Evaluation of the impacts of climate change on disease vectors through ecological niche modelling

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Abstract

Vector-borne diseases are exceptionally sensitive to climate change. Predicting vector occurrence in specific regions is a challenge that disease control programs must meet in order to plan and execute control interventions and climate change adaptation measures. Recently, an increasing number of scientific articles have applied ecological niche modelling (ENM) to study medically important insects and ticks. With a myriad of available methods, it is challenging to interpret their results. Here we review the future projections of disease vectors produced by ENM, and assess their trends and limitations. Tropical regions are currently occupied by many vector species; but future projections indicate poleward expansions of suitable climates for their occurrence and, therefore, entomological surveillance must be continuously done in areas projected to become suitable. The most commonly applied methods were the maximum entropy algorithm, generalized linear models, the genetic algorithm for rule set prediction, and discriminant analysis. Lack of consideration of the full-known current distribution of the target species on models with future projections has led to questionable predictions. We conclude that there is no ideal 'gold standard' method to model vector distributions; researchers are encouraged to test different methods for the same data. Such practice is becoming common in the field of ENM, but still lags behind in studies of disease vectors.

Introduction

Climate change is happening more quickly and strongly than predicted, and the anthropic influence in this process is now clear (IPCC, 2014). Projections from several greenhouse gas emission scenarios agree on an increase of the mean earth surface temperature by the end of the 21st century, with continents heating more than oceans and high latitude regions heating more than the tropics. Longer and more frequent heat waves will probably occur, as well as more intense precipitation events in several regions (IPCC, 2014). Increased floods, droughts, fires, heat waves and air pollutants will directly impact human health. Indirect impacts on human health will arise from ecological disturbances and social responses to disruptions to agriculture, and to water and food supplies. Vector-borne diseases will also increase, compounded by human migrations towards endemic areas (Woodward *et al.*, 2014).

Vector-borne diseases are exceptionally sensitive to climate change because they emerge from complex transmission

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cycles involving several species of pathogens, vectors and hosts (Parham *et al.*, 2015). Most disease vectors are arthropods, including insects and ticks. Climate change should, therefore, cause changes in disease distribution, density, seasonality and prevalence, and might prompt adaptation of vectors and hosts to new transmission cycles (Kovats *et al.*, 2001; Brooks & Hoberg, 2007; Rosenthal, 2009; Mills *et al.*, 2010).

The ecology of arthropod vectors should be impacted by climate change at three levels of biological organization: (i) at the individual level – being ectothermic organisms, vectors' metabolism varies with daily fluctuations in temperature, which may affect physiological traits related to vector competence (Paaijmans *et al.*, 2013) such as muscle activity (Harrison & Roberts, 2000) and biting rates, although this latter influence is not entirely clear (Rogers & Randolph, 2006; Ready, 2013); (ii) at the population level – changes in climate should influence abundance, density, seasonality, survival rates, generation time, fecundity and dispersion ability, allowing vectors to colonize new habitats more efficiently (Mills *et al.*, 2010; Stange & Ayres, 2010; Eisen *et al.*, 2014); (iii) at the community level – parasite–vector interactions can be influenced by temperature (Hlavacova *et al.*, 2013), and new species of vectors or hosts can adapt to existing transmission cycles (Kovats *et al.*, 2001; Rosenthal, 2009; Parham *et al.*, 2015).

Knowledge of vectors' spatial distributions is essential to assess transmission risks in different regions. Predicting vector occurrence in specific regions is a challenge that many disease control programs must meet in order to plan and execute control interventions and adaptation measures more efficiently. With the popularization of GIS (geographic information systems), increasing availability of species occurrence data, disease information and environmental variables, various methods of spatial analysis and mathematical modelling have become common in the scientific literature. The methods that correlate these available data in order to predict species' distributions are known as ecological niche models (ENMs) or species distribution models and have been widely used in studies of ecology, biogeography and conservation (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith & Leathwick, 2009). Recently, an increasing number of scientific articles have applied these models to study distributions of many medically important insect and tick species.

Ecological niche models are perhaps the most used methods to link climatic and environmental conditions to the distribution of species. In an ENM, an algorithm takes as input occurrence records of the studied species and calculates their relation with environmental variables, producing a surface of environmental suitability or probability of occurrence (Guisan & Zimmermann, 2000; Franklin, 2010; Peterson *et al.*, 2011). There are two basic approaches to apply an ENM in studies of vector-borne diseases. The first considers the entire transmission cycle and their ecological relationships as a 'black box', and analyses the geographical distribution of the disease occurrence, as if it were a single species (e.g. Nieto *et al.*, 2006; Yé *et al.*, 2007; Williams *et al.*, 2008; Arboleda *et al.*, 2009). This approach indirectly groups all component species of the transmission cycle, as well as their environmental needs and ecological interactions, losing, therefore, important details of the transmission process. However, the occurrence of the disease is often the only information available, and this becomes the only modelling option. The second approach is to model each species from the transmission cycle individually, and evaluate areas of co-occurrence afterwards. This approach

offers the opportunity to distinguish different reasons for the presence or absence of disease transmission in certain locations. For example, the disease may be absent due to the lack of the pathogen, an appropriate vector or a reservoir host (Peterson *et al.*, 2011). Areas with the presence of only vectors and competent hosts may be treated as vulnerable – a particularly important situation nowadays, when species are artificially transported by humans and new diseases emerge in areas where they would not naturally occur (Komar, 2003; Ready, 2008, 2010; Daszak *et al.*, 2013).

Comparative studies show that most of uncertainty in ENM comes from using different modelling algorithms (Buisson *et al.*, 2009; Diniz-Filho *et al.*, 2009; Elith & Graham, 2009). With the wide variety of methods, it is an additional challenge to interpret and compare the results of studies on vector distributions, so that they can be effectively used in control programs. Here we review the future projections of disease vectors produced by ENMs, and assess trends and limitations of the methods applied.

Methods

We performed a systematic review of the literature using four online databases: (i) Web of Science (http://isiwebofknowledge.com); (ii) Scopus (http://www.hub.sciverse.com); (iii) Pubmed (http://www.ncbi.nlm.nih.gov/pubmed); and (iv) Scientific Electronic Library Online (SciELO) (http://www.scielo.org). The Web of Science is the most comprehensive database of peer-reviewed articles published in English, as well as being the most used in systematic reviews (Falagas *et al.*, 2008; Gavel & Iselid, 2008). However, Scopus covers a larger number of journals that publish articles in languages other than English (Falagas *et al.*, 2008; Gavel & Iselid, 2008). PubMed is the most frequently consulted source for information in the biomedical field (Falagas *et al.*, 2008). The SciELO database, although less comprehensive, includes many Latin American journals that are not included in the other consulted databases.

Searches were conducted in March 2015, through different combinations of the following key words: 'ecologic* niche model*' 'species distribution model*', 'climat* model*', 'vector', 'disease'. The initial results ($N = 572$) were limited to articles published until 2014 that applied ENMs to predict areas of occurrence or environmental suitability of arthropods vectors of diseases. Articles that used models to explain the relationship of the vectors with environmental variables, without predictive mapping, were excluded from the analysis. Studies with models based only on the occurrence of disease or risk maps generated without vector information were also discarded. After removing duplicates and refining selections, 146 articles were reviewed (Table S1).

The articles were described under the following categories: vector species and main associated disease; study area; types of biological data; types of environmental data; applied method; inclusion of future projections (Table S1). Studies including future projections were analysed in greater detail in relation to biological data (number of records, data source), environmental data (number of variables, approximate spatial resolution), methods (algorithm employed, use of ensemble models based on different algorithms) and future projections (years, general circulation model, climate change scenario) (Table S2). The main results of the future projections were summarized by vector group and further described.
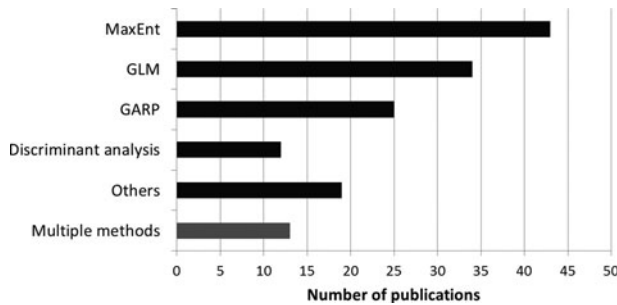
Fig. 1. Methods applied in the literature of ecological niche modelling of arthropod vectors of diseases.

Results and discussion

Application of different modelling methods

Seventeen different modelling methods were used to predict vector distributions. The most common was the maximum entropy algorithm (MaxEnt, 43 articles) (Phillips *et al.*, 2006), followed by generalized linear models (GLM, 34) (Guisan *et al.*, 2002), the genetic algorithm for rule set prediction (GARP, 25) (Stockwell, 1999), and discriminant analysis (12) (Rogers *et al.*, 1996) (fig. 1, Table S1). Other methods were less frequently applied, such as CLIMEX (5) (Sutherst & Maywald, 1985), ENFA (3) (Hirzel *et al.*, 2002), BRT (2) (Elith *et al.*, 2008), BIOCLIM (1) (Booth *et al.*, 2014) and Random Forests (1) (Breiman, 2001) (fig. 1, Table S1). For comprehensive descriptions of ENM algorithms, see Franklin (2010) and Peterson *et al.* (2011).

The predictive performance of MaxEnt has exceeded other algorithms in several comparative studies (Elith *et al.*, 2006; Foley *et al.*, 2009, 2010; Larson *et al.*, 2010; Arboleda *et al.*, 2012). In addition, its popularity can probably be explained by the fact that it is implemented in free software with a user-friendly interface, good documentation and many options for parameterization. Generalized linear models were the second-most frequent method because they offer more flexibility than machine learning algorithms (e.g. MaxEnt and GARP), thus improving model fit and ecological interpretations of parameters (Franklin, 2010). Also noteworthy is the use of CLIMEX, a mechanistic (process-based) algorithm. Mechanistic models are based on vector's biological processes, such as duration of life cycle, biting rates, dispersal ability, temperature limits for larvae development, etc. The inclusion of this type of data improves the biological meaning of models, but they require solid empirical knowledge about the vectors' physiology, which makes parameterization a challenge (Kearney & Porter, 2009; Dormann *et al.*, 2012; Fischer *et al.*, 2014).

Models produced by different algorithms may have dissimilar, even contrasting outputs (Dormann *et al.*, 2008; Diniz *et al.*, 2009; Elith & Graham, 2009; Li & Wang, 2013). Independent evaluations have often been unable to identify a single recommended algorithm for all circumstances (Elith *et al.*, 2006; Elith & Graham, 2009; Li & Wang, 2013; Qiao *et al.*, 2015). An alternative to avoid the choice of a particular method is to test models produced by a set of algorithms (Qiao *et al.*, 2015) and combine their results as an ensemble model (Araújo & New, 2007; Marmion *et al.*, 2009). With a set of models produced by a number of algorithms, uncertainty can be properly quantified, thus improving the study's result

(Pearson *et al.*, 2006; Owens *et al.*, 2013; Qiao *et al.*, 2015). The use of multiple algorithms was present in over 70% of general ENM studies published recently (Guillera-Arroita *et al.*, 2015), but it was under-represented in ENM of disease vectors for the same period (approximately 10%). This represents a significant delay in disease vector studies in relation to what is currently being published.

A good example of the multiple algorithm approach was a comparison between models produced by BIOCLIM, DOMAIN (Carpenter *et al.*, 1993), GARP, GLM (logistic regression) and MaxEnt to identify areas of high density of *Aedes* mosquitoes in Bermuda (Khatchikian *et al.*, 2011). The results varied between the different algorithms, but since GLM and MaxEnt performed better, both were used to predict risk areas of mosquito infestations (Khatchikian *et al.*, 2011). Another example was a study of the distribution patterns of natural breeding sites of *A. aegypti* in Colombia, where models produced by GARP had fewer omission errors than those produced by MaxEnt (Arboleda *et al.*, 2012). Models produced by MaxEnt performed better in certain regions, although areas predicted as suitable by the two algorithms coincided closely. The two algorithms were combined into an ensemble model, where coincident areas were considered suitable with greater confidence. The combination of methods improved the detection of natural breeding sites, allowing the optimization of effort and financial investment in dengue control programs in the region (Arboleda *et al.*, 2012).

Future projections of vector distributions

Over 700 vector species were studied in the 146 reviewed papers, including mostly mosquitoes (63 articles) and sand flies (29), followed by works on kissing bugs (18), biting midges (17), ticks (14), tsetse flies (3), fleas (1) and water bugs (1) (Table S1). The geographic extent of the reviewed studies varied from local to global (Table S1). The 31 studies with future ENM projections mostly point to expansions in response to climate change scenarios, accompanied by poleward shifts (table 1). This trend is being observed for several taxonomic groups, where long-term field studies demonstrate recent species' movements towards higher latitudes and higher altitudes in response to climate change (Hickling *et al.*, 2006; Stange & Ayres, 2010; Chen *et al.*, 2011). There is, however, a noteworthy methodological issue in about half of the reviewed studies (table 1). When projecting into future scenarios, models should be trained with the full-known distribution of the species. If only a subset of the realized niche is used, future predictions may underestimate environmentally suitable areas and quantifications of range changes become questionable (Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Araújo & Peterson, 2012). An additional source of uncertainty in future forecasts is the extrapolation of models into climatic conditions that do not presently exist (Fitzpatrick & Hargrove, 2009). Some ENM algorithms have standard ways of controlling extrapolation, such as MaxEnt, by limiting output values to the range of environmental variables under which the model was calibrated (Phillips *et al.*, 2006). Alternatively, out-of-range values can be masked directly in model predictions (Owens *et al.*, 2013; Carvalho *et al.*, 2015).

Aedes aegypti and *Aedes albopictus* (Diptera: Culicidae)

The main vector of dengue, *A. aegypti*, is currently distributed throughout most tropical regions of the world.

Table 1. Overview of the future projections of the distributions of arthropod vectors of diseases.

Species	Main disease	Study area	Full current distribution of species	Algorithm	Year of projections	Difference of projected area	General range shift directions	Reference
Diptera: Culicidae								
Aedes aegypti	Dengue	Australia	No	GARP	2030, 2050	Expansion	Central, south	Beebe *et al.* (2009)
Aedes aegypti	Dengue	Global	Yes	Alpha-shapes	2010–2040	Expansion and contraction	Several directions	Capinha *et al.* (2014)
Aedes aegypti	Dengue	Brazil	No	MaxEnt	2050	Contraction	South	Cardoso-Leite *et al.* (2014)
Aedes aegypti	Dengue	Global	Yes	CLIMEX	2030, 2070	Contraction, discrete expansion	Several directions	Khormi and Kumar (2014)
Aedes albopictus	Arboviruses	Trentino, Italia	No	GLM (logistic)	2050	Expansion	East, west	Roiz *et al.* (2011)
Aedes albopictus	Arboviruses	Europe	Yes	MaxEnt	2040, 2070, 2100	Expansion	North, east, west	Fischer *et al.* (2011*c*)
Aedes albopictus	Arboviruses	Australia, global	Yes	MaxEnt, CLIMEX	2030, 2050	Discrete expansion	Central	Hill *et al.* (2014)
Aedes stictus	Arboviruses	Sweden	No	Other	2020, 2050, 2080	Expansion	North	Schäfer and Lundström (2009)
Anopheles arabiensis	Malaria	Sudan and North of Egypt	No	MaxEnt	2050	Expansion	Not given	Fuller *et al.* (2012)
Anopheles arabiensis	Malaria	Africa	Yes	LOBAG-OC	2050	Contraction	East, southeast	Drake and Beier (2014)
Anopheles gambiae and *Anopheles arabiensis*	Malaria	Africa	Yes	CLIMEX	Not given	Expansion	South, east	Tonnang *et al.* (2010)
Anopheles gambiae and *Anopheles arabiensis*	Malaria	Africa	Yes	GARP	2055	Expansion	South, east	Peterson (2009)
Anopheles gambiae and *Anopheles arabiensis*	Malaria	Africa	Yes	CLIMEX	Not given	Expansion	South, east	Tonnang *et al.* (2014)
Diptera: Psychodidae								
Lutzomyia antophora and *Lutzomyia diabolica*	Leishmaniasis	North America and Mexico	Yes	MaxEnt	2020, 2050, 2080	Expansion	North, northeast	González *et al.* (2010)
Lutzomyia longipalpis and *Lutzomyia evansi*	Leishmaniasis	Colombia	No	MaxEnt	2020, 2050, 2080	Expansion or contraction (at different scenarios)	North	González *et al.* (2014)
Lutzomyia spp. (three species)	Leishmaniasis	South America	Yes	GARP	2055	Expansion	South, southeast	Peterson and Shaw (2003)
Phlebotominae (28 species)	Leishmaniasis	North and Central Americas	No	GARP	2020, 2050, 2080	Expansion in 97% of species, contraction in 3%	Northwest (64% of species), northeast (35%), southeast (0,6%)	Moo-Llanes *et al.* (2013)
Phlebotomus papatasi	Leishmaniasis	Southeast Asia	No	Discriminant Analysis	Not given	Expansion	Not given	Cross and Hyams (1996)
Phlebotomus perniciosus	Leishmaniasis	Bavaria, Germany	No	MaxEnt	2040	Expansion	Not given	Fischer *et al.* (2011*b*)

Table 1. (*Cont.*)

Species	Main disease	Study area	Full current distribution of species	Algorithm	Year of projections	Difference of projected area	General range shift directions	Reference
Phlebotomus ariasi and *Phlebotomus perniciosus*	Leishmaniasis	Madrid, Spain	No	GLM (negative binomial)	2040, 2070, 2100	Expansion	Not given	Gálvez *et al.* (2011)
Phlebotomus spp. (five species)	Leishmaniasis	Southern Germany	No	MaxEnt	2040	Expansion	Central, northwest	Haeberlein *et al.* (2013)
Phlebotomus spp. (five species)	Leishmaniasis	Central Europe	No	MaxEnt	2040, 2070, 2100	Expansion	Mostly east	Fischer *et al.* (2011*a*)
Diptera: Ceratopogonidae								
Culicoides imicola	Bluetongue	Spain	No	GLM (negative binomial)	2040	Stability	Not given	Acevedo *et al.* (2010)
Culicoides imicola	Bluetongue	Europe	No	GLM (logistic)	Not given	Expansion	North	Wittmann *et al.* (2001)
Culicoides imicola	Bluetongue	Global	Yes	CLIMEX	2030, 2070	Expansion and contraction	Mostly north	Guichard *et al.* (2014)
Hemiptera: Reduviidae								
Triatoma gerstaeckeri and *Triatoma sanguisuga*	Chagas disease	Mexico and USA	Yes	MaxEnt	2050	Expansion	North, northeast	Garza *et al.* (2014)
Triatoma brasiliensis species complex	Chagas disease	Northeast Brazil	Yes	MaxEnt, GARP	2020, 2050	Stability	Not given	Costa *et al.* (2014)
Acari: Ixodida								
Ixodes ricinus	Lyme disease	Europe	No	GARP	2050	Expansion and contraction	North	Boeckmann and Joyner (2014)
Ixodes ricinus	Lyme disease	Europe and Asia	Yes	MaxEnt	2050, 2080	Expansion	North, east	Porretta *et al.* (2013)
Ixodes scapularis	Lyme disease	USA/Mexico border	Yes	MaxEnt	2050	Expansion	Northeast	Feria-Arroyo *et al.* (2014)
Ixodidae (six species)	Lyme disease	Mediterranean region	Yes	ENFA	Not given	Not given	Not given	Estrada-Peña and Venzal (2007)

Projections of its global distribution showed that most areas that are currently occupied should remain climatically favourable for its occurrence in 2030 and 2070, while new areas will become suitable for its range expansion, such as the Australian outback, the Arabian Peninsula, southern Iran and parts of North America (Khormi & Kumar, 2014). Further projections for the near future indicate that suitable macroclimatic conditions for this vector should begin to expand between 2010 and 2039 (Capinha *et al.*, 2014). In Brazil, models predict a contraction of its range in the northern and northeastern regions, accompanied by a probable expansion in the south by 2050 (Cardoso-Leite *et al.*, 2014). Since *A. aegypti* is a vector with high adaptability to urban environments, its local distribution is also influenced by the occurrence of artificial breeding sites such as water tanks and swimming pools. In Australia, models based only on climatic variables failed to detect locations of its known occurrence and of human cases of dengue (Beebe *et al.*, 2009). This inconsistency was attributed to human behaviour, as residents began to store water during a regional drought attributed to climate change (Beebe *et al.*, 2009). The study pointed out, therefore, not only the local-scale limitations of ENM, but also the importance of implementing climate change adaptation measures that are compatible with disease control programs (Beebe *et al.*, 2009). Despite not using the full-known distribution of the vector in model training, predictions of future range contraction in Brazil (Cardoso-Leite *et al.*, 2014) and of future inland expansion in Australia (Beebe *et al.*, 2009) were similar to those predicted by models based on its global distribution (Capinha *et al.*, 2014; Khormi & Kumar, 2014).

In contrast to the highly anthropophilic *A. aegypti*, the Asian tiger mosquito *A. albopictus* prefers less disturbed environments and has predominantly zoophilic habits, participating in sylvatic transmission cycles of a number of arboviruses, such as chikungunya, yellow fever and dengue. Despite having relatively lower importance in human disease transmission than *A. aegypti*, the distribution of *A. albopictus* has been much studied because it is considered the most invasive mosquito species in the world (Benedict *et al.*, 2007; Medley, 2010; Porretta *et al.*, 2012). Its original distribution in Southeast Asia has expanded in recent decades to various countries in the Americas, Africa and Europe, mostly through cargo transportation (Reiter & Sprenger, 1987; Tatem *et al.*, 2006). In Europe, the species is currently established in the Mediterranean region, where local vector populations are already expanding (Roiz *et al.*, 2011). Future projections of ENM point to an increase of climate suitability areas for *A. albopictus* in central and western parts of Europe by 2040, with eastern areas becoming suitable from 2070 onwards (Fischer *et al.*, 2011*c*). Based on these projections, an assessment of the main cargo shipment routes concluded that certain areas of the continent, such as Rotterdam, Hamburg and Antwerp, have the dangerous combination of high incoming cargo from countries where *A. albopictus* occurs and high future climatic suitability for the vector (Thomas *et al.*, 2014). In Australia, where there are currently no records of *A. albopictus*, niche models based on the global distribution of the vector show that the coastal region is climatically suitable for its establishment, with projections for the coming decades indicating expansion of this suitable area towards the interior of the country (Hill *et al.*, 2014).

Anopheles spp. (Diptera: Culicidae)

The distributions of two malaria vectors in Sub-Saharan Africa, *Anopheles gambiae* and *An. arabiensis*, will also likely expand southwards and southeastwards, according to ENMs involving climate change scenarios (Peterson, 2009; Fuller *et al.*, 2012; Tonnang *et al.*, 2010, 2014). By adding mosquito survival rates to niche models, it was concluded that East African countries will have greater climatic suitability for these vectors in the coming decades than West African countries (Tonnang *et al.*, 2014). Although the models predict local regions of both increase and decrease of climatic suitability for the vectors, 11–30% fewer people should be exposed to the vectors in the coming decades, as seen by overlaying model predictions and human distribution (Peterson, 2009). A more recent study pointed to a contraction of over half of the distribution area of *An. arabiensis* in West African countries (Drake & Beier, 2014). The overall contraction of the full range of the vector might erroneously suggest less exposure to vector-borne diseases with climate change. The association with human distribution demonstrates the caution needed when interpreting predictions of ENMs of vectors. Vector occurrence *per se* does not necessarily implies higher risk of disease transmission, and a closer look at other risk factors is needed.

Lutzomyia spp. and *Phlebotomus* spp. (Diptera: Psychodidae)

Leishmaniases are neglected tropical diseases widely distributed in 98 countries, with approximately 0.2–0.4 million cases of visceral leishmaniasis and 0.7–1.2 million cases of cutaneous leishmaniasis occurring every year (Alvar *et al.*, 2012). The vectors of leishmaniases, sand flies, are classified in two genera according to their distributions: *Lutzomyia* in the Americas and *Phlebotomus* in other continents. Areas climatically suitable for the South American vectors *L. whitmani*, *L. intermedia* and *L. migonei* should expand by the year 2050 (Peterson & Shaw, 2003). Expansion areas are located in different regions of the continent, but their most evident direction is south, where *L. whitmani* will have larger suitability areas than the other two vectors (Peterson & Shaw, 2003). In contrast, in Colombia, future projections from regional distribution models indicate reduction of the total predicted area of occurrence of *L. longipalpis* and *L. evansi* associated with changes in their altitudinal distribution (González *et al.*, 2014). Unfortunately, failure to consider the full distribution of *L. longipalpis* might have produced biased predictions for Colombia (González *et al.*, 2014), because the vector occupies a broad range of latitudes from Mexico to Argentina (World Health Organization, 2010).

The vectors *L. anthophora* and *L. diabolica*, currently distributed in Mexico and the USA, are projected to expand northwards (González *et al.*, 2010). These projections were associated with predictions of the distributions of rodent hosts and human populations, and indicated that the expected number of people exposed to leishmaniases in North America will at least double by 2080 (González *et al.*, 2010). Future northward expansions of suitable areas to leishmaniasis vectors are also expected for 27 of 28 species with current occurrence in Mexico, Guatemala, Belize, USA and Canada, the exception being *L. vexator* (Moo-Llanes *et al.*, 2013). However, the predictions for species whose distributions include South America, such as *L. longipalpis* and *L. shannoni*, should be interpreted with caution because the models were only calibrated with data from Canada, USA, Mexico, Guatemala and Belize (Moo-Llanes *et al.*, 2013).

Europe is currently on alert for the emergence of leishmaniasis and the expansion of its vectors, especially in the countries in central regions of the continent, predicted to become

increasingly climatically similar to the Mediterranean region, where there are endemic areas of these diseases (Ready, 2008; Medlock *et al.*, 2014). In a region of canine leishmaniasis in Spain, an increase in the abundance of *P. ariasi* in higher altitude areas was observed, pointing out to a possible migration of the vector to these areas in response to rising temperatures (Gálvez *et al.*, 2010). Future projections predict expansions of the range and increase of local densities of both *P. ariasi* and *P. perniciosus* in the 21st century (Gálvez *et al.*, 2011); however, models were restricted to Spain, which represents only part of the range of both species at the Mediterranean region (World Health Organization, 2010). In Germany, Austria and Switzerland, there are predicted areas of increased climate suitability for five species of *Phlebotomus*, but most are unlikely to be reached by the vectors by the end of this century due to their limited dispersal ability (Fischer *et al.*, 2011*a*). This finding was reinforced by later field sampling in the region of Bavaria, southern Germany, where no sand flies were caught (Haeberlein *et al.*, 2013). However, field studies show that several species of *Phlebotomus* from the Mediterranean region already have records of the expansion of their distributions towards central Europe (Maroli *et al.*, 2008; Medlock *et al.*, 2014).

Culicoides spp. (Diptera: Ceratopogonidae)

Bluetongue disease, a zoonotic infection transmitted by *Culicoides* spp. (biting midges) to various ruminants, has important economic impacts in temperate zones of Europe, Africa and the Americas. Some authors suggest that in the Mediterranean region there is evidence of northward expansion of *C. imicola* in recent decades (Purse *et al.*, 2005), while others refute this (Conte *et al.*, 2009). Future expansions of *C. imicola* in climate change scenarios are predicted for most of its occurrence areas in the northern hemisphere (mainly central and western Europe and the USA) and some contraction areas in Africa (Guichard *et al.*, 2014). In Europe, their distribution is currently known in the Iberian Peninsula, with future climatically suitable areas predicted in the northwest direction, in climate change scenarios (Wittmann *et al.*, 2001). In Spain, niche models of wild hosts of Bluetongue virus (deer and wild boar) were used as predictors of the occurrence of *C. imicola*, in addition to other environmental variables, showing that in the near future (2011–2040), its predicted distribution will not suffer many changes, but its abundance is expected to increase in currently occupied areas (Acevedo *et al.*, 2010).

Triatoma spp. (Hemiptera: Reduviidae)

Chagas disease, also known as American trypanosomiasis, is transmitted by many species of kissing bugs from Triatominae subfamily. It was originally restricted to Latin America, but in past decades it has been detected in the USA, Canada, European and Asian countries, due mostly to human migration from endemic areas Schmunis & Yadon, 2010). In Brazil, *Triatoma brasiliensis*, a species complex (Monteiro *et al.*, 2004), is considered the main vector in the northeast region (Monteiro *et al.*, 2004). Future projections of its distribution indicate few areas of both expansion and contraction, so its distribution may remain stable, at least until 2050 (Costa *et al.*, 2014). In contrast, ENMs of two vectors of Chagas disease in the USA, *T. gerstaeckeri* and *T. sanguisuga*, predict northwards expansions of their distributions in response to climate change in 2050 (Garza *et al.*, 2014).

Ixodes spp. (Acari: Ixodida)

Several species of *Ixodes* ticks are involved in the transmission of Lyme disease, which is the most prevalent vector-borne disease in the USA and Europe. It is vectored by *I. scapularis* and *I. pacificus* in North and Central America, and by *I. persulcatus* and *I. ricinus* in Europe and Asia (Lane *et al.*, 1991).

The distribution of *I. ricinus* in Europe may nearly double by 2080 (Porretta *et al.*, 2013). This predicted expansion includes areas north and east of its current range, reaching the northernmost regions of Eurasia, such as Sweden and Russia (Porretta *et al.*, 2013). A model developed from a subset of its distribution records showed overall similar future predictions for Europe, with some local differences in the Iberian Peninsula and Scandinavia (Boeckmann & Joyner, 2014). In the USA, models indicate current greater probability of occurrence of *I. scapularis* in the Gulf of Mexico, and future projections point to relative stability in its range by 2050 (Feria-Arroyo *et al.*, 2014).

Further considerations on niche models of disease vectors

Vector occurrence data often present spatial bias towards endemic areas where disease surveillance programs are active. In addition, having presence and absence data that are required for some ENM algorithms is rarely the case when studying disease vectors. Most studies that used absence data based on field studies were restricted to regional and local scales, due to the inherent limitations of sampling effort (Eisen *et al.*, 2006; Mushinzimana *et al.*, 2006; Reiter & Lapointe, 2007; Khatchikian *et al.*, 2011; Cardo *et al.*, 2014). Absence data can be replaced by pseudo-absences generated according to several criteria (Lobo & Tognelli, 2011; Senay *et al.*, 2013). Real absence data, however, can also be a source of bias in model outputs if they are not treated appropriately. After all, a species may be absent from a sampled region for various reasons besides the lack of environmental suitability, such as dispersion barriers, historical factors or biotic interactions (Lobo *et al.*, 2010). In a modelling exercise to test different absence datasets of *C. imicola*, the removal of false absences improved all model outputs (Peters *et al.*, 2011).

Most ENMs are correlative approaches based on abiotic factors; they do not consider species' dispersion (Guisan & Zimmermann, 2000; Barve *et al.*, 2011). Thus, knowledge of vector ecology becomes essential for interpretation of model outputs. Accessible localities in climatic suitability areas can be either hypothesised *a priori* (Barve *et al.*, 2011; Carvalho *et al.*, 2015) or mapped *a posteriori* for vectors with limited dispersal ability, such as sand flies (Fischer *et al.*, 2011*a*). In contrast, ticks' dispersion is facilitated by their hosts' movements, favouring their range expansion in suitable areas (Porretta *et al.*, 2013).

Health data are commonly grouped into administrative areas, such as municipalities, districts, states or countries. Automatically converting vector records from this format to point localities can generate positional errors, depending on the spatial resolution of the study, which might lead to wrong estimates of the species–environment relationship (Naimi *et al.*, 2014). Even if the vector records for an ENM are aggregated into area units, they can be analysed using statistical methods, considering the spatial limitations of model predictions. This approach was applied in a GLM (logistic regression) of the environmental suitability of *L. whitmani*, cutaneous leishmaniasis vector in the state of Mato Grosso, Brazil,

where both vector occurrence and environmental data were grouped at the municipal level (Zeilhofer *et al.*, 2008).

To correctly interpret future ENM projections for disease vectors, it is important to remember that a vector's distribution represents only a fraction of the factors that determine human vector-borne diseases. Even if vectors, pathogens and hosts co-exist in a location, the disease might not become endemic for several reasons. Human social factors play an important role in disease establishment, such as migration, urbanization, population immunity and effectiveness of health systems (Gage *et al.*, 2008; Barcellos *et al.*, 2009). For example, the incidence of malaria has declined since 1900, mainly due to effective control (Gething *et al.*, 2010). However, in the areas of predicted expansion of distribution of malaria vectors in Africa there is more poverty and fewer resources to control the disease, which are important determinants of transmission risk (Peterson, 2009). International travel has contributed to increased numbers of imported cases of dengue in the USA and Europe (Gardner *et al.*, 2012). Chagas disease, a chronic and silent infection currently treated as an emergent vector-borne disease in southern USA, may have been established in the region for over 70 years (Garcia *et al.*, 2015), so the predicted expansion of vectors may increase transmission risk (Garza *et al.*, 2014). Canine leishmaniasis transmission cycles, known to precede human outbreaks of the disease have been recorded in areas with no records of human cases, not only in European countries (Ready, 2010), but also in the USA and Canada (Duprey *et al.*, 2006). These and other evidence points to the need for a multidisciplinary view of the impacts of climate change on vector-borne diseases.

Conclusions

Changes in the geographical distribution of vectors are expected with climate change, therefore impacting the spatial epidemiology of vector-borne diseases. Tropical regions of the world are currently occupied by many vector species, however future projections indicate poleward increases of suitable climates for their occurrence. These are the scenarios for Mediterranean vectors of several arboviruses, leishmaniasis, bluetongue disease and tick-borne infections, which are expected to find climatically suitable areas in central Europe for their expansions by the end of this century. In Sub-Saharan Africa, malaria vectors are expected to shift their distributions southward and eastward, losing climatic suitability in western countries in the process. Leishmaniasis vectors from tropical America are projected to expand their ranges both northwards and southwards in temperate zones, while inland Australia should increase in climatic suitability for mosquitoes.

The results discussed here are for the distribution of vectors only, which are a fraction of the determinants of the occurrence of these diseases. These likely vector expansions will only translate into increased risk of human disease if they are accompanied by hosts and parasites themselves. Human social factors and control efforts also play important roles in transmission risk. It is recommended that entomological monitoring activities are made, especially in the areas projected to become suitable for the occurrence of these vectors. Long-term monitoring studies can contribute substantially to the knowledge of the ecology of these species and how their distributions change in response to climate change.

Adoption of multiple ENM methods to study disease vector distributions is slow relative to the general ENM literature.

Another concern is the lack of consideration of the full-known current distribution of the target species on models that include future projections; about half of the reviewed studies had this issue, potentially leading to questionable predictions. An extra effort from authors is necessary in order to better understand the details of these methods so that models are produced with greater reliability and a clear description of their uncertainties. With this, these studies can support disease control policies more efficiently.

Supplementary Material

The supplementary material for this article can be found at https://doi.org/10.1017/S0007485316001097

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