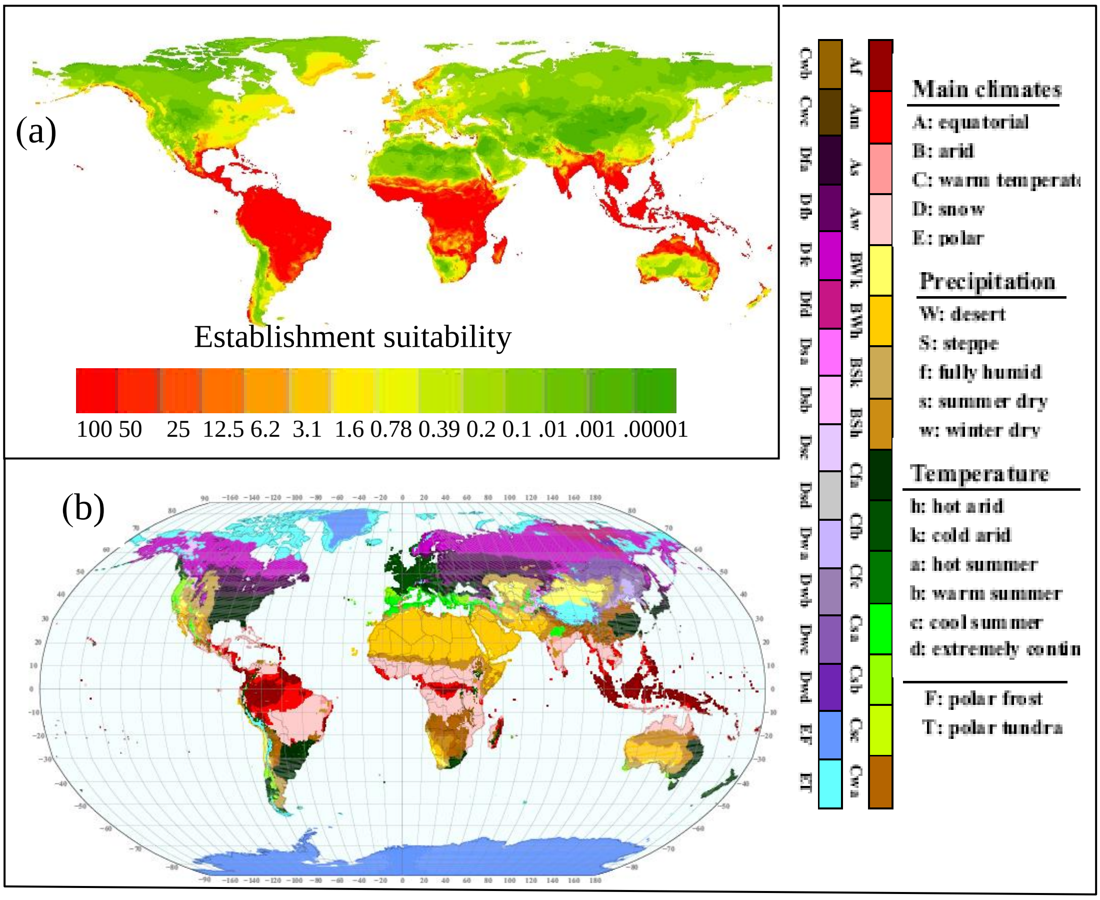

Fig. 14. Comparison of spatial patterns of the *W. auropunctata* global model map (a) and the world map of Köppen-Geiger climate classification updated by Kottek et al. (2006) (b).

Like the global model, the prediction map of the local model was found to overlap closely with a map of Israel's climate regions (Fig 15). Regions of high establishment potential approximately overlap the semi-arid climate zone with a small shift toward the Mediterranean climate. Large parts of the Mediterranean climate zone show intermediate establishment potential and most of the arid climate zone show low potential for establishment. These spatial patterns of prediction are due to the climatic characteristic of the climatic zones. The arid zone in Israel is primarily characterized by relatively high Evap and Max-temp values and by low Prec-wet and P-E values. Compared to the arid zone, most of the Mediterranean climate zone is characterized by lower Evap values, higher Prec-wet and higher P-E values. Within the Mediterranean zone the coastal plain is characterized by higher Prec-CV values. Within Mediterranean zone in Israel, high mountains have different climate characteristics (Csb in Fig. 15). These mountain areas are characterized by lower temperatures that presumably lead to lower prediction of *W. auropunctata* establishment in these areas. High prediction establishment values correspond to the narrow semi-arid climatic zone between the arid and the Mediterranean zones (Bs in Fig. 15). The high prediction for establishment in this zone indicates that the combination of climatic variables is the most suitable for *W. auropunctata*, relative to other climatic zones in Israel. Presumably, the main limiting factors in the arid zone are high level of evaporation, low water inputs and high maximum temperatures. In the Mediterranean zone the main limiting factors may be low water inputs and low temperatures in the mountain regions.

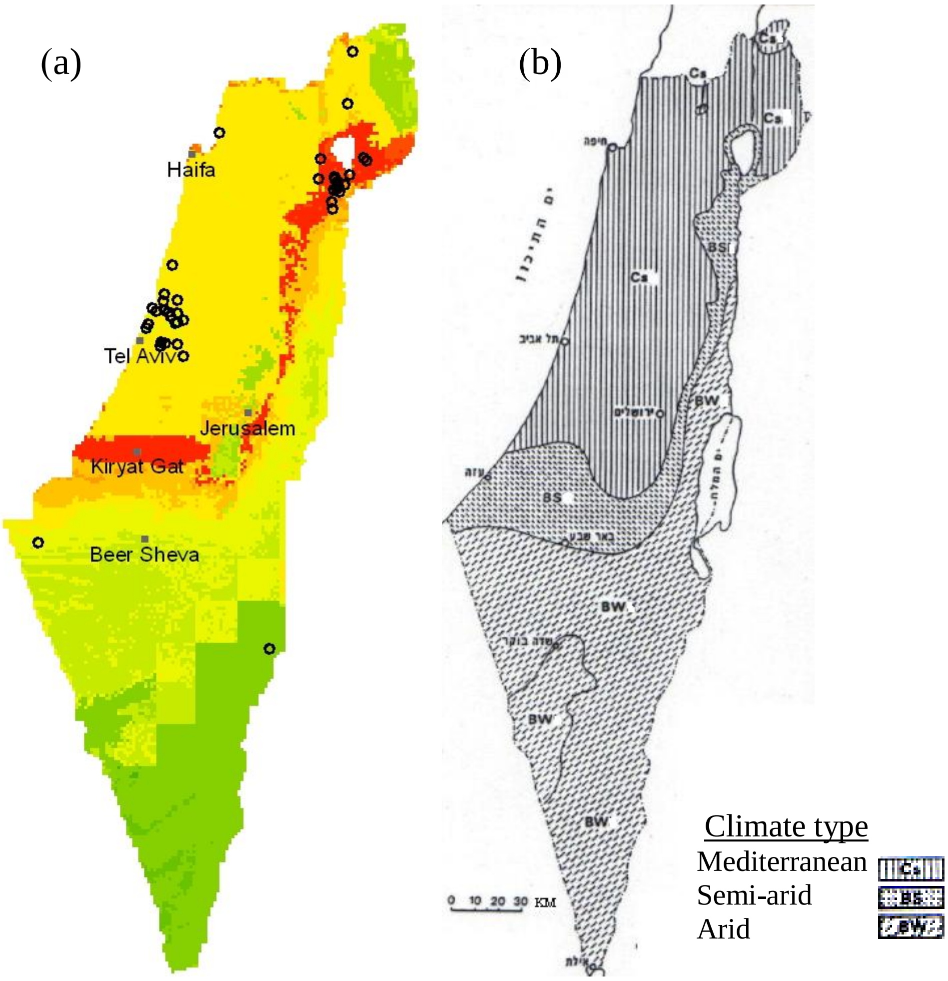

Fig. 15. Comparison of spatial patterns of the *W. auropunctata* local model map without irrigation correction (a) and Israel Map of Köppen climate classification with correction (modified after Potchter & Saaroni 1998) (b).

Irrigation correction

Urban and agricultural land uses affect the local microclimate conditions. The major effect is due to irrigation which boosts water availability within the habitat. Irrigation has been described as an important factor which alters the distribution of species that can establish anthropogenic land uses (Mendelssohn et al. 1971, Federman and Werner 2007, Menke et al. 2007). Surprisingly, SDM-based studies appear to ignore irrigation variables in their analysis, in contrast to the prominent use of climate variables in SDMs. This study incorporated irrigation data as a correction of precipitation data, and found a subsequent improvement in the predictive capacity of the models. The predictive capacity of the native range was tested using three different sets of occurrence records within the native range: calibration records, test data records and records in irrigated lands. The predictive capacity of the global projection was tested using the set of all invasive records. Five different sets of invasive records from different regions were used as additional validation for the global model. The predictive capacity of the local projection was tested using invasive records from Israel. Performance of models with irrigation corrections was better than the corresponding models without correction for nine out of ten test data sets. The only exception was the test data set within the native range that did not show change in prediction capacity following irrigation correction (Table 5). These results emphasize the importance of irrigation correction to the distribution model of *W. auropunctata* for the local and global scales. Improvement in the global model prediction due to irrigation correction occurred in five independent records sets from different geographical regions. These results demonstrate the importance of irrigation correction for various geographical and climatic regions.

Irrigation correction was based on estimation of irrigation characterization from non-equatorial regions. Accordingly, prediction improvement was higher for non-equatorial regions (Israel and Florida) than for equatorial regions (Oceania and pacific, West Africa and Caribbean) (Table 5.). In order to improve the prediction capacity in the equatorial region, irrigation characteristics of this region should be included in the irrigation correction. Irrigation correction in the local model was more effective for the Mediterranean climate zone than for the desert climate zone. The improvement in model performance in the Mediterranean climate zone is presumably due to the ability of irrigation in this region to simulate a subtropical or tropical climate conditions (Bytinski-Salz 1966).

Accounting for irrigation inputs is expected to improve SDMs of a variety of species that inhabit areas of anthropogenic land use. These species include invertebrates, reptiles, amphibians, birds, small mammals and plants.

The irrigation correction was effective despite its reliance on rough estimates of irrigation inputs. Volumetric irrigation data are difficult to obtain in a spatial format, specifically at large scales, since irrigation intensity varies over time and between various crops and land uses. Because of this limitation, water input in irrigated lands was estimated using general logical principals**.** An examination of the correction-related shift in the variable range of the invasive occurrence records relative to the native records indicated that the estimate was not accurate in all cases. For example, correcting the coefficient of variation of monthly precipitation (Prec-CV) to a value of zero in irrigated lands shifted those records from the upper limit of the native niche to below the minimum record of Prec-CV of the native niche. Prec-CV is smaller in irrigated than in non-irrigated areas, but the difference is likely to vary between regions and between different crops. Since empirical data were not available, I assumed that water input due to precipitation in the wet season is similar to the water input due to irrigation in the dry season and accordingly I changed the Prec-CV in irrigated areas to zero. This assumption of equal water input in the dry and wet seasons is probably inaccurate, and I presume that actual values of Prec-CV are larger than zero. However, any other CV value that would be assigned to irrigated areas without using empirical data, would not be more reliable. I recommend that future studies, especially those dealing with small spatial scales, will use volumetric empirical data on monthly variation of water input. Except for Prec-CV, correction of other variables did not result in unreasonable shifts with respect to the native niche.

Another aspect of irrigation correction in SDMs is native records located in irrigated lands. Using these records for model building could bias the model results following inaccurate representation of microclimate conditions. Despite this potential bias, no studies that omit species records from irrigated agriculture and urban land-use were found in the scientific literature. An exceptional study partly considered this limitation by omitting *W. auropunctata* records from greenhouses and heated buildings, but keeping records from irrigated lands in the analysis (Harris et al. 2005). One novelty of the present study is that the models are based on records from only non-irrigated lands. Habitat descriptions from the species data sets, land use layers and visual examination of satellite images were used to determine the irrigation status in species occurrence locations. These methods are simple to use and recommended for other SDMs studies.

An alternative possibility to build a model without omitting native records is to build the model using precipitation-corrected versions of these records. This approach should better describe the species distribution, assuming that accurate irrigation data is available. However, if accurate irrigation data is not available, using inaccurate records to build the model could drastically bias model results. Unlike the risk inherent in the correction of irrigated lands, where any potential bias affects data of this land use alone, using records from irrigated lands as input for the model could bias the entire model prediction. In the present study, records from irrigated lands were not used to build the model, since no irrigation data was available for the native range of *W. auropunctata*.

An indication for the need of irrigation correction in the native range is the relatively low predictive capacity that was found when testing the model using records from irrigated lands of the native range (Table 5). This low predictive capacity was found although the native records in irrigated lands are geographically close to the records used to build the model.

To summarize, irrigation was found to control *W. auropunctata* distribution in many areas, and should be considered when building SDMs for this and for other species.

Model Validation

This study used the area under the curve (AUC) of the Receiver Operating Characteristic (ROC) based on independent validation records sets. The AUC of the ROC-curve is a recommended method for SDMs validation (Elith et al. 2006, Hernandez et al. 2006, Marmion et al. 2009), since it provides a single measure of model performance that is not dependent upon a particular threshold (Fielding and Bell 1997, Pearce and Ferrier 2000, Pearson 2007) and thus is less sensitive to errors in threshold choice. Using independent validation sets is also a preferred approach (Fielding and Bell 1997, Elith et al. 2006, Jeschke and Strayer 2008) since other common methods either reuse the same data for building and testing the model ("re-substitution") or employ artificial data splitting. The strength of this study, similar to other SDMs studies of invasive species, is its use of independent datasets from remote locations for model evaluation.

An important aspect of model validation is that absence data can not be used for model validation of invasion sites. Absence data is unsuitable for model validation since absence from a site does not reflect unsuitable conditions for an invasive species, and may represent a potential future invasion site. Thus, robust validation is only possible in regions with species occurrence records, although this validation is used for the entire model extent. Despite these spatial differences in validation performance, occurrence records are the only method to validate the model.

Scale comparison and output format

A comparison between global and local models of the same region was conducted in order to evaluate whether the high resolution of the local model is essential for exact determination of assessing establishment potential at the global and local scales. High and significant correlations between the maps of local and global models (Fig. 13) point to the latter alternative. Accordingly, the coarse resolution used for the global model provides sufficient information for local purposes. These results were found despite the use of different climatic datasets, and the higher accuracy of the data used for irrigation correction in the local model. The cell size used for the global model (~18X18 km) enables to distinguish between regions with different establishment suitability of the prediction map. However, differences between establishment suitability of single irrigated area and its surroundings cannot be distinguished from this model map (Fig 13.). These differences can be recognized in the higher resolution map (~1X1 km) of the local model (Fig 11). The decision on data resolution depends on the research purpose. For specific purposes such as examining establishment potential in a single settlement, the resolution used for the global model is not satisfying. However, most of the SDMs studies focus on more general issues such as general patterns of potential distribution, which may be examined by a coarse resolution data. Furthermore, fine resolution data are more difficult to obtain, require greater computing power and longer processing time.

Examination of the modeled area of Israel within the global scale model revealed another important conclusion. In this study a preliminary model run was executed using the logistic output format. Phillips and Dudi'k (2008) designed this format to represent the probability of species presence given a set of environmental variables. Using this format, this study found that establishment probabilities for Israel in the local model differed from those within the Israeli extent of the global model. Since probabilities must be constant a priori, this inconsistency indicates that the logistic format does not accurately represent the probability of species presence in this model. I hypothesize that this inconsistency originates in the Mexent method, which estimates probability distribution for whole pixel sets, as opposed to calculating individual probabilities for each pixel. To avoid a misinterpretation of logistic output, this study used the cumulative output format, which assigns a percentage value to each pixel. This percentage represents establishment suitability in a pixel relative to other pixels. The suitability value is first assigned within the native extent, and then assigned to the projected region based on the variables (features) coefficient found and the environmental variables in the invaded range. Accordingly, the cumulative values in Israel did not range from 0-100 in both the local model and within the Israel extent of the global model (0-48 and 0-71, respectively). The reason for higher values within Israel extent of the global model is the relative high suitability of Israel compared to large areas (many pixels) of low suitability. The differences between the values of prediction in the same area (Israel) emphasize that the prediction is not absolute and depends on the extent of projection. Accordingly, setting a single threshold for determining suitability for species establishment is problematic; examining all ranges of thresholds using the AUC parameter is more appropriate.

Limitations and suggestions for further study

Nature is too complex and heterogeneous to be accurately predicted by a single model (Guisan and Zimmermann 2000). Accordingly, the central aim of models is to provide simplified descriptions of a complex reality. Prediction models deal with even more complex situations and more unknown factors; their function is to predict outcomes that cannot be forecasted using other methods. This study provides new information about the potential distribution of *W. auropunctata*. This potential distribution does not forecast an unavoidable future scenario, since invasion potential could be affected by factors outside the realm of this study. I recommend that future studies include additional variables representing human impact on microclimate conditions. Variables such as climate change, human trade and the urban heat island effects are expected to influence the predictions of *W. auropunctata* distribution, as well as those of other species that inhabit anthropogenic land-use. The urban heat island effect is a characteristic warming of urban areas as compared to their non-urbanized surroundings (Voogt 2002). This warming could have a large effect on the establishment potential of species in urban habitats. Accounting for this effect is complicated in large scale models, since urban heat island effects differ from one city to another and depend on variables such as city density, surface structure, wind speed and more (Voogt 2002). Climate change could dramatically change *W. auropunctata* potential distribution following changes in temperature and precipitation patterns at large scales. Modeling the potential distribution of this species under different climate change scenarios can reveal important conclusions about its future potential distribution. Transport of goods, the main dispersal vector for this species, is recommended to be considered in future studies. The prediction maps in this study represents only the establishment risk of the species in case it reaches a given site, but it does not represents the probability of reaching the site. This probability can be estimated using product import and trade data.

The addition of other environmental variables could also improve the models prediction of *W. auropunctata* distribution. Considering this study's finding that water input and soil moisture are crucial for *W. auropunctata* distribution, the presence of surface water (rivers, lakes, puddles, etc.) in areas of low or medium precipitation quantities can potentially create suitable habitats for this species. In addition, direct soil moisture should be included as a variable in the modeling process. This variable was not included in this study since it was not available at large scales. Two other potentially important climatic variables that were not included in this study are the length of the dry and wet seasons and precipitation therein. These variables may be more important than the precipitation during the driest and wettest months alone.

Models are useful when experimental data is lacking. In the case of *W. auropunctata* no experimental data on climatic preferences were found (Harris et al. 2005). Further investigation of climatic preferences and limiting factors through lab experiments is essential to improve our understanding of the potential climatic niche and the potential distribution of *W. auropunctata*.

Improving the monitoring method

Introduction

Monitoring is an important process for the discovery of a newly invasive species. Early discovery of an invasive species might increase the probability of its successful eradication, owing to its limited distribution (Myers et al. 2000). In addition, an efficient and reliable monitoring method is essential for the validation of eradication measures. Eradication of *W. auropunctata* requires long-term treatments, accompanied by extensive monitoring for several additional years (Wetterer and Porter 2003). However, monitoring is an expensive procedure (Hauser et al. 2006) and improving the monitoring method could reduce costs and labour investment. For *W. auropunctata*, nest and habitat characteristics, as well as its foraging activities, are important factors that influence the monitoring procedure.

Characteristics and habitats of the nest

As opposed to most ants that dig nest tunnels in the ground, *W. auropunctata* has an unstructured nest, which it establishes close to the surface. It can nest in a variety of sites, such as under stones, under leaf litter, between a tree trunk and the soil, in tree holes, under bases of palm leaves or in spaces between plants and soil (Spencer 1941, Clark et al. 1982). Nests can be found in dry or moist areas, due to the ants' response to environmental changes. A possible response could be nesting deeper in the soil during dry periods and moving into trees during floods (Smith 1965). The social structure of the nest is "unicolonial," i.e., a colony composed of many aggregates (Holldobler and Wilson 1990). Three types of aggregations were distinguished in the Galapagos: only workers, workers and ants at immature stages (larvae, pupae, eggs), or one to several queens together with workers and ants at immature stages (Clark et al. 1982).

Foraging activity

The foraging activity of *W. auropunctata* depends on weather and microhabitat conditions. Some reports suggest that *W. auropunctata* prefers heat and humid conditions for its foraging activity. For example, on Santa Cruz Island, more baits were visited by *W. auropunctata* in the hot and wet season (mean temperature of 25°c) than in the dry season (mean temperature of 22°c), and ant density was higher after a greater amount of rainfall (Clark et al. 1982). On Santa Fe Island, it was easiest to find *W. auropunctata* after El Niño event, while in dry conditions it was harder to find the ants, since they remained in the soil or in subterranean parts of shrubs (Abedrabbo 1994). On the other hand, Mikheyev (2008) found that *W. auropunctata* frequently ceased foraging in the heat or under rain, and Meier (1994) found most foraging trails on the shadowed sides of cacti. Despite the influence of weather on foraging activity, Causton et al. (2005) suggested that *W. auropunctata* would be attracted to baits under most climatic conditions (including strong wind, heavy rain, and full sunlight) and at all times of the day. Reports of the foraging distance of this species also varied: Deyrup (2000) found that foraging trails often move for many meters, while Orivel et al. (2009) assumed, based on field observation, that baits could potentially attract workers from any nest located up to 2 meters away. In summary, studies on *W. auropunctata's* foraging distances and the species' behaviours under various climatic conditions are not sufficiently systematic, and further study is needed to improve monitoring methods and to determine optimal conditions for monitoring (Causton et al. 2005).

Monitoring methods

There are many methods for sampling ground-dwelling ants: pitfall traps, Winkler extraction (extraction of soil and litter), artificial nesting sites, hand collection and baits (Delabie et al. 2000). Some of these methods, especially pitfall traps, baits and direct search, have been used in a variety of studies to search for *W. auropunctata* (Ulloa-Chaco´n and Cherix. 1994, Causton et al. 2005, Null 2006, Walker 2006, Vonshak et al. 2010). A comparison study of different sampling methods for *W. auropunctata* showed that the most efficient method (most of the ants were collected) was a direct search in leaf litter, followed by use of baits, pitfall traps and the dissection of decomposing logs (Ulloa-Chaco´n and Cherix. 1994). Direct search and use of baits are the current monitoring methods used in Israel and, given their proven performance, they were chosen for comparison in this study. With the exception of a single, non-detailed guideline for testing for the possible presence of the species (Humburger 2010), there is no authoritative Israeli protocol specifying how and when each of the monitoring methods should be used. Consequently, there is no routine monitoring procedure in Israel, and monitoring parameters are determined by the surveyors.

Only one protocol for surveying *W. auropunctata* was found in the scientific literature (Hawaii-ant-group 2003). This protocol was written for detecting the ant in Hawaii using the bait method, and it specifies the food substance for the baits, the time lag between bait installation and examination, the preferred time for survey and the recommended intervals between baits. Parameters used in surveys can be found in reports of studies performed in different areas and for different purposes (Causton et al. 2005, Null 2006, Walker 2006, Mikheyev et al. 2008, Orivel et al. 2009).

Bait method

Bait method protocol requires the specification of four parameters: food substance, time interval between bait installation and examination, bait locations, and distance between baits. In a comparison of various food substances, the most attractive food for *W. auropunctata* was peanut butter (Williams and Whelan 1992); thus, it is used by the Israeli authorities and was chosen for use in this study.

The second parameter, the time interval between bait installation and examination, ranged between 45 to 90 minutes in different studies (Hawaii-ant-group 2003, Null 2006, Orivel et al. 2009). Instructions provided by the Israeli authorities concerning the time interval are inconsistent. The Israeli Ministry of Environmental Protection (IMEP) recommends maintaining one hour interval between bait installation and examination (IMEP, 2010) while the Ministry of Agriculture recommends maintaining only half an hour interval (Humburger 2010).

The scientific literature provides limited recommendations regarding bait location (third parameter). Null (2006) and Orivel (2009) recommended placing baits at the base of plants and trees. Orivel (2009) recommended that baits be placed on soils in which surface temperatures range from 10°c to 37°c and most preferably where soil-surface temperature is 30°c.

The fourth parameter is distance between baits. Studies use different distances to detect the species in new locations. These distances vary between 3-5 meters (Hawaii-ant-group 2003, Causton et al. 2005, Null 2006, Orivel et al. 2009). A distance of 1 meter between baits was used to confirm successful eradication (Causton et al. 2005). The above mentioned distances do not specify detection probability nor are they based on experimental evidence.

Direct search method

Direct search is a common method for monitoring *W. auropunctata*. The search is focused on ants' foraging trails and common sites of nests, e.g., under rocks, logs, debris and potted plants (Lubin 1984, Armbrecht and Ulloa-Chacon 2003, Vonshak et al. 2010). The monitoring time per area has varied, ranging from one man-hour for an area of 100 m^2 (Mikheyev et al. 2008) to 5 minutes for 1 m^2 (equivalent to 833 hours for 100 m^2) (Walker 2006). None of the studies examined the detection probability for specific monitoring times per area.

Objectives

The main objective of this of this portion of the study is to improve the method of monitoring *W. auropunctata*. The specific objectives are:

1. To define the ideal bait distribution, i.e., the number of baits per area that is most efficient for determining presence or absence of the species within a monitored area, to a designated level of statistical significance.

2. To characterize the optimal microclimate conditions of soil-surface for bait location.

3. To characterize the preferable weather conditions for surveying *W. auropunctata* using the bait method.

4. To estimate the time required for determining presence or absence of the species within a monitored area using direct nest search method.

5. To compare the monitoring efficiency of baits and direct search in different seasons.

Methods

In order to improve the monitoring of *W. auropunctata*, I assessed the time needs and detection probability of bait and direct search methods. In addition I characterized the effects of soil-surface microclimate conditions on bait detection. Data were collected between March 2009 and January 2010 in a sample of infested settlements located in various regions in Israel.

Bait method

Detection probability

Bait method efficiency is based on time interval between bait installation and examination and the specification of the ideal bait distribution required for determining presence or absence of the species within a monitored area. To determine whether the one hour time interval between bait installation and examination, as used by the Israeli authorities, is sufficient, a field test was performed. Prior to the test, seven nests of *W. auropunctata* were identified in the infested area of Ein Hamifratz. Between 1-3 baits were set around each nest, at 1, 2 and 3 meters distances, allowing no nest to be any closer to the baits. Accordingly, a total of 13 baits were installed around the seven nests mentioned. The baits were left in their locations for 3 hours, and were examined for *W. auropunctata* presence at half hour intervals. The field test was repeated twice: in the spring (March 22, 2009) and in the early summer (May 31, 2009). A sufficient time interval was defined as the time after which no more baits were visited by *W. auropunctata*, in at least one of the field tests. The time interval determined by the field tests was then used in this study’s subsequent experiments.

The ideal bait distribution for determining presence or absence of the species within a monitored area to a designated level of statistical significance was assessed based on the distance between visited baits and their nearest nests. I measured these distances during the study period (~one year), in the following settlements: Ein-Hamifratz, Kvutsat Kineret, Dgania B, Afiqim, Beit Zera, Haon, Dafna and Maabarot. Each of these settlements is characterized by different climatic conditions, stage of invasion and eradication intensity. Baits were located in random locations within the known infested area of the settlements, keeping a distance of at least 30 meters between baits. When a visited bait was found, the distance to the nearest nest was measured and recorded. A histogram of the combined results of the distance frequencies was constructed. Based on the histogram shape, I selected from among ten types of continuous probability distributions the one which best fits the data. Pearson's Chi square test was used to examine whether the selected distribution fits the histogram. The null hypothesis of the Chi square test states that the frequency distribution observed in the sample is consistent with a theoretical distribution. The tests-statistic for this test is $\chi^2 = \sum_{i=1}^{i=k} \frac{(O_i - E_i)^2}{Ei}$, where O_i is the observed frequency in bar *i*, E_i is the expected frequency in bar *i* and *K* is the total number of histogram bars. The degrees of freedom are defined as *K-L-1*, where *L* is the number of parameters used in fitting the distribution. The χ^2 test statistic asymptotically approaches χ^2 distribution, and thus *P*-value is calculated by comparing the value of the statistic to a chi-squared distribution. The selected distribution function was used to calculate the probability of finding *W. auropunctata* at a specific distance from a nest. This probability is 1 minus the area under the curve of the distribution function at the defined distance. The calculated detection probabilities were used to determine the probability of bait visitation as a function of the nearest nest distance.

Microclimate soil conditions and bait detection

Twenty seven baits were located at a 2 meter distance from twelve known *W. auropunctata* nests in Ein-Hamifratz. Bait installation made sure that there would be no other nests closer to it than the intended nest site. Examination of *W. auropunctata* presence on the baits was performed, and top soil moisture and temperature in all bait locations were recorded. Top soil moisture was measured by weighting a top soil sample before and after 3 days of oven-drying at 60°C. A T-test was preformed to compare the mean soil moistures and temperatures in visited and unvisited baits. A Mann-Whitney U Test was performed for non-normally distributed data. Statistical tests were performed using the SPSS program.

Air temperature

Air temperature was measured after bait placing in seven monitoring sessions in Ein Hamifratz. Bait placing was executed in the morning hours and lasted for about one and a half hours. Statistical correlation between air temperature and the portion of visited baits among those set up in the experiment was examined using Spearman's rank correlation.

Direct search method and detection efficiency comparison

The locations of *W. auropunctata* nests were recorded in an irrigated 60,000 m^2 infested plot in Ein-Hamifratz. In the same plot, a repetition of 5 different surveys was conducted. Each repetition was performed by two different surveyors searching for *W. auropunctata* nests in a period of 75 minutes. The ratio between the mean number of nests detected in the five surveys and the total number of nests detected in the plot was used to estimate the probability of a single nest being found by any two surveyors working in a defined area and time. This estimation is site-specific for Ein-Hamifratz.

In order to compare the efficiency of direct search and bait method, each of the five direct method surveys in Ein-Hamifratz was accompanied by an additional bait method survey conducted in the same time and plot. Baits were located exactly in the same locations in every one of the five surveys. The surveys represent four seasons and were carried out in March, June, August and October of 2009 and in January, 2010. The number of nests found during each visit and in each monitoring method was recorded and compared.

Results

Detection probability of bait method

The first test of time interval between bait installation and examination showed the following bait visitation time by *W. auropunctata:* the first bait was visited during the first half hour, another one during the second half hour, and four baits during the third half hour. Seven baits were not visited during the 3 hours of the test. In an identical test conducted 3 months later, nine baits were visited during the first half hour, one bait after the second half hour and three baits were not visited. According to these tests, a one-hour time lag between bait installation and examination is sufficient. This timing protocol was used in subsequent experiments in this study.

A histogram of distances from visited baits to the nearest nest in the sample of infested settlements was produced (Fig. 16). Based on the shape of the histogram an exponential distribution was selected as the best-fit model for the data. The exponential distribution function was: $f(x) = \lambda e^{-\lambda x}$ ($\lambda = 2.93 \times 10^{-3}$) for $X \geq 0$, otherwise 0. The null hypothesis: Xi~ exp ($\lambda = 2.93 \times 10^{-3}$) was accepted following statistical testing ($\chi^{2(2)}$ =0.38, α=0.83).

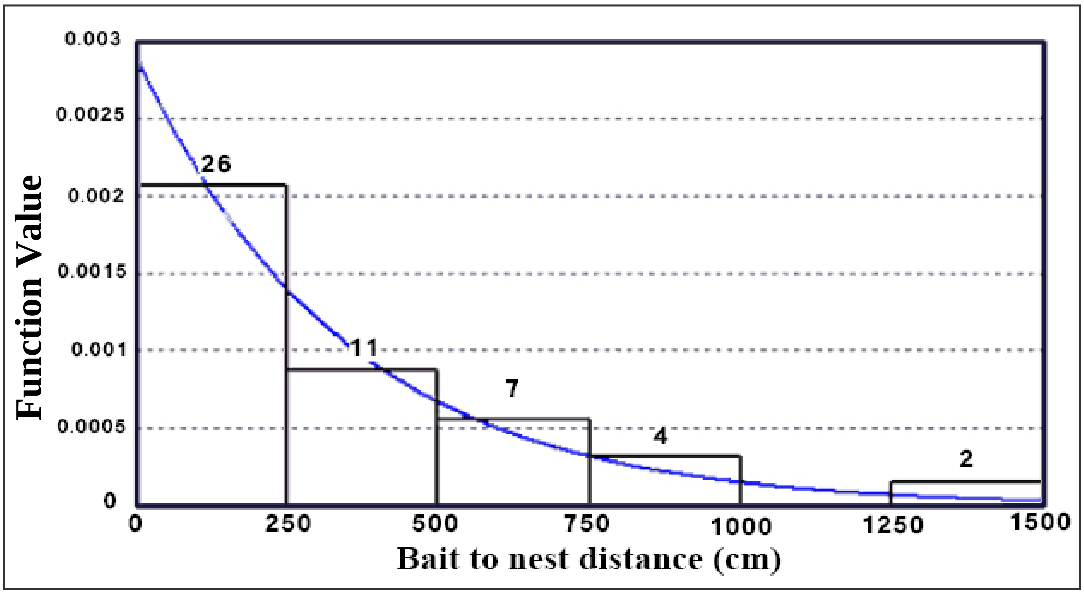

Fig. 16 . Distance between visited baits and their nearest nest recorded in a sample of infested settlements in Israel. The number on top of each column indicates the number of observations. Blue line indicates the exponential function fitted to the histogram.

The probability of finding *W. auropunctata* in a specific distance from a nest is 1 minus the area under the curve of the distribution function at the corresponding distance. The calculated detection probabilities were used to determine the probability of bait visitation as a function of the nearest nest distance: y = $1.0068e^{-0.003x}$ (y is the detection probability and x is a specific bait to nest distance; Fig. 17).

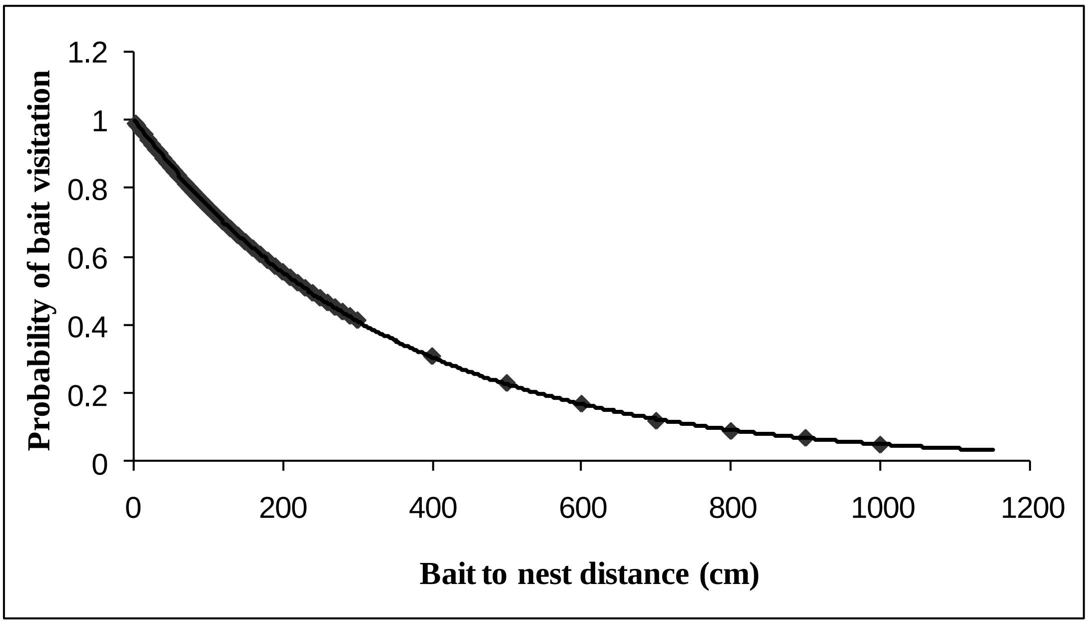

Fig. 17 . Probability of bait visitation by *W. auropunctata* as function of bait to nearest nest distance

Environmental effects on bait detection

Air temperature

Air temperature and the proportion of visited baits were measured in 7 monitoring sessions in Ein-Hamifratz (Fig. 18). A significant correlation was found between air temperature and the proportion of baits visited (Spearman's r=0.955, p=0.001).

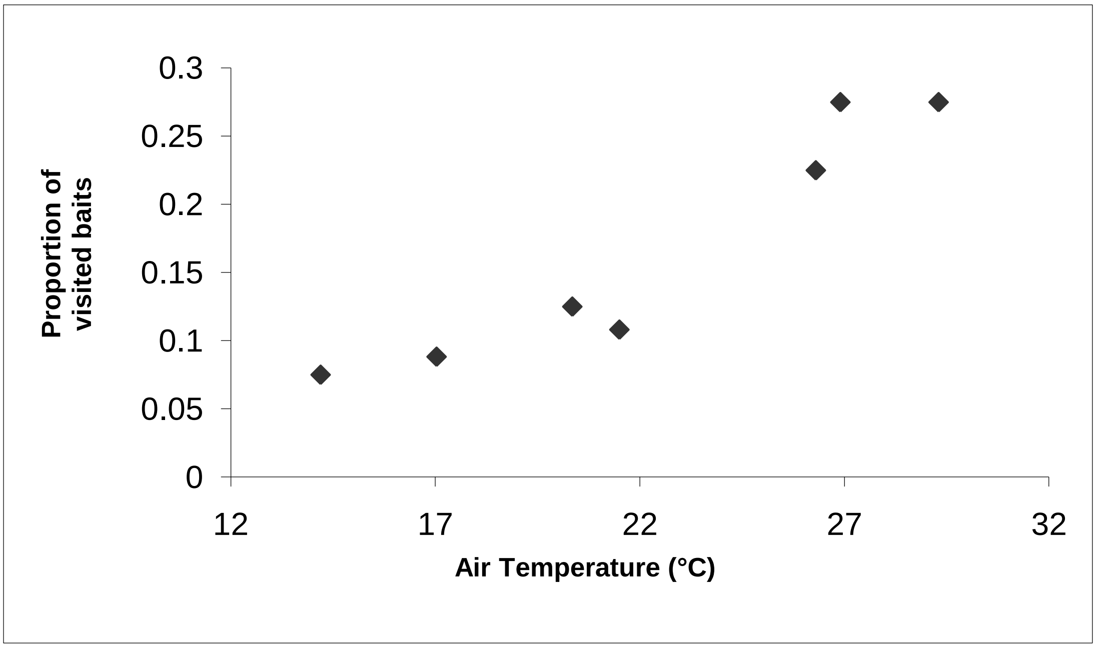

Fig. 18. Proportion of visited baits plotted against air temperature in 7 monitoring sessions at Ein-Hamifratz

Microclimate soil conditions and bait detection

Soil-surface temperatures ranged between 24.4-31.2°c at visited bait sites and 29.8-39.4°c at unvisited bait sites. The results of a T-test indicate a significant difference between the average soil-surface temperature of visited and unvisited baits located at a distance of 2m from 12 nests in Ein-Hamifratz ($P<0.001$; Fig. 19). A Mann-Whitney U Test found no significant difference between average soil-surface moisture of visited and unvisited baits (Fig. 20).

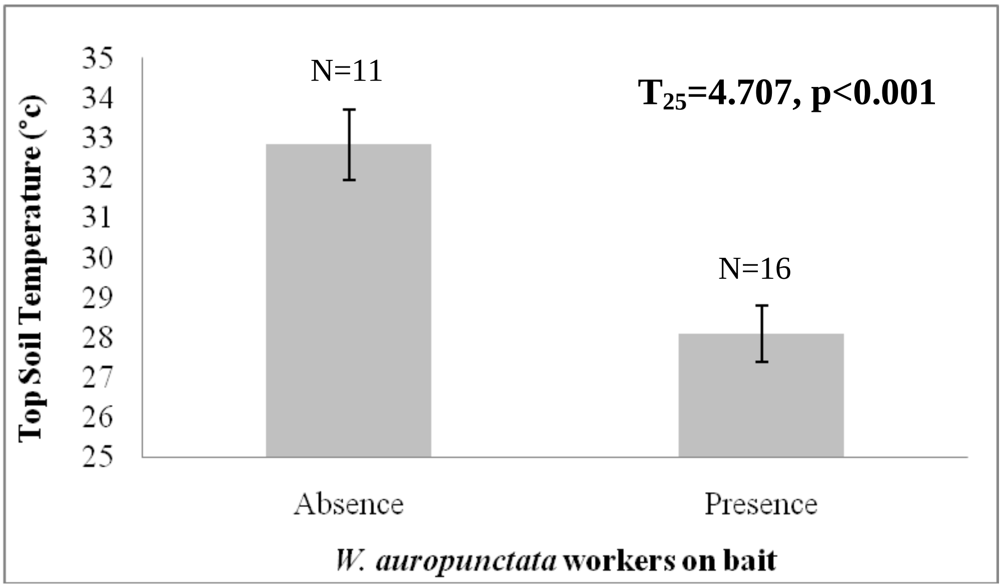

Fig. 19 . Average top soil temperature of visited (N=16) and unvisited (N=11) baits (±S.E.) located at a distance of 2m' from 12 nests.

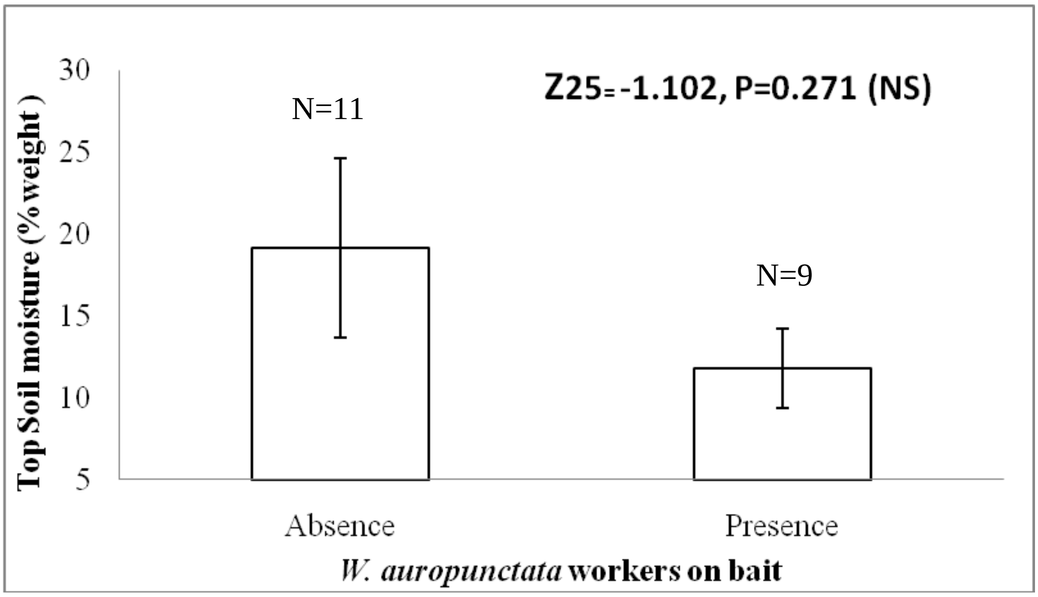

Fig. 20. Average top-soil moisture content (% weight) (±S.E.) for visited (N=9) and unvisited (N=11) baits. Baits were located at distance of 2 m' from 12 nests.

Direct search method and detection efficiency comparison

A total of 56 ant sites (nests or foraging trails) were identified within a 60,000 m^2 research plot in Ein-Hamifratz (0.93 nests/1000 m^2). In 5 independent 75 minutes direct searches, performed by 2 surveyors in the same plot, an average of 14 nests were found (0.23 nests/1000 m^2/1.25 hours).

A comparison between the direct search and the baiting method in terms of the number of ant sites (nest or foraging trails) found within the same plot per time unit shows that the direct search performed better in 4 out of 5 monitoring sessions (Fig. 21).

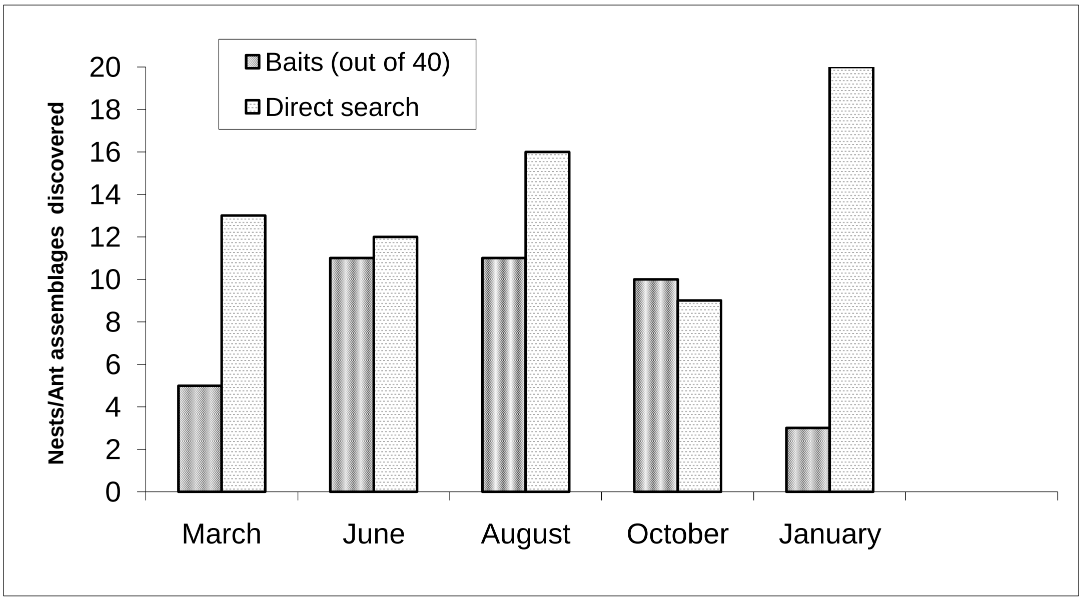

Fig. 21. Number of ant sites (nest or foraging trails) found in direct search and bait method in the same plot in Ein-Hamifratz.

Conclusions and discussion

The main objective of this portion of the study was to improve the monitoring method used by Israeli authorities dealing with *W. auropunctata*. Although the method currently in use is partially based on the scientific literature, it is not consistent, has not been evaluated for efficiency, and lacks definitions of preferable conditions for execution as well as for determining presence or absence of the species. The definition of these parameters, provided in this study, could lead to early detection of infested sites, which in turn could both boost successful eradication and contribute to the validation of eradications measures. In addition, defining these parameters could help reduce the labour investment and costs of the current method used.

In the scientific literature, the parameters indicated for monitoring (e.g., distance between baits, time allotted for direct search) are diverse and there is a paucity of systematic studies that attempt to optimize these parameters. In addition, to date, no information has been collected on the statistical significance of presence or absence of the species related to specific bait distribution patterns or time allotments in the direct search method. Given the lack of systematic studies on *W. auropunctata* foraging distances and behaviours in different climatic conditions, Causton et al. (2005) recommended performing repeated examinations of foraging traits in different climates and with populations of various sizes (including those that have been damaged by eradication attempts). The current study followed this recommendation, and included observations of foraging characteristics in baits established under different climate conditions within various regions in Israel.

Bait Method

This study examined the level of effort required to determine the presence or absence of the species at a predefined level of statistical significance, for the existing methods used by the Israeli authorities. The bait method was the main focus of this examination, since it was the only method in use by the authorities at the onset of this study. The effort needed to detect the species using the baits method depends mainly on bait distribution per unit of area. The ideal bait distribution for determining presence or absence of the species was calculated based on observations of the distances between visited baits and their nearest nests in different seasons and sites. Each site was characterized by a unique set of parameters that potentially influence the foraging distance from the nest, including climatic conditions, stage of invasion, eradication success and nest density. The representation of a variety of conditions and colony characteristics provides information that is not site-specific and thus could be relevant for various climates and regions in Israel. A potential confounding factor in this method is the fact that there is no evidence that the ants on a given bait came from the nest nearest the bait. One potential solution to this uncertainty would be to follow the foraging trail; however, in most cases this is not possible, due to the small size of the ant workers and the low ant densities found on the foraging trails. Another possible approach would be to mark ants at their nest by feeding them with coloured sugar and cataloguing ant colours at the bait site, as used by Schline (1987) in the *Phlebotomus papatasi* (sand fly) study.

The equation for *W. auropunctata* visitation probability at a given bait as a function of bait to nest distance makes it possible to calculate the probability of not detecting the ant while it is present (Type II error). Accordingly, Orivel (2009) had a Type II error probability of 0.52 when using 5 meter intervals between baits, while Causton et al. (2005) had a Type II error probability of 0.14 when using 1 meter bait intervals (the shortest on record). The distance between baits is proportional to the required number of baits and accordingly to the time and effort needed to install them in the field. Thus, for example, a 5 meter interval requires 40 baits per 1000 m^2, while a 1 meter interval means installing 1000 baits per 1000 m^2. Therefore, selection of bait distribution should depend on the goals of the monitoring plan, the size of the monitoring area and the time and resources available. Using 1 m intervals between baits requires a lot of effort, but is essential for verifying species absence. Despite the large sampling effort required, this interval has been used to monitor a large area of 210,000 m^2 (Causton et al. 2005).

To improve the efficiency of the bait method, the optimal microclimate and weather conditions for bait locations were examined. In determining the presence of *W. auropunctata*'s workers on baits, environmental conditions are more significant than competition with other species, since other species tend to retreat due to the *W. auropunctata*'s aggressiveness (Holldobler and Wilson 1990). Microclimate examination at visited bait locations indicated that soil temperature at the bait location was a predictor, whereas soil moisture was not predictive of ant workers' presence. The average soil-surface temperature was 28°c at visited baits and 32.8°c at unvisited baits. Another result that shows a similar effect of temperature on bait visitation is the significant positive correlation that was found between the proportion of visited baits and air temperature within the range of 17-29^{0}c. Despite the positive correlation within this temperature range (17-29^{0}c), the proportion of visited baits in air temperature of 29^{0}c was slightly lower than that in 27°c (Fig. 18). Monitoring at this site (Ein-Hamifratz) was not performed in temperatures higher than 29^{0}c, and thus it would be interesting to examine if the proportion of visited baits further decreased at higher air temperatures. These findings indicate that in order to maximize the efficiency of bait method, monitoring should be performed when the air temperature nears 27°c. When the temperature is higher, I recommend placing the baits in shaded locations. These findings are consistent with those of the study by Clark et al. (1982), which detected more *W. auropunctata* workers on Santa Cruz Island at an average temperature of 25°c than at an average temperature of 22°c; with the findings of Mikheyev (2008), who found that *W. auropunctata* frequently ceased forging in the heat; and with those of Meier (1994) who found the foraging trails of this species on the shaded sided of cacti. In contrast, Orivel (2009), found that *W. auropunctata* was active on baits when soil-surface temperatures were between 10-37°c and most active when the soil surface temperature was 30°c.

These varied findings indicate that other factors, such as precipitation, food availability and nest densities, could affect ant presence on baits. Another indication that other factors (in addition to temperature and humidity) affect the presence of *W. auropunctata* on baits is the differences in bait detection rates in different seasons in Israel, found in this study. These differences show that most of the baits (in the same locations) were highly visited in June and August and the least visited in January. Summer irrigation in the monitored plot caused hot and wet micro-climatic conditions. These conditions are probably the main reason for the increased activity during the summer (Vonshak, Pers. Comm.). To further improve this monitoring method, it is recommended that researchers compare species' activity in irrigated versus non irrigated plots. In addition, it is recommended to examine the microclimate conditions inside *W. auropunctata* nests during different seasons as compared to its surrounding environment, in order to learn more about the microclimatic preferences of this species.

Direct search and detection efficiency comparison

The sampling effort required for direct searches was estimated in this study. Estimates were based on comparing the number of nests detected in a specific plot in Ein-Hamifratz, to the average number of nests that were detected in the same plot in five limited time sessions of direct search. The results of this comparison are restricted to this site with its specific conditions and nest distribution. A comprehensive, direct search survey of this plot detected 0.93 nests/1000 m^2, as compared to an average of 0.23 nests/1000 m^2 detected in 5 direct search surveys. This result revealed a single nest detection probability of roughly 25% for 2 people surveying an area of 60000 m^2 during 1.25 hours. In our experience, monitoring the same area under same time and effort limitations using baits required an interval of approximately 30 meters between baits. The calculated equation shows a probability of ~1% for detecting a single nest following this interval. Consistent with this result, a comparison of the direct search and the bait methods in different seasons showed better performance of the direct search in most of the cases.

The use of direct search is simple to perform but requires participants who know how to identify the ants. The disadvantages of this method are that nests located in sites that are hard to reach (like tree tops) will not be detected; and the efficiency of the method depends on the skill of the surveyors. An incomprehensive survey or a survey executed by unskilled surveyors could be crucial when verifying successful eradication. Therefore, the direct search method is recommended as the main monitoring method, but it is recommended to use the bait method as an additional precaution, especially in potential nest locations where detection by humans is difficult.

Recommendation

In view of these results and the conclusions mentioned above, the recommended monitoring method when surveying a known infested site is the direct search method, and in addition of baits installed in locations where humans are unable to conduct effective observations. Summer is the recommended season for conducting surveys in Israel, and these should be performed during the morning hours, when air temperature is around 27°c. Baits should be installed in shaded sites, where surface soil temperature is below 30°c. For surveys intended for verifying successful eradication or discovering new infestations, stricter monitoring parameters should be implemented, in order to preclude false negative results. To this end, I recommend conducting a direct search supplemented with baits installed at a grid of 1 meter intervals (86% probability detection per each nest). The combination of these two methods performed as recommended here will minimize the probability of false negative results.

Summary

This study extended our knowledge regarding the influence of climate on *W. auropunctata* distribution and activity at different scales. Using SDM, I examined the climate influence on species distribution at a continental scale (species native range), and the limiting variables for distribution at local scale (Israel). The field work examined the effect of microclimatic conditions on monitoring efficiency at local scale. At large continental scale, variables representing soil moisture and minimum temperature were the most important factors in determining *W. auropunctata* distribution. These factors limited the distribution of the species within Israel, however, within irrigated lands, water input was not a limiting factor, and the main limiting factor was minimum temperatures. Maximum temperature of the warmest month was the least important variable factor in determining the species native distribution. At finer scale (hundreds of meters), *W. auropunctata* workers were more active in summer (at irrigated site), but less active in extreme high soil temperatures. This difference between factors determining activity and distribution are expected. Every ant species is depended on temperature and humidity (distribution at large scales), but the tolerance of a foraging worker (activity at fine scales) is different from that of an entire colony. The forager is more sensitive to ambient microclimate conditions, whereas a colony can partly control it by shifting deeper into the soil or by clustering to retain metabolic heat and moist (Holldobler and Wilson 1990).

A model that uses a smaller scale (and finer resolution) than those used in this study is recommended for further investigation of environmental variables affecting *W. auropunctat's* distribution. As opposed to distribution at large scales that are typically influenced by climatic variables, distribution at small scales more likely to be influenced by resources availability, micro-topographic variation or habitat fragmentation (Guisan and Thuiller 2005).

Integration of the results of the two parts of this study provides knowledge that can be implemented to prevent further spread of *W. auropunctata* in Israel, and in other countries. The first part that modelled the potential distribution can direct monitoring actions to areas of high potential establishment. The second part contributes to the improvement of the efficiency of the monitoring actions. Efficient monitoring actions in areas of high establishment potential may lead to early exposure of infested sites

which can contribute to successful eradication. In addition, other management actions may be performed in high establishment risk areas and countries. Management actions include examination of imported goods, instructions for local citizens and restrictions on soil and vegetal exporting from the infested region or country. In summary, human activity is the main vector for the spread of *W. auropunctata* as well as for the establishment of new areas which were not suitable without irrigation. Following this anthropogenic-related spread of the harmful invasive species *W. auropunctata*, it is recommended that human action will be taken to prevent further spread to other countries and other region in Israel.

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Appendix

<u>Appendix 1:</u> Simplified theoretical example of probability distribution estimation using a maximum entropy principle and linear feature constraint:

- **<u>Model inputs (expressed in the 2X2 matrix)</u>:**

10	**20***
18*	**20**

4 pixels' study area

One environmental variable (values inside the pixels)

2 species records (marked by * inside the relevant pixels)

- The constraint imposed by the linear feature: the Mean variable ($\overline{X}$) of the species records locations (=19) should be close to $\overline{X}$ of the environmental variable distribution.

{For probability distribution: $\overline{X} = \sum X_i P_i$ (X_i - variable value, P_i - probability)}

-Without constrains, by the maximum entropy principle, each pixel gets a value of 0.25 and $\overline{X}$ = 0.25*(10+20+18+20) =17

A possible solution satisfying the constraint is presented in the following matrix (values are probabilities):

0.05	**0.35***
0.25*	**0.35**

In this case:

$\overline{X}$ =(0.05*10)+(0.35*20)+(0.25*18)+(0.35*20)=0.5+7+4.5+7= 19.

Among all the possible distribution that satisfies the constraint, the model will use the one with maximum entropy (the most close to uniform).

Appendix 2: correlations matrix between the variables used in the study

Bold indicates correlation higher than 0.8. Strikethrough indicates variables that were not used for model building.
* Correlation is significant at the 0.05 level (2-tailed).
** Correlation is significant at the 0.01 level (2-tailed).

	Min-cold	Max-warm	~~Ann-temp~~	~~Temp-range~~	~~Ann-prec~~	Prec-wet	Prec-dry	Prec-CV	P_E	Evap
Min-cold		0.132	**0.808****	**-0.837****	0.416**	0.439**	0.305**	-0.116	0.136	0.045
Max-warm	0.132		0.639**	0.423**	-0.357**	-0.282**	-0.288**	0.335**	-0.234*	0.437**
~~Ann-temp~~	**0.808****	0.639**		-0.388**	0.092	0.141	0.068	0.141	-0.028	0.303**
~~Temp-range~~	**-0.837****	0.423**	-0.388**		-0.582**	-0.560**	-0.434**	0.282**	-0.247**	0.200*
~~Ann-prec~~	0.416**	-0.357**	0.092	-0.582**		**0.906****	**0.821****	-0.515**	0.314**	-0.520**
Prec-wet	0.439**	-0.282**	0.141	-0.560**	**0.906****		0.550**	-0.204*	0.182*	-0.441**
Prec-dry	0.305**	-0.288**	0.068	-0.434**	**0.821****	0.550**		-0.755**	0.391**	-0.489**
Prec-CV	-0.116	0.335**	0.141	0.282**	-0.515**	-0.204*	-0.755**		-0.276**	0.435**
P-E	0.136	-0.234**	-0.028	-0.247**	0.314**	0.182*	0.391**	-0.276**		0.270**
Evap	0.045	0.437**	0.303**	0.200*	-0.520**	-0.441**	-0.489**	0.435**	0.270**	

לביצוע הניטור בעונה זאת הוא שעות הבוקר המוקדמות. מיקום פיתיונות בקרקע בטמפרטורה גבוהה משלושים מעלות מוריד את סיכויי הגילוי, לכן בעונת הקיץ יש למקמם במקומות מוצלים. לחות הקרקע במיקום הפיתיון לא נמצאה כגורם המשפיע על גילוי הפיתיון. שיפור שיטות הניטור יאפשר איתור הנמלה בשלבי פלישה מוקדמים ובכך יקל על פעולת ההדברה להכחדה מלאה. בנוסף שיפור שיטות הניטור יאפשר למקבלי ההחלטות להגדיר הכחדה מלאה של המין לאחר פעולות הדברה.

מחקר זה מזהה אזורים בעלי התאמה גבוהה להתבססות נמלת האש הקטנה ובנוסף מאפשר ניטור יעיל יותר של מין זה. גורמים אלו מאפשרים למקבלי ההחלטות לבצע החלטה יעילה יותר לגבי האזורים המועדפים לביצוע פעולות ניטור ומשפרים את פעולות ניטור אלו. שילוב זה בין מסקנות המחקר עשוי לתרום לצמצום ההוצאות הכרוכות בניטור נמלת האש הקטנה ולהאטת ההתפשטות של מין פולש מזיק זה.

תוצאות אלו ממחישות את חשיבות זמינות המים לנמלת האש הקטנה, ואת חשיבות תיקון ההשקיה לחיזוי יותר מדויק של ההתבססות הפוטנציאלית של מין זה. תיקון המשקעים חשוב בסקאלות השונות שנבדקו ובאזורים גיאוגרפים בעלי מאפיינים אקלימיים שונים. שיטת תיקון המודל והחלתו לשטחים מושקים באופן המייצג את תוספת ההשקיה, יכולה לשמש גם לשיפור חיזוי תפוצה של מינים אחרים.

למעט אזורים מושקים, מפות חיזוי המודלים בסקאלות השונות הראו תוצאות המתאימות למפות המייצגות אזורי אקלים. בסקאלה הגלובאלית אזורים בעלי פוטנציאל התבססות גבוה נמצאו בעיקר באזורים הטרופים והסב-טרופיים. המודל בסקאלה גלובאלית ללא תיקון ההשקיה חזה הסתברות בינונית להתבססות המין ברוב שטחה של ישראל, אך המודל עם תיקון משקעים הראה ערכים גבוהים להתבססות המין באזורים מושקים בחבל הים תיכוני בישראל. המודל עם תיקון ההשקיה בסקאלה של ישראל הראה ערכי התבססות גבוהים באזור המעבר בין האזור הים תיכוני לאזור החצי יובשני. בנוסף חזה המודל הסתברות גבוה להתבססות גם במרבית האזורים המושקים בחבל הים תיכוני. אזורים הררים גבוהים בחבל הים תיכוני הראו ערכי התבססות נמוכים גם באזורים מושקים. המודל חזה ערכי התבססות נמוכים באזור המדברי בישראל הן לגבי שטחים טבעיים והן לגבי שטחים מושקים. מחקר זה מראה כי נמלת האש הקטנה לא מנצלת את כל השטח הפוטנציאלי להתבססותה בישראל והיא צפויה להמשיך להתפשט ולהתבסס באזורים נוספים, בעיקר באזורים מושקים בחבל הים תיכוני.

מטרה נוספת של מחקר זה הינה לשפר את שיטות הניטור המשמשות כיום בישראל לגילוי הנמלה. שיטות אלו הכוללות שימוש בפיתיונות וחיפוש ישיר של הנמלה, נבחנו בעזרת תצפיות וניסויי שדה. שיפור שיטות הניטור כלל אפיון מדדים כמותיים של שיטות אלו. מדדים אלו כוללים: צפיפות פיזור פיתיונות, תנאי טמפרטורה ולחות קרקע במיקום הפיתיון, הגדרת עונת השנה המועדפת לניטור והשוואה בין היעילות של פיזור פיתיונות שיטתי לזו של חיפוש ישיר של הנמלה. אפיון מדדים אלו נעשה על ידי מדידות התנאים בפיתיונות שבהם התגלתה הנמלה ומדידת המרחק בין פיתיונות אלה לקן הקרוב במדגם של ישובים נגועים בישראל. ניסוי שדה שימש להשוואה בין תנאי הטמפרטורה והלחות בפני הקרקע במיקומי פיתיונות שבהם התגלתה הנמלה ובין תנאים אלו במיקומים שבהם הנמלה לא התגלתה. כל הפיתיונות בניסוי זה מוקמו בסמוך לקינים של נמלת האש הקטנה. המסקנות העיקריות מחלק זה של המחקר הן ששימוש בחיפוש ישיר מומלץ לניטור הנמלה באזורים הידועים כנגועים. ניטור זה ילווה במיקום פיתיונות במקומות שבהם יש קושי לבצע חיפוש ישיר (מתחת לשיחים, לדוגמא). לצורך גילוי אתרים חדשים שבהם לא ידועה הימצאות נמלת האש הקטנה ווידוא הכחדה לאחר פעולת הדברה, מומלץ לבצע בנוסף לחיפוש ישיר, ניטור בעזרת פיתיונות הממוקמים במרחק של מטר אחד מהשני. בבדיקת הסתברות גילוי הנמלה כתלות במרחק בין הפיתיונות נמצאה הסתברות גילוי של 86% כאשר הפיתיונות ממוקמים במרחק של מטר אחד מהשני. שימוש בחיפוש ישיר בנוסף לפיתיונות יעלה את הסתברות גילוי זו. שילוב זה של שתי שיטות הניטור, מצריך השקעת זמן רב יחסית לשטח המנוטר, אך היא נחוצה כדי למנוע טעות של הגדרת השטח כלא נגוע בנמלה בעוד הנמלה נמצאת בו (טעות מסוג II). צפיפות זו של פיתיונות אפשרית לביצוע ושימשה לווידוא הכחדה לאחר פעולות הדברה באי בגלפאגוס. העונה שנמצאה כטובה ביותר לביצוע ניטור היא עונת הקיץ, אך ניתן לבצע ניטור לאורך כל השנה. הזמן הטוב ביותר

תקציר

מינים פולשים הם בעיה עולמית הפוגעת במגוון המינים, בבתי גידול טבעיים, בחקלאות ובבריאות האדם. מבין משפחות המינים הפולשים, הנמלים הן מהנפוצות והמזיקות ביותר. נמלת האש הקטנה (*Wasmannia auropunctata*), היא מין פולש שמקורו בדרום ומרכז אמריקה. במאה השנים האחרונות פלש מין זה לאזורים טרופיים וסב-טרופיים אחרים בעולם. נמלה זו נמצאת ברשימה העולמית של 100 המינים הפולשים הגרועים ביותר כפי שהגדיר ארגון ה-IUCN (International Union for Conservation of Nature). השפעותיה על המערכות האקולוגיות אליהן היא פולשת כוללות: פגיעה בנוכחות ובמגוון המינים של נמלים וחסרי חוליות אחרים, פגיעה בפעילות ובמגוון המינים של זוחלים ותקיפת עיניים של זוחלים ויונקים. הימצאות הנמלה באזורים מיושבים מהווה מטרד לתושבים בשל עקיצתה הכואבת. נמלת האש הקטנה זוהתה לראשונה בישראל בסוף שנת 2005 ומאז היא אותרה בעשרות ישובים. לא נעשתה כל הערכה לגבי המשך התפשטות הנמלה ופוטנציאל ההתבססות שלה באזורים שונים בארץ. שיטות הניטור המשמשות כיום בישראל למעקב אחר התפשטות נמלת האש הקטנה הם ניטור בעזרת פיתיונות וחיפוש ישיר של הנמלה. הסתברות גילוי המין בעזרת שיטות אלו כתלות במאמץ הדיגום לא נבדקה. כמו כן, חסרות הנחיות לגבי תנאי מזג האוויר והעונה המומלצת לביצוע ניטור. המטרות העיקריות של מחקר זה הן: הערכת פוטנציאל ההתבססות של נמלת האש הקטנה בסקאלה של ישראל ובסקאלה גלובאלית ושיפור השיטות המשמשות כיום בישראל לניטור מין זה. לצורך הערכת פוטנציאל ההתבססות של המין, נעשה שימוש ב"מודל של בית גידול". שיפור המודל והחלתו גם לשטחים מישובים וחקלאיים, מהווה מטרה נוספת של מחקר זה. "מודלים של בתי גידול" הם מודלים ממוחשבים המספקים חיזוי להתבססות פוטנציאלית של מין על ידי שימוש בנתונים על מיקומים בהם נצפה המין ומשתנים סביבתיים במרחב. מודלים אלו חזו במקרים רבים, בדיוק גבוה את המרחב הגיאוגרפי בו יכולים מינים פולשים להתבסס. המודל ששימש במחקר זה הוא MAXENT, מודל בית גידול נפוץ בשימוש אשר הראה תוצאות טובות במחקרים המשווים בין ביצועי מודלים שונים. תפוצה של נמלים מושפעת מאוד ממשתנים סביבתיים אקלימיים, בעיקר מטמפרטורה, משקעים ולחות. בהתאם לכך, המודל הורץ על בסיס 7 משתנים אקלימיים הכוללים 2 משתני המבטאים טמפרטורה ו-5 משתנים המבטאים משקעים ולחות. מיקומי תצפיות המין עליהם התבסס המודל הם מיקומים ללא השקיה באזור התפוצה הטבעי של המין (דרום ומרכז אמריקה). תצפיות באזורים שאליהם פלשה הנמלה שימשו לבדיקת טיב המודל. ערכי משתני המשקעים שונו בשטחים מושקים חקלאיים ועירוניים באזורי החיזוי, כך שייצגו השקיה. השינוי כלל הורדת השונות הבין חודשית של המשקעים, הוספת משקעים לממוצע המשקעים השנתי ולממוצע המשקעים בחודש היבש. ערכנו השוואה בין תוצאות החיזוי עם התיקון ובלעדיו. המודלים הכוללים תיקון השקיה הראו תוצאות טובות יותר הן בסקאלה הגלובאלית והן בסקאלה של ישראל. בנוסף, חלוקת התצפיות באזורים שאליהם פלש המין בעולם לחמישה אזורים גיאוגרפים, הראתה כי המודל עם תיקון השקיה תפקד בצורה טובה יותר מהמודל הלא מתוקן בכל האזורים המוגדרים.

תודות

המחקר נעשה בהנחיית פרופ' יוחאי כרמל בפקולטה להנדסה אזרחית וסביבתית, הטכניון.

אני מודה לפקולטה להנדסה אזרחית וסביבתית במוסד הטכניון על התמיכה הכספית הנדיבה בהשתלמותי.

התפשטות פוטנציאלית וניטור המין הפולש "נמלת האש הקטנה"

(*Wasmannia auropunctata*)

לשם מילוי חלקי של הדרישות לקבלת התואר
מגיסטר למדעים במדעי איכות הסביבה

רועי פדרמן

טבת תשע"א חיפה דצמבר 2010

התפשטות פוטנציאלית וניטור המין הפולש "נמלת האש הקטנה"

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רועי פדרמן