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Geographical distribution modelling of the bronze bug: a worldwide invasion

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Abstract

1 The present study investigated the environmental variables that define a suitable climate for the bronze bug, *Thaumastocoris peregrinus* Carpintero & Dellapé, using presence-only data, with the aim of identifying areas that have a suitable climate (and thus high probability) for future colonization and generating a spatially explicit predictive map of environmental suitability. An occurrence database (293 records) was compiled mainly from the literature.

2 The environmental data were obtained from the WorldClim 1.3 dataset, and the models were performed using MAXENT, version 3.3.3k. Model performance was evaluated through cross-validation. We used the null models approach to test our models. For model calibration, two datasets were defined (a non conservative dataset and a conservative one) by comparing the bioclimatic variables between native and introduced range using boxplots.

3 According to both models, the range for *T. peregrinus* will continue to expand. In South America and Africa, the distribution of the bronze bug may expand mainly to the north-east and central areas. Special attention should be given to the regions of southern U.S.A., Central America, and southern China and nearby countries, where conditions are highly suitable but the bronze bug has not yet been recorded and could only arrive by human means.

4 Because *Eucalyptus* species, many of which are highly susceptible to infestation by the bronze bug, are increasingly being planted around the world, and because the bronze bug has spread so rapidly over the past 8 years, the bronze bug may be expected to appear in many areas where it has not yet been recorded.

Keywords *Eucalyptus*, Heteroptera, invasive species, Maxent, species distribution modelling, *Thaumastocoris peregrinus*.

Introduction

Invasive species are a worldwide problem with several different consequences on human health, the economy and natural ecosystems (Pimentel *et al.*, 2005; Angetter *et al.*, 2011; Bidinger *et al.*, 2012). Predictive modelling of the geographical distribution of a species based on the climatic conditions of sites of known occurrence constitutes an important technique in analytical biology (Phillips *et al.*, 2006). When applying this approach, it is important to distinguish between fundamental, realized and climatic niches. The fundamental niche represents the complete set of environmental conditions under which a species can persist (Hutchinson, 1957); the realized niche is the portion of the fundamental where the species occurs at a point in time as a consequence of biotic and abiotic interactions (Wiens *et al.*, 2009); and the climatic niche consists of the set of climatic conditions where the species may occur (Quintero & Wiens, 2013). Models that are based on the relationship between climate parameters and species response represent the climatic niche of a species, which is a subset of the fundamental niche (Pearson & Dawson, 2003). Climatic niche models have been increasingly used for predicting the potential distribution of invasive species (Jiménez-Valverde *et al.*, 2011; Zhu *et al.*, 2012a).

Many true bugs (Hemiptera: Heteroptera) have extended their distributions remarkably over the last century, and some of them have increased their pest status after introduction beyond their

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native range (Zhu *et al.*, 2012b). *Thaumastocoris peregrinus* Carpintero & Dellapé (2006), commonly known as the bronze bug, is exclusively associated with several *Eucalyptus* species and has become an economically important pest of *Eucalyptus* not only in Australia (i.e. its native range), but also in South America, Africa and Europe (Laudonia & Sasso, 2012; Nadel & Noack, 2012; Garcia *et al.*, 2013). The bronze bug is a typically gregarious insect that occurs in large groups of both adults and nymphs on *Eucalyptus* leaves (Jacobs & Neser, 2005). It has a short life cycle (approximately 35 days) and the females are capable of lying approximately 60 eggs during their lifespan (Jacobs & Neser, 2005; Bouvet & Rodríguez 2009), thus allowing several generations per year. Adults and nymphs can run fast and unpredictably when disturbed, suggesting that they could easily be dispersed by many vectors, such as wind, transporting plants or branches (Ide *et al.* 2011) and birds (Noack & Rose, 2007). Their rapid reproductive rate and ability to disperse may facilitate their successful establishment in newly-invaded environments (Noack & Rose, 2007; Nadel *et al.*, 2009).

Eucalyptus spp. are the most planted tree species in the world (FAO, 2006; Corcuera *et al.*, 2010); and, in the tropics, they represent approximately 50% of the plantation areas (Evans & Turnbull, 2004). Several *Eucalyptus* species are susceptible to infestation by the bronze bug, as reported in several recent studies (Jacobs & Neser, 2005; Bouvet & Rodríguez, 2009; COSAVE, 2009; Rodrigues Barbosa *et al.*, 2010; Ide *et al.*, 2011; Noack *et al.*, 2011; FAO, 2012; Laudonia & Sasso, 2012; Sopow *et al.*, 2012). To date, the bronze bug has been reported for 14 *Eucalyptus* species in Australia (Noack *et al.*, 2011); Nadel *et al.* (2009); one in New Zealand (Sopow *et al.*, 2012); 26 in South Africa; 11 in South America (Carpintero & Dellapé, 2006; Bouvet & Rodríguez, 2009; Martínez & Bianchi, 2010; Wilcken *et al.*, 2010); and 21 species and hybrids in Europe (Laudonia & Sasso, 2012; Garcia *et al.*, 2013). Currently, the host range of the bronze bug includes approximately 43 *Eucalyptus* species and hybrids worldwide. Infested *Eucalyptus* trees show leaf silvering, ranging from chlorosis to bronzing, giving the bronze bug its common name (see Supporting information, Doc. S1). Heavy infestations cause leaves to become red/brown, after which defoliation occurs.

Subsequent to the dramatic infestation of eucalypts in Sidney in 2001 (Noack *et al.*, 2011) the bronze bug has rapidly become established as a severe pest in South America (Carpintero & Dellapé, 2006; Noack & Coviella, 2006; Martínez & Bianchi, 2010; Rodrigues Barbosa *et al.*, 2010; Wilcken *et al.*, 2010; Ide *et al.*, 2011; Savaris *et al.*, 2011; Benítez Díaz *et al.*, 2013; Magalhães Pereira *et al.*, 2013), Africa (Jacobs & Neser, 2005; Chilima, 2007, 2008; Nadel *et al.*, 2009; Noack *et al.*, 2011), Europe (Laudonia & Sasso, 2012; Garcia *et al.*, 2013), and New Zealand (Sopow *et al.*, 2012).

In invasive species management, the areas identified by niche modelling are those where an invasive species may be present or where it may appear in the future, and so the results could be valuable for planning and prioritizing areas for monitoring (Ward, 2007). Such information can also help to determine the extent, cost and likelihood of success of control and monitoring programmes. Thus, the predictive modelling of the potential distribution of a species is an important tool for invasive species management (Kadoya *et al.*, 2009).

The present study aimed: (i) to identify the environmental variables defining suitable climate for the bronze bug using presence-only data; (ii) to identify areas with suitable climate (and thus a high probability) for future colonization; and (iii) to generate a spatially explicit predictive map of environmental suitability.

Materials and methods

Occurrence data

An occurrence database for the bronze bug was compiled from a few specimens held at the Museo de La Plata (Argentina) and from the literature (Jacobs & Neser, 2005; Carpintero & Dellapé, 2006; Noack & Coviella, 2006; Chilima *et al.*, 2008; Bouvet & Rodríguez, 2009; COSAVE, 2009; Nadel *et al.*, 2009; Noack *et al.*, 2009, 2011; Martínez & Bianchi, 2010; Rodrigues Barbosa *et al.*, 2010; Wilcken *et al.*, 2010; Dovey *et al.*, 2011; Ide *et al.*, 2011; Savaris *et al.*, 2011; Laudonia & Sasso, 2012; Martins *et al.*, 2012; Mascarin *et al.*, 2012; Nadel & Noack, 2012; Sopow *et al.*, 2012; Souza *et al.*, 2012; Benítez Díaz *et al.*, 2013; Garcia *et al.*, 2013; Magalhães Pereira *et al.*, 2013; Oumar *et al.*, 2013). Some African records reporting the bronze bug lack locality data: Kenya (Noack *et al.*, 2011), Zimbabwe (Chilima, 2007; Nadel *et al.*, 2009), Mozambique (Nadel & Noack, 2012) and Malawi (FAO, 2012). We confirmed some localities in Kenya by personal communication with Mr E. Mutitu (Forestry and Agricultural Biotechnology Institute, South Africa), who also informed us of the presence of the bronze bug in Uganda and Tanzania (the latter was not included in the present study because of the lack of locality information). From Malawi, locality data were obtained from a pest alert flyer (Chilima *et al.*, 2008) sent to us by Dr C. Chilima (Forestry Research Institute of Malawi).

We assembled 293 occurrence localities: 171 from South America, 59 from Africa, four from Europe and 59 from Oceania (see Supporting information, Doc. S2). When coordinates were published, we used them but, in most cases, only localities were mentioned, and the geographical coordinates were obtained from Google Earth. If only distributional maps were available, the localities were geo-referenced using ARCMAP, version 10 (ESRI, 2011).

There were variations in the occurrence data in different continents for spatial density, which depends on sampling intensity, mainly because of the proximity of the tree plantations to roads. Therefore, to avoid overemphasizing a sampled area, we selected points for model calibration using a subsampling regime to reduce sampling bias and spatial autocorrelation that could distort potential distributional models (Dormann *et al.*, 2007; Veloz, 2009; Nuñez & Medley, 2011; Zhu *et al.*, 2012a,b). In accordance with Nuñez & Medley (2011) and Zhu *et al.* (2012a,b), we developed a model for each continent (except Europe, where there were only four records) using all occurrence points, and spatial autocorrelation was defined among pseudo-residuals (1 − probability of occurrence generated by model) by calculating Moran's I at multiple distance classes using SAM, version 4.0 (Rangel *et al.*, 2010). Significance was determined by permutation tests.

Distances where spatial autocorrelation was minimal differed by continent: South America, 258 km; Africa, 188 km; and Oceania, 716 km. Grids were created for each continent with the cell dimensions of the minimal distances detected and one occurrence point per cell was selected. As a result, the dataset was reduced from 293 to 51 occurrence points: 25 from South America, 15 from Africa, seven from Oceania and four from Europe. This procedure greatly reduced sampling bias and spatial autocorrelation, resulting in evenly distributed occurrence points across space. We used all 51 occurrence points from native and introduced records for model calibration.

Selection of variables

Environmental dimensions in which to characterize ecological niches were selected by considering the climate, which has been recognized as the main characteristic that is significantly associated with invasive species across biological groups (Hayes & Barry, 2008; Bomford *et al.*, 2009; Elith *et al.*, 2010). The environmental data were obtained from a set of 19 bioclimatic variables in the WorldClim 1.3 dataset (Hijmans *et al.*, 2005). WorldClim contains climate data (monthly precipitation and monthly mean, minimum and maximum temperature) at a spatial resolution of 2.5 arcmin (approximately 5 km^2) obtained by interpolation of climate station records from 1950 to 2000. To exclude correlated variables used for modelling, Pearson's correlation coefficient (r) was calculated between each pair of the 19 WorldClim variables for all the points from the geographical extent. For each comparison with $r \geq 0.90$ one variable was selected for modelling.

Direct climate comparisons

The climatic similarity of the invaded area compared with the source ecosystem is often a useful predictor (Peterson & Vieglais, 2001; Bomford *et al.*, 2009; Rödder & Lötters, 2010). Zhu *et al.* (2012b) hypothesized that, if the environmental dimensions selected are those with low discrepancy between native and introduced populations, then niche model transferability might be improved among these areas, and thus more accurate models might be obtained. This is valid for species that are conservative of their niche during the invasion of new areas, although a climatic niche shift could also be expected. We defined two datasets to consider the two possibilities: that the bronze bug will be conservative of its niche during biological invasion or that climatic niche shift will occur. Accordingly, we analyzed the similarities of the environmental dimensions between native and introduced populations. Raw environmental data were extracted from environmental rasters in species' occurrence records using DIVA-GIS (http://www.diva-gis.org/) and compared in boxplots. By comparison of the boxplots, we were able to identify those variables with low discrepancy between native and introduced populations (variables with overlapping columns). With this information, we defined two datasets: one highly dimensional (non conservative) and a simpler one with only those variables with low discrepancy between native and introduced populations (highly conservative). Both datasets were used to calibrate the models.

Ecological niche modelling

Presence/absence models are frequently used to predict species distribution, although there is a common problem related to the uncertainty in determining absences (Phillips *et al.*, 2006), especially where the species does not occupy all available suitable habitats (Gibson *et al.*, 2007). This is frequently the case in invasive species (Kadoya *et al.*, 2009) whose distribution ranges are still spreading. In such cases, methods to model presence-only data such as maximum entropy modelling are powerful tools for predicting the potential distributions of species across new areas (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Phillips *et al.*, 2006; Pearson *et al.*, 2007; Raes & ter Steege, 2007).

The models were performed using MAXENT, version 3.3.3k (Phillips *et al.*, 2006), which was specifically developed to model species distributions with presence only data and has outperformed most other modelling applications. Default settings were used to run the models and were built through cross-validation. We used a 10-fold cross validation, which leaves out 10% of the data as a testing set at each of 10 iterations, building the model on the remaining 90% of the data in each iteration. Model evaluation was carried out via the area under the curve (AUC). We used the null models approach to test whether our models provide a better fit than would be expected by chance. Ninety-nine null models were built by drawing random occurrence points without replacement. Each null model was based on an equal number of occurrence points and modelled under the same conditions as the real models. The AUC of these null models were used to test the significance of the real models. If the AUC of the real models fell in or above the highest 5% of the AUCs of the null models, the real models were considered statistically significantly better than random (Raes & ter Steege, 2007).

Results

Pearson results

The exploratory analysis to identify the environmental variables defining suitable climate led to a combination of 14 minimally correlated variables (see Supporting information, Doc. S3). These are: annual mean temperature (BIO1), mean monthly temperature range (BIO2), isothermality (BIO3), temperature seasonality (BIO4), minimum temperature of coldest month (BIO6), mean temperature of wettest quarter (BIO8), mean temperature of driest quarter (BIO9), mean temperature of warmest quarter (BIO10), annual precipitation (BIO12), precipitation seasonality (BIO15), precipitation of wettest quarter (BIO16), precipitation of driest quarter (BIO17), precipitation of warmest quarter (BIO18) and precipitation of coldest quarter (BIO19).

Direct comparisons

Figure 1 provides an overview of climate conditions at sites with records of native and introduced bronze bug. From the visual comparison of the boxplots of the 14 variables occupied by native and introduced populations, we were able to identify nine variables with low discrepancy in which the interquartile range overlaps. These are: BIO1, BIO2, BIO8, BIO10, BIO12, BIO15, BIO16, BIO17 and BIO19. These results allowed us to define the two datasets used for model calibration; dataset I, which includes 14 variables (the only variables excluded are the highly

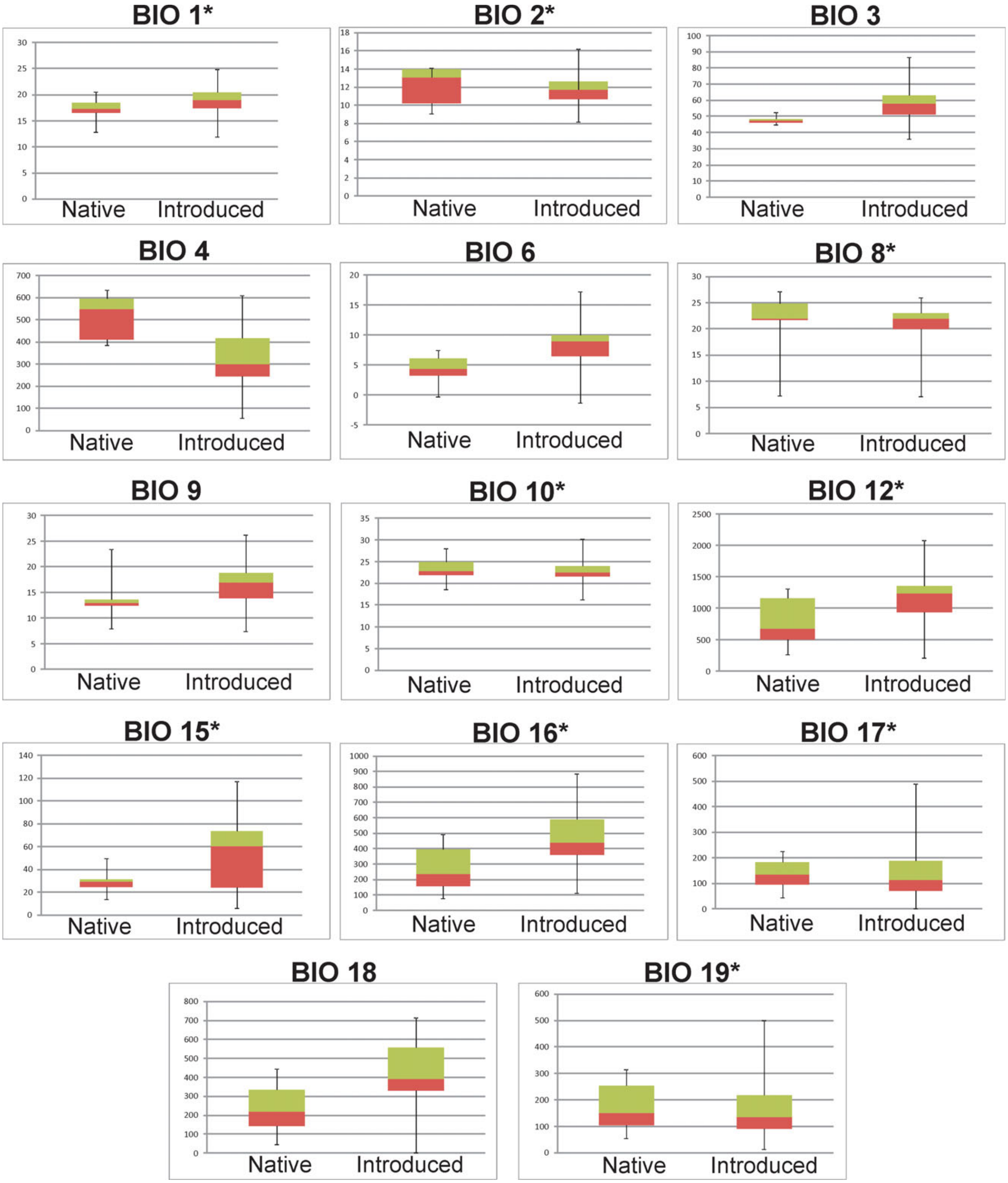

Figure 1 Direct comparison of the bronze bug occurrence-associated variables between native and introduced distributional areas. Asterisk (*) indicates variables with overlapping columns (i.e. interquartile range) between the two areas, representing variables of low discrepancy; variables of high discrepancy were excluded from Dataset II. BIO1, annual mean temperature; BIO2, mean monthly temperature range; BIO3, isothermality; BIO4, temperature seasonality; BIO6, minimum temperature of coldest month; BIO8, mean temperature of wettest quarter; BIO9, mean temperature of driest quarter; BIO10, mean temperature of warmest quarter; BIO12, annual precipitation; BIO15, precipitation seasonality; BIO16, precipitation of wettest quarter; BIO17, precipitation of driest quarter; BIO18, precipitation of warmest quarter; and BIO19, precipitation of coldest quarter.

correlated ones), and dataset II, which includes the nine variables with reduced discrepancy between native and introduced range.

Model comparisons: predicted range of suitable climates for the bronze bug

The two environmental datasets, dataset I (non conservative) and dataset II (highly conservative) showed very good model projection. For dataset I, the average test AUC was 0.957, the standard deviation was 0.031 and the AUC ranged from 0.876 to 0.981. For dataset II, the average test AUC was 0.951, the standard deviation was 0.032 and the AUC ranged from 0.862 to 0.979. Both models provide a significantly better fit than expected by chance alone (see Supporting information, Doc. S2). Models trained on the two datasets showed the same general pattern of distribution, although dataset I was more reduced (Fig. 2). The model built with environmental dimensions with low discrepancy between native and introduced populations (highly conservative) (Fig. 3) shows larger areas of climatic suitability for the bronze bug, mainly in southern U.S.A., along the north-east of the Andes in South America, in central Africa and in south-eastern Europe. The climatic variables that appear to constrain the distribution of the bronze bug are mostly related to temperature (BIO3, BIO4, BIO6 and BIO9).

According to our models (Figs 2 and 3), in Oceania, climate conditions are suitable in southern and eastern Australia, Tasmania and New Zealand. In Africa, climate conditions are suitable in south-east South Africa, Madagascar, middle-east Africa, and coastal regions of Morocco, Algeria and Tunisia; and the most suitable conditions are found where the bronze bug is already established, extending to the north mainly in Ethiopia. In Asia, climatic conditions are suitable for the bronze bug in southern China, Myanmar, Cambodia, Laos and India.

In South America, suitable climatic conditions for the bronze bug primarily include the currently known range of the species, extending northward along the Brazilian coast, and to the west to Paraguay, Bolivia and northern Argentina. A narrow suitable area also appears along the east of the Andes from Bolivia to Venezuela. In Chile, the suitable area spans south from known records of the bronze bug. In North and Central America, conditions are suitable from southern North America to Nicaragua, on most of Caribbean Islands, and along a narrow fringe on the west coast of U.S.A.

In Europe, climate conditions are suitable in most of western and southern Europe; the most suitable areas being in Italy, France, Spain and Portugal.

Discussion

Climatic model predictions are an important tool and a valid first approach to the potential magnitude and distributional pattern of future impact of invasive species, although they should be interpreted carefully because they do not consider important factors other than climate, such as biotic interactions. Thus, populations will not necessarily become successfully established in an area predicted as climatically suitable because other factors may be unsuitable (e.g. an absence of their host plant or the presence of competitors, predators or pathogens). Moreover, these models cannot predict the full extent of the invasion in the new range. There are several examples of invasive species occupying new niches during biological invasion (Broennimann *et al.*, 2007; Angetter *et al.*, 2011; Bidinger *et al.*, 2012). There is as yet insufficient evidence to confirm whether the bronze bug is conservative of its niche or if a climatic niche shift could be expected during the invasion. These two possibilities are considered in the two datasets that we used to

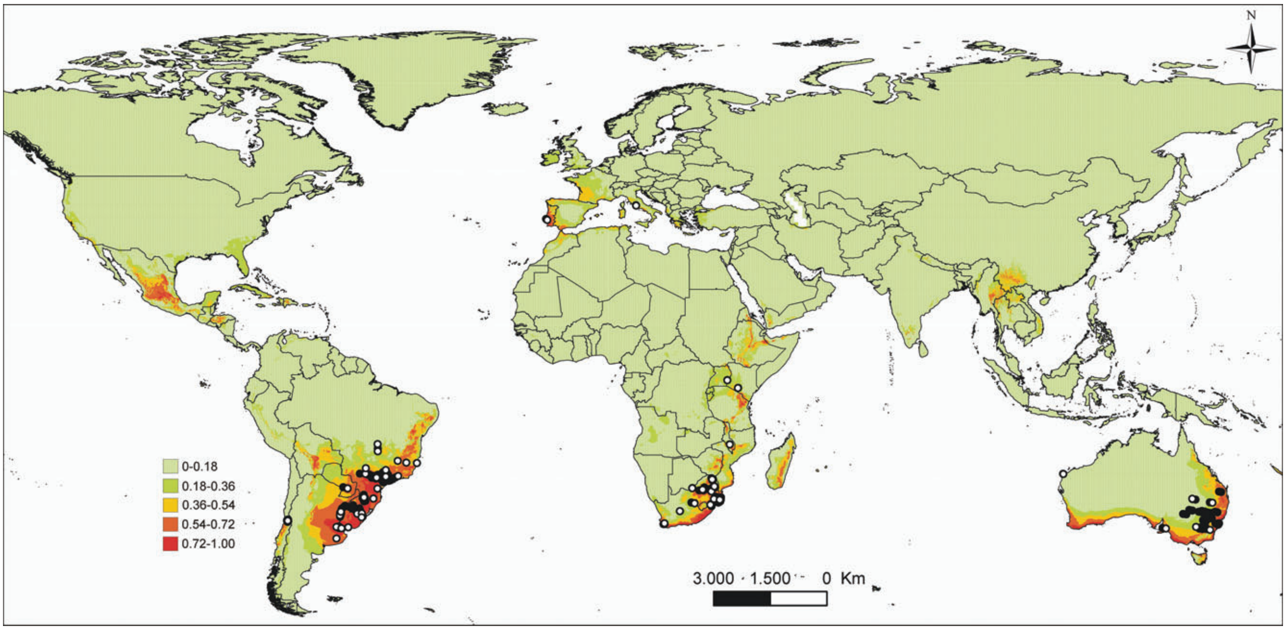

Figure 2 Niche models based on 51 records (white dots) and transferred worldwide. Based on dataset I. Black dots represent occurrences of the bronze bug excluded from model calibration. Darker tone /red colour represents high suitability, lighter tone/green colour indicates low suitability.

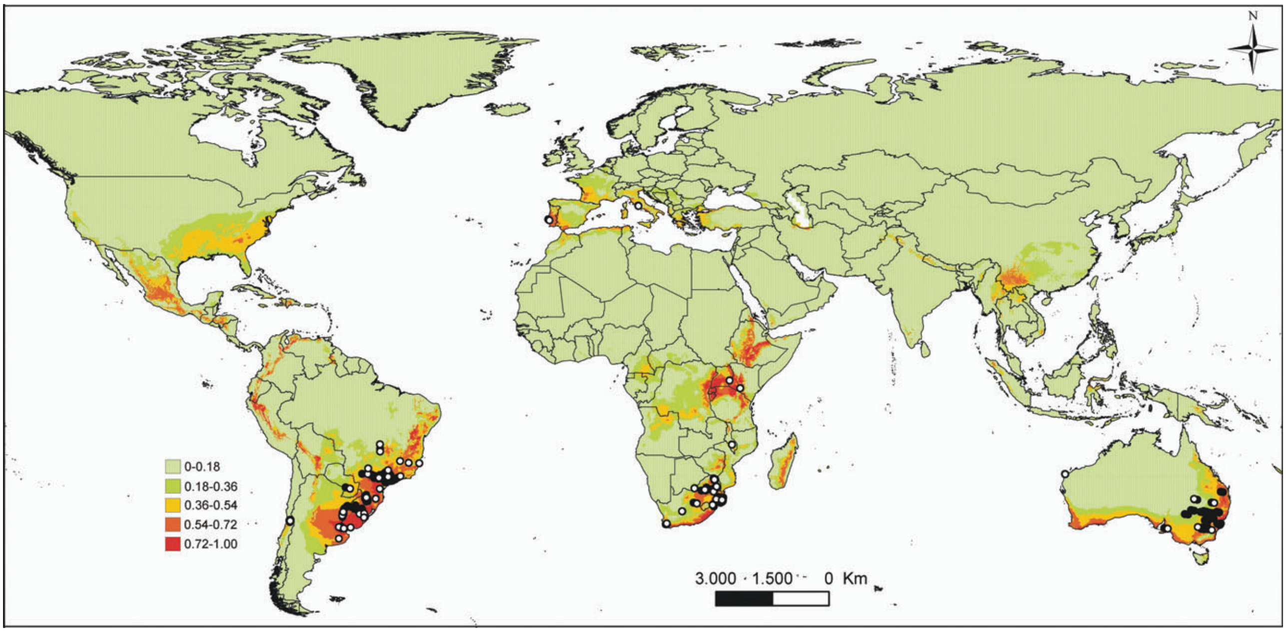

Figure 3 Niche models based on 51 records (white dots) and transferred worldwide. Based on dataset II. Black dots represent occurrences of the bronze bug excluded from model calibration. Darker tone /red colour represents high suitability, lighter tone/green colour indicates low suitability.

build our models. According to both models, the most probable scenario is that the range of the bronze bug will continue to expand. In South America and Africa, the distribution of the bronze bug may expand mainly to the north-east and central areas. Special attention should be given to the regions of southern U.S.A., Central America, and southern China and nearby countries, where conditions are highly suitable but the bronze bug has not yet been recorded and could only arrive by human means.

In Asia, there is no record of the bronze bug, although particular attention must be paid to regions where *Eucalyptus* is cultivated and our models predict good climatic suitability. These regions are located in India, China, and Myanmar. India has over 3.9 million ha of *Eucalyptus* plantations, ranking second in the world (Booth, 2012). In China, the *Eucalyptus* plantation industry has undergone rapid development, and there are over 2.6 million ha of these plantations, ranking third in the world (Booth, 2012). In this vast country, the region endangered, according to our results, is the Yunnan province (Figs 2 and 3), where *Eucalyptus* plantations cover more than 60 000 ha (Wang *et al.*, 2011).

In the U.S.A., where there is increasing interest in establishing short rotation eucalypt plantations in the south-eastern region to meet biofuel needs (Booth, 2012), special care should be taken to prevent the introduction of the bronze bug. Historically, the use of eucalypts in southern U.S.A. has been limited by their freeze tolerance (Meskimen *et al.*, 1987; Rockwood *et al.*, 2008), although selection and genetic modification are increasing that range (Gordon *et al.*, 2012). The demand for hardwood, pulp and bio-energy in southern U.S.A. is increasing and, in the specific case of bio-energy and pulp demand for biomass from eucalypts, the projection by 2022 could approach 20 million tons/year (Dougherty & Wright, 2012).

In Central America, mainly in Mexico, *Eucalyptus globulus* and *Eucalyptus camaldulensis* are the most common species (Kiwanja, 2007), both of which are susceptible to infestation by the bronze bug. At present, these trees are used for various purposes, including windbreaks, aesthetic purposes, cellulose for paper production and, in some rural areas, fuel (Álvarez Zagoya & González Lozano, 2012). Although only approximately 25 000 ha are currently cultivated, the number is increasing every year (Pérez-Vera *et al.*, 2005). Some studies report that Mexico has 11 million ha suitable for cultivation of *Eucalyptus*, mainly in the south-east of the country (Martínez Ruiz *et al.*, 2006).

In Europe, where the bronze bug is only known from a few localities in Italy and Portugal, the climatic suitability predicted shows that there could be a major increase in its range. In these two countries and Spain, *Eucalyptus* spp. are cultivated on a large scale for industrial purposes (Tomé *et al.*, 2001; Facciotto & Mughini, 2003; Tolosana *et al.*, 2010). The Mediterranean region, where highly susceptible species of *Eucalyptus* are common (e.g. *E. camaldulensis*), would be the most highly threatened area. Laudonia & Sasso (2012) have warned that the bronze bug may become a serious pest for the eucalyptus plantation industry, as well as in parks and urban areas. Some studies (Laudonia & Sasso, 2012; Garcia *et al.*, 2013) suggest that South America and South Africa are the source of the pest through the importation of wood; the hypothesis of introduction via South America is reinforced by the discovery in Portugal of a South American neuropteran predator of the bronze bug.

Because *Eucalyptus* plantations are increasing worldwide, and the most commonly planted species are highly susceptible to infestation (Jacobs & Neser, 2005; Bouvet & Rodríguez, 2009; Laudonia & Sasso, 2012), and because the dispersion of the bronze bug has increased rapidly over the last 8 years, the occurrence of this invasive species should be expected in many areas where it has not yet been recorded.

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Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference:
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Doc. S1. List of *Eucalyptus* species reported as a host plant of bronze bug *Thaumastocoris peregrinus.*

Doc. S2. Occurrence data and sources.

Doc. S3. Correlation matrix of all variables and performance of the calibrated species distribution models against the performance of the null models.

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