The use of occurrence data to predict the effects of climate change on insects

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Experimental information on the roles played by climatic factors in determining the ecology and distribution of insect species is scarce. This has stimulated the increasing use of the climatic characteristics of the localities in which the species are observed to derive predictions under different climatic scenarios (the so called species-distribution models or SDMs). This text reviews the main limitations of these correlative models when they are applied to organisms, such as insects, that are characterized by a high degree of collector bias and incompleteness. It is argued that SDMs must rely solely on presence information, rejecting the use of background or pseudoabsences, and that we are not predicting the future distribution of a species but exploring the future location of the climatic conditions in which a species was observed. The scarcity and bias of the available occurrence information in insects as well as our ignorance about the non-climatic factors delimiting species ranges forces us to be extremely careful. It is therefore desirable to avoid the use of central tendency measures reflecting supposed optimum niche conditions because they are particularly dependent on the quantity and biases of the occurrence information. The use of simple algorithms and procedures aimed at extracting information on environmental limits from the available occurrences would be more convenient in this case.

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Introduction

Insects are the most diverse group of terrestrial animals [1]. This is sufficient by itself to qualify insects as the group for which our distributional and ecological ignorance is greatest. In addition, the comparative lack of taxonomical facilities and workforce in entomology [2], as well as the substantial effort needed to carry out comprehensive entomological surveys and taxonomical identifications [3,4], has led to biases and gaps in the taxonomical and biogeographical information about insects being considered proverbial [5,6•]. For example, only 10% of total Animalia occurrences included in a publicly accessible internet portal, such as the Global Biodiversity Information Facility (GBIF; www.gbif.org/), belong to insect species, despite insects representing 73% of all known species of animals worldwide (www.catalogueoflife.org/) according to the Catalogue of Life (accessed in March, 2016). As distributional information is crucial for both basic and applied purposes, this shortcoming hinders the use of insects in the advance of evolutionary, biogeographic and ecological knowledge as well as in conservation policies.

The lack of exhaustive information about insect distributions and climatic requirements is an argument in favour of using shortcuts to estimate the current, past and future ranges of insect species, as well their ecological niches, by using the occurrence of species as the basic source of information. The models using occurrences are thus simply a representation of unknown and dynamic realities (the geographical distributions or the niches), which are estimated by correlating a dataset of geographic occurrences with the environmental characteristics of the localities in which these occurrences are observed [7]. Such correlative models have been given various names (species-distribution models, ecological niche models, bioclimatic models or habitat-suitability models) but are hereafter referred to as species-distribution models or SDMs. Be that as it may, the basic procedure followed by all these approaches is that species observations are the main source of information to infer the environmental conditions under which the species can maintain sustainable populations, and these conditions are transferred spatially to derive probable or potential distributions.

A vast of amount of primary biodiversity data has been made freely available for users during the last three decades, via web portals as GBIF. The ease of access to this information, coupled with the development of free digital sources of environmental data such as WorldClim (www.worldclim.org/), CliMond (https://www.climond.org/) or the IPCC Data Distribution Centre (http://www.ipcc-data.org/index.html), as well as the revolutionary advance in the processing power of computers (a microprocessor in 2013 was 1.5 million times faster than one in 1971; see [8]), are the main factors that have given

rise to an exploding interest in SDMs. Consequently, the number of manuscripts published on this topic in scientific journals has grown exponentially since 1995, such that a new SDM study is now published approximately every day [9].

The estimation of potential insect distributions from observed occurrences and climatic data has been the subject of study for nearly 100 years [10], but early studies were generally based on the available physiological information rather than on correlations. Currently, only a small subset of studies attempt to derive niche estimations and potential insect distributions (e.g., [11–14]), mainly by using more or less sophisticated modelling procedures with presence-only data. An examination of the 503 studies published during 2014 and 2015 in three relevant entomological journals addressing ecological questions (*Ecological Entomology*, *Journal of Insect Conservation* and *Insect Conservation and Diversity*) indicates that only 2.8% of them (14) use SDMs as a tool of analysis (another 0.4% use physiological data to derive predictions). However, this percentage reaches 19.9% (49 out of 246 studies) in the case of *Diversity and Distributions*, one of the generalist journals devoted to conservation and biogeography. Interestingly, only 11.5% of the SDM studies published in *Diversity and Distributions* have addressed Arthropoda species. Hence, SDMs seem to be underused in insects, and, when applied, the correlative modelling procedure seems to be also the rule as occur in groups with a comparatively higher level of distributional and taxonomical knowledge. Without wishing to discredit the possibilities of a correlative approach to provide useful distributional and niche predictions, the present work will discuss the possibilities, uncertainties and drawbacks of carrying out reasonable simulations for climate change scenarios using only the available occurrence information about insect species.

The causality limitation

According to Legendre and Legendre [15], it is necessary to distinguish between forecasting and prediction. Although predictive models are based on well-known causal processes, forecasting models are those based on correlations that cannot be extrapolated beyond the observed range of conditions used in the process of model building. In forecasting models, the function describing the variation in the dependent variable in response to explanatory variables is used to derive new values in different situations. SDMs should thus be considered forecasting models in which the more accurate the relationship between climate and species distribution is, the more reliable their predictions under a climatic change scenario will be.

It is a well-known fact that the limits and ranges of species distributions are caused by a high number of non-climatic factors that are often spatially correlated with each other

and with the climatic variables [16]: biological interactions (competitors, facilitators or parasites), environmental variables such as soil composition or vegetation characteristics, historical contingencies and dispersal limitations may together or separately explain the distribution of a species. For example, as consequence of dispersal limitations a species can be geographically restricted to southern Europe. A model using climatic predictors may erroneously infer in this case that the climatic conditions in this southern region are causing this distribution, thus providing a wrong climate change prediction. This is the case of the highly specialized troglobitic beetles which thermal physiology indicates broad thermal tolerances, while their occurrences could suggest restricted thermal niche distributions [17]. Thus, it is always difficult to surpass the limitations imposed by forecasting models to make reasonable predictions for climate change scenarios without knowing the weight of these other non-climate factors.

If some factor related to temperature is important for delimiting the distribution of an organism, the challenge is to discriminate the effect of climatic variables from the effects that can also be attributed to other correlated non-climatic variables; this is the classic dilemma between correlation and causation [18]. Some authors have proposed calculating the pure effect of climate by simply including covariates such as altitude range or using partial regressions [19–24]. As expected, the effect of climate on distribution extrapolations decreases significantly when other explanatory variables are included, thus minimizing the shifts in the predicted distributions under different climate change scenarios. Which predictions are closest to reality? Few studies have tried to evaluate the outputs of these correlational models using distribution data from a different period. When accomplished [25–32], the results of these exercises clearly show the limited capacity of these forecasting models to predict the changed areas, as well as the need to include other non-climatic variables, the frequent overestimation of the obtained validation results, or the inability of the common validation measures used to account for statistically significant differences in the obtained geographical representations.

## Other drawbacks: absences versus pseudoabsences

Beyond the inescapable 'causality problem', other shortcomings hinder the development of reliable distribution extrapolations under climate-change scenarios. Apart from the appearance of new environmental conditions, unknown biotic interactions and novel species responses, all of which remain disregarded in the process of model training, some basic concerns should be considered in the case of insects. As happens all too frequently, the available geographic information about insects is usually scarce and biased, even in countries with a long-standing tradition of entomological studies [6•]. Under these circumstances,

the response variable (the occurrence of species) lacks the minimum requirement needed to generate consistent statistical inferences: a random variable well distributed across the selected gradient of environmental conditions. Furthermore, this survey incompleteness also negatively affects the essence and information content of the response variable itself. A variable must be an outcome that does vary or change, and our deficiency of knowledge about the spatial variation of insect abundances usually prevents delimiting the location of 'true' or probable absences. Thus, we generally can only have a number of occurrences whose density and aggregation may reflect the variation in abundance of the species and/or the differences in the sampling effort of collectors.

The lack of reliable absence data is a direct consequence of insufficient survey effort [33]. The frequent lack of information on the sampling intensity prevents identifying the degree of completeness of the local inventories, and therefore prevents obtaining information about the detectability of species and the location of probable absences. Only when the insect species is economically important, as in the case of crop or forest pest species, the level of survey effort allowed obtaining and using reliable absences [34]. Under these circumstances, the only available information is the presence of the species, and this kind of information cannot be considered a variable (a value that changes). This important shortcoming has been attempted to overcome by the use of pseudoabsences: absences generally selected at random within the study area in which the model is made (the so-called background absences). This is the classic procedure of the Resource Selection Functions [35], which compare the environmental conditions in the occurrence localities against those existing in the whole study area. It has been proven that this widely used procedure does not allow us to estimate the probability of occurrence or the prevalence of species [36] because false zeros of background absences do not have the statistical significance of 'true' absences. Furthermore, the continuous values generated by these presence/background absence models can only reflect the intensity of the own data used in the model training [37]. In other words, the suitability values so generated will reflect the density of observations. On the other hand, the location and number of these 'false' absences are highly dependent on the geographical extent considered. It is always possible to select the most adequate geographical extent to provide an apparently reliable geographical representation according to the standard measures of accuracy [38].

Figure 1
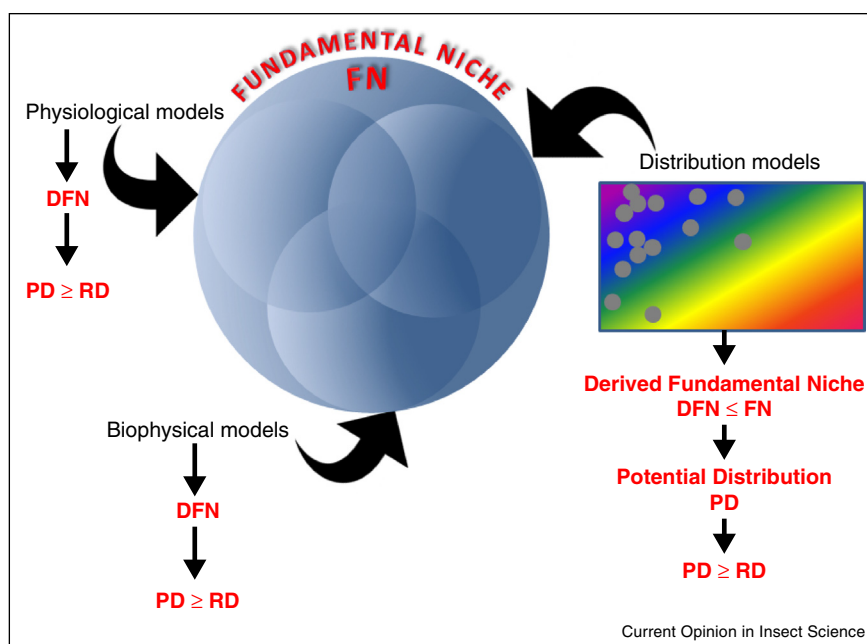
The fundamental niche of an organism (the set of conditions and resources that allow a given organism to survive and reproduce in the absence of biotic interactions and dispersal limitations; FN) can be approached considering different sources of knowledge, such as physiology [56], biophysics [57] or distributional data. All these sources of information are complementary and probably none will yield a perfect prediction. Each one of these sources of information can be used to infer the niche of an organism (the derived fundamental niche or DFN) to subsequently translate geographically this niche in order to generate a potential distribution (PD). These potential distributions can be equal to or greater than the realized or 'real' distributions (RD) as a consequence of the role played by species interactions or dispersal limitations, which limit the number of environmentally suitable localities that have been colonized.

What, then, is to be done?

The lack of equilibrium in distribution ranges due to the role played by non-climatic factors, the difficulty of estimating the 'true' causal influence of climatic variables, the pervasive biases and deficiencies in the available occurrence data, and the difficulties in documenting absences are all especially relevant shortcomings when SDMs are carried out for insect species. These shortcomings may seriously influence the distribution estimations of species under different climatic scenarios when using a forecasting approach. In view of these circumstances, the use of simple algorithms and procedures seems more justified than using complex modelling techniques based on regressions or machine learning methods which necessarily require the use of 'true' or background absences (maximum-entropy, generalized additive models, multivariate adaptive regression splines, genetic algorithms, random forests or support vector machines). These methods are so powerful that they are capable of

modelling the intrinsic errors and bias contained in the data [39•].

Presence information is the only empirical available evidence in most cases and for many groups of organisms such as insects. Thus, the only option is to be confident regarding what we have (presences) and not to use what does not exist (absences) to derive predictive functions by means of powerful regression or machine-learning methods. Although the use of mechanistic, biophysical or physiological information may provide complementary and more robust estimations, occurrences also constitute a valuable, less limited, and highly accessible source of data on species' biological requirements (Figure 1). These niche conditions obtained from distribution observations can be subsequently translated geographically using current or future scenarios in order to infer the potential distribution: a provisional image of the inhabited localities when the set of contingent factors preventing the colonization of

Figure 2
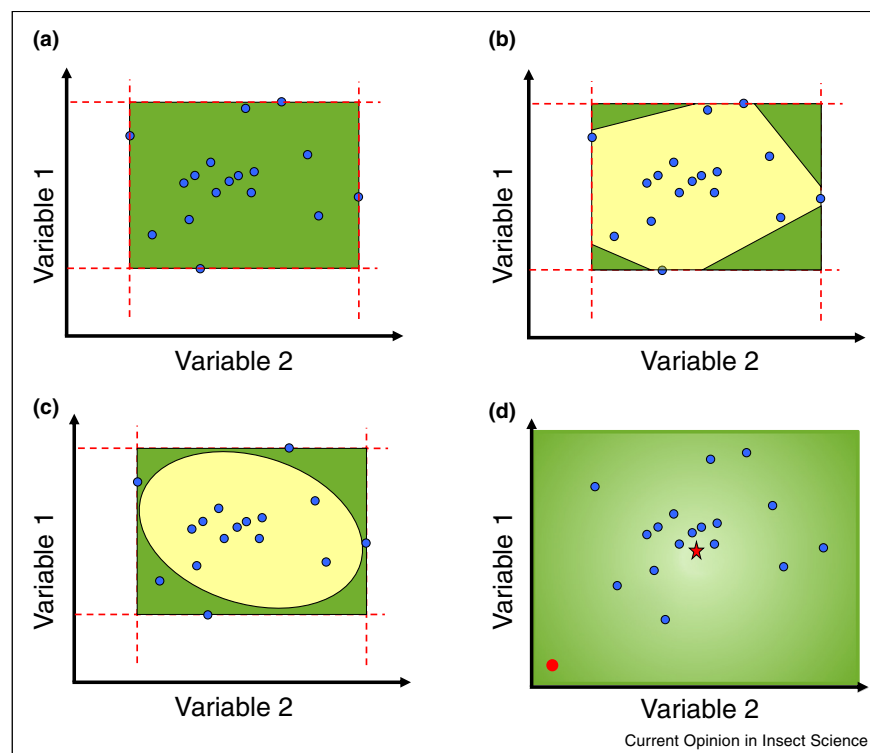
Available insect occurrence data are usually scarce and biased. When occurrence data are scarce, the environmental limits of species could remain unrecognized. When the occurrences are biased the locality with a high number of observations does not necessarily correspond to the most favourable conditions. One could, for example, use the available presences to derive niche estimations in an environmental space, here represented by two variables. Environmental values of these two variables in the presence localities (blue points) can be used to delimit a simple parallelogram **(a)** that would include the set of a priori suitable localities. In a further step it is possible to cut out this parallelogram delimiting a convex polygon **(b)** or a spheroid **(c)**, thus discarding as potentially suitable those environmental areas not represented by the data, or that have a low density of observations. The optimum conditions can be inferred using any measure of central tendency (here represented by a star), and the distance from this optimum used to generate continuous suitability values **(d)**. In this case, one must assume both the form of the response curve and a causative relationship between frequency of occurrence and density or abundance of the species. If, as a result of a survey, we detect a new locality record (red point in D) far from known conditions, the potential distribution and niche space will be extended dramatically. Thus, when distribution data are scarce and biased, the simplest parallelogram envelope may provide good predictions whereas continuous suitability values are misleading.

suitable regions have not affected the distribution. If we wanted to obtain an estimation of real distributions, we would require predictors capable of accounting for the factors responsible of the absence of species, as well as reliable absences to train models [40]. Validation of model results also requires reliable absences. However, potential distributions cannot be validated using occurrence data because absence observations may always be influenced by the contingent factors that hinder the occurrence of species in *a priori* favourable locations.

The aforementioned shortcomings also suggest not using the environmental values of occurrence observations to estimate optimum niche conditions by calculating central tendency measures (as mean, mode or median). Such measures may be particularly dependent on the quantity and biases of the used occurrence information (Figure 2). Instead, it would be better to trust in the environmental limits [41,42] as indicated by the available observations. In not exhaustively surveyed groups of organisms, the known range of species is always expanding because of new collections. These new occurrences constitute the best and simplest information that can be obtained regarding the climatic or environmental tolerances and limits of the species. The continued enlargement of these limits is an additional argument supporting the use of simple modelling procedures that do not try to infer optimum conditions from occurrences (Figure 2).

Several authors advocate the use of simple modelling procedures focused on using only the available presence information as well as the observed climatic limits of species [43,44••,45] when the purpose is extrapolating the potential distribution of species and there are no good-quality data. These authors propose that generalized intersections, multidimensional enveloping, Mahalanobis distances or multi-environmental convex hulls are more appropriate techniques for deriving geographical representations of potential distributions in the case of climatic change, especially when the data are insufficiently exhaustive. Key requirements such as selecting the most appropriate predictors according to their biological relevance [46,47] or covering as much as possible of the whole geographical and environmental range of species occurrences [48] will be always important decisions in these procedures, and these criteria must be clearly stated. In any case, the translation at other temporal scenarios of the tolerances or climatic ranges based on current data must be treated as geographical representations: risk maps in which the extent of the species will be conditioned by their opportunity to colonize distant but suitable places. Only a supplementary knowledge about the dispersal capacity of the target species [49,50] may help to discriminate the climatically favourable areas that probably will be colonized from those with a lower risk of being inhabited. It should not be forgotten that we are not predicting the future distribution of a species, a huge

challenge considering our data deficiencies and the multiplicity of the involved factors and their interactions. Our purpose was exploring the future location of the climatic conditions in which a species was observed. This is not a lot, but it may be sufficient for making important conservation decisions.

Conclusions

Distributional data are necessary for the ecological and biogeographical study of insect species, as well as to estimate the probable shift of geographical ranges under changing scenarios or to design conservation actions. The ecological, physiological and biophysical study of insect species may assist us in delimiting the climatic and environmental conditions under which these species are able to maintain their populations and thus their probable geographical distributions. Unfortunately, obtaining this type of information for such a heterogeneous and ecologically diverse group of organisms as insects is almost unattainable. Although affected by the diversity of interacting factors influencing species distributions, available occurrence data may often constitute the only source of information from which to derive niches and geographical ranges for most insect species. However, this distributional evidence must be used cautiously, avoiding the application of sophisticated and complex algorithms and procedures when the data does not possess sufficient quality [51,52]. When the occurrence data are scarce and biased, the use of complex modelling methods may give a false impression of accuracy [37], when actually we could be facing a case of 'garbage in, garbage out'. Given that insects are hyperdiverse and comparatively little-known, I argue that the best option is to use simple modelling techniques that rely on occurrence, rather than absence, observations. In the near future, the most promising avenue is to combine physiological, biophysical and occurrence data [53–55].

Acknowledgements

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