The impact of climate change changes over time

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A B S T R A C T

Species distribution models (SDMs) have become an important tool to predict the impact of climate change on the distribution of a given species. Generally, projections for a chosen time horizon in the future are compared with the size of the species’ current distribution. In this study, we show that selection of the target time horizon can qualitatively alter the prediction of a species’ future distribution. We illustrate this by assessing the potential distribution of 15 invasive ant species in 2020, 2050 and 2080 at a global scale. Our results indicate that for 6 out of the 15 species modelled, the trend of potential habitat size (i.e., decrease or increase) changed over time following climate change. In four species, the sign of the trend changed, from an initial expansion to a subsequent reduction or vice versa, depending on the date projected to. In some cases, these changes were great (e.g., from an initial increase of 36.5% in 2050 to a decrease of –64.3% in 2080). Our findings stress the importance of using several projection horizons to avoid misled species management decisions.

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1. Introduction

Many species from diverse taxonomic groups have already been affected by anthropogenic climate change, forcing them to change their phenology, physiology or distribution (Bellard et al., 2012). But climate change is happening at such a fast rate that many species will not be able to adapt rapidly enough. In fact, a large proportion of global biodiversity is predicted to go extinct before the end of this century (Bellard et al., 2012; Pereira et al., 2010). One way for species to persist, despite climate change, is to change/shift their geographic distribution. Shifts in species distributions will be one of the most dramatic consequences of climate change. Understanding the potential impacts of climate change on species’ distributions is therefore crucial to enable stakeholders and biodiversity managers to make informed decisions to mitigate biodiversity loss (Pressey et al., 2007). Currently, the tool most widely used to predict species’ future distributions are species distribution models (Sinclair et al., 2010; Pereira et al., 2010). This approach is based on the assumption that a species’ current habitat reflects its ideal climatic conditions and is in equilibrium with its climatic niche. Species distribution models relate the species’ current distribution to a set of climatic variables, which define its “climatic niche”. It is then possible to project the species’ niche to future climatic scenarios, based on different combinations of CO2 emission scenarios and global circulation models. Projections at different dates in the future can then be compared to the current climatically suitable area to evaluate changes in a species’ potential distribution. A recent review has shown that almost all major global studies on the impact of climate change on biodiversity project to a single future time horizon, which can vary widely among studies, and is usually between 2050 and 2100 (Bellard et al., 2012). The choice of that time is rarely discussed and management recommendations are made based on a single “snapshot” in time. This implicitly assumes that the trend of the impact of climate change on a species’ distribution will be the same in, for example, 2050 as in 2100. For example, if the potential range of a species decreases with climate change, it should decrease further at a later date. Conversely, a species that benefits from climate change is supposed to do so at different time horizons in the future. Quantitative differences are to be expected as climate change is continuing. The intuitive expectation is that climate change will accentuate any change in a species’ distribution observed at an earlier date. Whether linear or non-linear, there is an implicit assumption that potential species’ ranges, which expand by 2050, should further expand at a later date and that potential ranges which start by retracting should retract further.

In this study, our aim was to test the hypothesis that the choice of the future time horizon does not qualitatively influence the prediction of the trend of climatically suitable habitat for a given species. We used climatic data, which was available for three future time periods, which are in fact averages over 10-year periods and are centred around three dates in the future (2020, 2050, 2080) (Hijmans et al., 2005). For clarity, we will refer to those three dates in this paper. Using a range of 3 different time horizons for our projections allowed us to

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challenge the implicit assumption that the effects of climate change on species distributions are generally unidirectional and monotonic.

As a model system, we used 15 species of the same family and comparable ecology, in order to draw robust conclusions. We chose ants because they are widespread and dominant members of many ecosystems. Because they are poikilotherms, many features of their biology are very sensitive to temperature and humidity, including foraging (Brightwell et al., 2010), oviposition rate (Abril et al., 2008), and survival (Abril et al., 2010). It has been shown that climate is the most important factor in determining their distribution (Roura-Pascual et al., 2011) and therefore, climate change is highly relevant to future invasions of ants (Bertelsmeier et al., 2013). We also focused on invasive ants, because they allowed us to assess distributions at a global scale. Additionally, their projected distributions are of paramount importance for conservation biology. These 15 invasive ant species are responsible for numerous species displacements and local extinctions, as well as the perturbation of many interspecific relationships and ecosystem functions (Holway et al., 2002; Rabitsch, 2011; Lach and Hooper-Bui, 2010). In addition, many of these species are important agricultural pests (Rabitsch, 2011) and a nuisance to humans because they have a powerful sting and may transmit pathogens (Moreira et al., 2005). Management measures against these invasive ant species primarily rely on predictions of their current and future invasion “risk zones” (Hoffmann et al., 2010). In our study, we assessed the temporal change in potential habitat of 15 invasive ant species out of 19 listed by the Invasive Species Specialist Group of the IUCN (Lowe et al., 2000). All of these 15 species are known for their impacts on native species or human health and are present on several continents (IUCN SSC Invasive Species Specialist Group, 2012).

The 15 species are the Argentine ant, Linepithema humile, the yellow crazy ant, Anoplolepis gracilipes, the invasive garden ant, Lasius neglectus, the destroyer ant, Monomorium destructor, the flower ant, Monomorium floridum, the pharaoh ant, Monomorium pharaonis, the European fire ant, Myrmica rubra, the long-horned ant, Paratrechina longicornis, the big-headed ant, Pheidole megacephala, the tropical fire ant, Solenopsis geminata, the red imported fire ant, Solenopsis invicta, the black imported fire ant, Solenopsis richteri, the white-footed ant, Technomyrmex albipes, the ghost ant, Tapinoma melanocephalum and the electric ant, Wasmannia auropunctata.

We assessed the amount of climatically suitable landmass for each of these 15 species, with species distribution models at four different time horizons (current, 2020, 2050, 2080). The quantification of the effect of climate change on predicted suitable area worldwide at three future points in time allowed us to examine, for each species, the trend of these effects, and their possible reversal.

2. Materials and methods

2.1. Species distribution data

Species distribution models search for a non-random association between environmental predictors and species occurrence data to make spatial predictions of its potential habitat (Franklin, 2009). Because our models should include the full set of climatic conditions under which the species can thrive, we included occurrence points from both its invaded and native habitats (following Liu et al., 2011; Rödder and Lötters, 2008; Beaumont et al., 2009; Broennimann et al., 2007). It has been shown that models calibrated based on only native range data often misrepresent the potential invasive distribution and that these errors propagate when estimating climate change impacts (Beaumont et al., 2009; Broennimann et al., 2007).

In total, we used an average of 239 points of occurrence per species to model the species’ distribution (366 points of occurrence for A. gracilipes, 153 for L. neglectus, 519 for L. humile, 116 for M. destructor, 228 for M. floridula, 112 for M. pharaonis, 123 for M. rubra, 476 for P. longicornis, 208 for P. megacephala, 443 for S. geminata, 88 for S. invicta, 66 for S. richteri, 59 for T. albipes, 335 for T. melanocephalum and 288 for W. auropunctata) (Fig. A1 Supplementary Online Material). The number of points was sufficient to achieve good model performance for all species (Table A1 in Supplementary Online Material). The occurrence records came from the literature, researchers, government agencies, student projects and private collectors, compiled in two public databases; the ISSG database for invasive species (IUCN SSC Invasive Species Specialist Group, 2012) a database for ant distributions (Harris and Rees, 2004). We did not include points where the species was present in artificial climatic conditions, such as greenhouses. For this, points were removed from the distribution whenever they were obviously lying outside the species requirements. For models requiring absence data, 10 000 randomly and globally distributed pseudo-absence (background) points were generated.

2.2. Climatic predictors

We modelled the species niche based on 6 of the 19 bioclimatic variables provided by the Worldclim database (Hijmans et al., 2005). We selected for each species the 6 variables, which had the highest contribution to the Maxent model (most relevant for determining its distribution) and that were not collinear (pair-wise Pearson r < 0.75) (Table A2). The bioclimatic variables are derived from monthly temperature and rainfall values from 1960 to 1990 (Hijmans et al., 2005) and are known to influence species distributions (Root et al., 2003). We used a spatial resolution of 10 arcmin (approx. 18.5 × 18.5 km pixel).

Future climatic data was also provided by the Worldclim database which uses data from the 4th IPCC assessment report and which had been calibrated and statistically downscaled to match the data for “current” conditions (GIEC, 2007). In order to consider a range of possible future climate conditions, we modelled the species potential future distribution based on downscaled climate data from the 3 available Global Circulation Models (GCMS) provided by different climate modelling centres: The CCCMA-GCM2 model, the CSIRO-MK2 model and the HCCPR-HADCM3 model (GIEC, 2007). These GCMS are frequently used in species distribution modelling (Bradley et al., 2010; Synes and Osborne, 2011). In addition, projections for two different Special Report on CO2 Emission Scenarios (SRES) were included in our models: the optimistic B2 scenario (CO2 concentration 800 ppm, 1.4–3.8 °C temperature increase) and the pessimistic A2 scenario (CO2 concentration 1250 ppm, 2–5.4 °C temperature increase) (GIEC, 2007). In total, we used 6 future climatic scenarios per future time horizon (2 SRES × 3 GCMS).

2.3. Species distribution modelling

We used five different machine learning modelling techniques, which are among the most widely used algorithms and are known for their robustness (Franklin, 2009) to generate the ensemble forecasts. Machine learning methods are among the recently developed tools especially designed for modelling complex relationships and prediction (Lorena et al., 2011) and their predictive performance often exceeds that of more conventional techniques (Eilith and Leathwick, 2009; Guyon and Elisseeff, 2003). They are used to characterise the function that explains species distribution based on climatic variables inductively, directly from the input
data (Franklin, 2009). That means that these types of learning algorithms do not assume a certain type of distribution. Their predictive performance often exceeds that of more conventional techniques (Elith and Leathwick, 2009).

The first two models are based on Support Vector Machines (SVM), which are a new generation of learning algorithms. In a classification problem, two-class SVMs seek to find a hyperplane that maximally separates the two target classes. Recently, one-class SVMs have also been developed. They distinguish one specific category from all other categories. We included a one-class SVM in addition to the two-class SVM because it is a promising new approach in species distribution modelling (Guo et al., 2005).

Third, we used Artificial Neural Networks (ANNs) that have been commonly used to model complex relationships (Manel et al., 1999). In particular, ANNs have been successfully used to predict species distributions (Franklin, 2009; Maravelias et al., 2003). Models were trained using a back-propagation algorithm (Guo and Liu, 2010).

We also used Classification Trees (CT), which partition the response variable into increasingly pure binary subsets with splits and stop criterion (De’ath and Fabricius, 2000). The result was an average across 10 Classification Trees iterations of the model algorithm.

Finally, the Maximum entropy method (Maxent) estimates a probability distribution of a species being present by maximising entropy: it seeks the most spread out distribution in space, given a set of constraints (Phillips et al., 2006). Maxent has generally a very good model performance and has been widely used for distribution models for invasive species and impacts of climate change (Stiels et al., 2011; Jimenez-Valverde et al., 2011; Murray et al., 2011; Jarnevich and Reynolds, 2011; Bradley et al., 2010; Ficetola et al., 2010; Rourea-Pascual et al., 2009).

A clear limitation of modelling is that outputs are dependent on the specifically chosen input settings; in this instance, the algorithms, global climate models and scenarios of human development. To minimise potential resulting variation, we conducted consensual forecasts (Aráujo and New, 2007) of combined models using the five different modelling techniques above with each of three climate models (GCMs) and two CO2 emission scenarios (SRES). The purpose of consensual forecasts is to separate the signal from the “noise” associated with the errors and uncertainties of individual models, by superposing the maps based on individual model outputs. Areas where these individual maps overlap are defined as areas of “consensual prediction” (Aráujo and New, 2007). This is different from averaging the individual projections, as the area predicted by the consensual forecast can be smaller than any individual forecast if there is little spatial agreement (i.e., overlap) between individual forecasts. Simple averaging across individual forecasts is considered unlikely to match the reality (Aráujo and New, 2007).

The contribution of the individual models (i.e., the spatial prediction of “suitable range”) was weighted according to their AUC (Section 2.4) in order to enhance contribution of models with higher model performance values (see Roura-Pascual et al., 2009). Only binary projections (present or absent) have been combined to generate the consensus model because continuous outputs can have different meanings for different models and cannot be simply added together (Guo and Liu, 2010). The combination of the individual forecasts then yields a projection, the consensus model, where the value of pixels vary between 0 and 1 and can be interpreted as a probability of the species being present in each pixel (Aráujo and New, 2007).

The consensus model was generated using all five modelling algorithms to 6 future climatic scenarios (2CO2 emission scenarios × 3 GCMs), yielding a single consensus projection for one particular time horizon. The value of the consensus model is preferred to an average value across all models because it has two important advantages: 1/it takes into account the spatial dimension and 2/it weighs the contribution of individual models according to their predictive accuracy. An average value (and associated variability) would therefore be much less informative.

All models were run using the ModEco Platform with default parameters (Guo and Liu, 2010) and combined to consensus forecasts, weighted according to their Area Under Receiver Operator Curve (AUC) in order to enhance contribution of models with higher model performance values (see Roura-Pascual et al., 2009). The modelling process was repeated to generate consensus predictions for 2020, 2050 and 2080.

2.4. Assessing suitable range and model validation

Potential habitat suitability was assessed by applying 5 different classification thresholds, whereby all pixels in which the probability of presence exceeded 0.5, 0.6, 0.7, 0.8 or 0.9 were classified as “suitable” range (Franklin, 2009). As results were similar and trend reversals could be observed under all classification thresholds, we present results obtained with a classification threshold of 0.5, which is frequently used for binary classification in the context of species distribution modelling (Franklin, 2009; Klamt et al., 2011; Nenzén and Aráujo, 2011). Spatial analyses were carried out using DIVA-GIS program (Hijmans et al., 2001) and ArcGis v. 9.3. Statistical analyses were carried out in R v. 2.15.2.

Model robustness was evaluated with AUC, which is a non-parametric threshold-independent measure of accuracy that is commonly used to evaluate species distribution models (Ward, 2007; Roura-Pascual et al., 2009; Manel et al., 1999; Pearce and Ferrier, 2000). We used the AUC because it does not depend on the classification threshold and is easily interpretable as the probability that a model discriminates correctly between presence and absence points (Pearce and Ferrier, 2000; Roura-Pascual et al., 2009). AUC values can range from 0 to 1, where a value of 0.5 can be interpreted as a random prediction. AUC between 0.5 and 0.7 are considered low (poor model performance), 0.7–0.9 moderate and >0.9 high (Franklin, 2009 and references therein). For model evaluation, the data needs to be split into a train and a test group. Here, we used 10-fold cross-validation, whereby the data had been split into 10 equal parts, with 9/10 of the observations used to build the models and the remaining 1/10 used to estimate performance; this was repeated ten times and the estimated performance measures were averaged (Franklin, 2009; Fielding and Bell, 1997). AUC values in this paper are given as mean ± SD.

2.5. Assessing the trend reversal

When a trend reversal occurred in the change of suitable area, we evaluated its strength in three complementary ways (see
First, we calculated the magnitude of the trend reversal. The magnitude is the difference between the range size in 2080 and the date at which the trend reversal occurred (either 2020 or 2050). The magnitude of the trend reversal is expressed as a percentage of the species’ current potential distribution. Second, we calculated a “reversal percentage”. This is the magnitude of the reversal in any trend divided by the value of the initial trend before its reversal (i.e., the value of change in size of potential habitat at the date where the trend reversal occurred). The size of the reversal percentage reflects the “error” that one would have if the projection had been based on an earlier date instead of 2080.

Finally, in order to test whether the amplitude of the trend reversal was of the same magnitude as the initial trend, we developed a simple Compensation Index (Smaller Change/Greater Change). This index tends towards 1 when the change of the trend reversal is of the same magnitude as the initial change. In those cases, the “net” impact of climate change in 2080 on the species’ range tends towards 0 (the trend is completely reversed, cancelling out the initial impact).

3. Results

Among the 15 species analysed, 6 showed a reversal in trend of range change over time: M. floricola, M. pharaonis, M. rubra, S. invicta, S. richteri and T. albipes. As the objective of this study is to detect potential trend reversals in potential habitat due to climate change, we present the results for these 6 species only. Although variation could be observed among different future climatic scenarios and classification thresholds, the general pattern persisted (see below). This is illustrated here for T. albipes (Fig. 2). There was a significant difference among projections made at different time horizons (Anova: $F_{(1,16)} = 29.9, p < 0.0001$). The trend reversal in change in range size over different time horizons was not due to an effect of the different CO2 scenarios or the different GCMs nor classification thresholds (SRES: $F_{(1,15)} = 0.0056, p = 0.9414$; GCMs: $(F_{(1,15)} = 0.0343, p = 0.9664$, classification thresholds: $F_{(1,13)} = 0.3719, p = 0.5525$).

Among all 6 species and all 6 climatic scenarios that have been used at different time horizons in the future, trend reversals could be observed in total in 32 out of 36 forecasts, which is higher significantly higher than expected by chance ($\chi^2 = 12.829, df = 1, p = 0.0003$). The same was observed using 5 different classification thresholds for consensus models of all 6 species, where 27 out of 30 projections showed a trend reversal ($\chi^2 = 11.4286, df = 1, p = 0.0007$).

4. Discussion

The forecasts of potential distributions today, in 2020, in 2050 and in 2080 indicated a tendency to reverse over time for 6 out of 15 species (Fig. 1). First, we calculated the magnitude of the trend reversal. The magnitude is the difference between the range size in 2080 and the date at which the trend reversal occurred (either 2020 or 2050). The magnitude of the trend reversal is expressed as a percentage of the species’ current potential distribution. Second, we calculated a “reversal percentage”. This is the magnitude of the reversal in any trend divided by the value of the initial trend before its reversal (i.e., the value of change in size of potential habitat at the date where the trend reversal occurred). The size of the reversal percentage reflects the “error” that one would have if the projection had been based on an earlier date instead of 2080.

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3.1. Model evaluation

Overall, model performance was good to excellent for all of the species. The mean AUC value was 0.935 ± 0.05 (min 0.794; max 0.998) (Table A1 in Supplementary Online Material).

3.2. Spatial predictions

The trend reversal observed in 6 species of invasive ants can be illustrated by the example of T. albipes, where a great initial expansion of the current potential range by 2020 is followed by a dramatic range contraction until 2080 (Fig. 3a–d).

3.3. Trend reversal

In total, three species M. floricola, M. pharaonis and T. albipes, showed first a range expansion, which was then followed by a range contraction (Fig. 4a, b and f). In M. floricola, the trend reversal was so strong that completely compensated for the initial expansion and in T. albipes the trend reversal even led to a decrease relative to the current potential habitat. The highest magnitude could be observed in T. albipes, where an initial range expansion by 36.5% in 2050 was followed by a net range contraction of −64.3% relative to the species’ current potential range.

One species, S. invicta, showed an initial increase of 13.4% in 2020, followed by a range contraction in 2050, resulting in a net range which was only 4.4% greater than under current climatic conditions (Fig. 4d). This was then again followed by another trend reversal, leading to an increase of 35% in 2080.

In two species, M. rubra and S. richteri, the opposite trend reversal could be observed: after the initial contraction, the potential habitat expanded (Fig. 4c and e). In M. rubra, the trend reversal was so strong that it eventually compensated the initial trend. In S.richteri, the potential habitat decreased by −10.9% in 2020, but showed subsequently expanded, leading to a net loss of only −2.3% relative to the current potential habitat. This was followed by a second trend reversal, leading to another contraction of −7.3% of currently suitable area in 2080.

Overall, in 3 species (M. floricola, M. rubra and T. albipes), the trend reversal changed the sign of the prediction, from an initial expansion to a subsequent contraction, or vice versa. This means that the result changed qualitatively depending on the time to which projections are made, i.e., a projection at one single time horizon produced a result opposite to that obtained by a projection to another date.

In order to evaluate the magnitude of these effects in the different species, we calculated the trend reversal magnitude (Fig. 5a), the reversal percentage (Fig. 5b) and a Compensation Index (Fig. 5c) for each of the six species. By far the most dramatic magnitude of trend reversal could be observed in T. albipes (100.8%), followed by S. invicta (30.6%) and M. floricola (12%) (Fig. 5a, dark red bars). In fact, the magnitude of the trend reversal was greater than the difference between the current potential habitat and the potential habitat in 2080 (Fig. 5a, light red bars). In other words, the net impact of climate change observed in 2080 (compared with today) was smaller than the intermediate effect, before the trend reversal. The reversal percentage reached 341% for S. invicta and 276% for T. albipes (Fig. 5b). The Compensation Index was highest for M. rubra, which lost −4.5% of its potential habitat in 2050, but eventually ended up with almost the same amount of habitat in 2080 as under present climatic conditions (Fig. 5c).
of 15 species of the same family studied here. In 3 species (M. floricola, M. rubra, T. albipes), the distribution trend changes qualitatively depending on the future time horizon to which a projection is made. Where predictions at one date in the future could, for example, suggest a range expansion, projecting to another date might predict the opposite. Furthermore, there was no general pattern in the direction of the trend reversal. In 4 species an initial expansion in potential habitat was followed by a subsequent contraction while in 2 other species the opposite happened; an initial contraction was followed by a subsequent expansion. In one species an initial expansion was followed by a contraction, which was again followed by an expansion in 2080.

Not only are the trend reversals frequent in this rather small and homogeneous species sample (6/15), but they are also substantial. For example, between two contiguous dates, M. rubra shows a complete (98.9%) compensation of the initial trend, while S. invicta shows a percentage trend reversal of 341%. T. albipes showed a trend reversal by 276% compared to the initial trend. The absolute magnitude of the trend reversal was 35% in S. invicta and 100.8% in T. albipes.

These trend reversals are unlikely to be due to “noise” in the projections as the consensus models used for predicting potential distribution showed high model performance (high AUC values, Fielding and Bell, 1997). The models were designed to include an extreme range of climate change scenarios, with an optimistic B2 and a pessimistic A2 CO2 emission scenario as well as three very different and widely used global circulation models (GIEC, 2007). Uncertainty due to a single modelling method has been reduced by building models with five different algorithms that contributed to the final consensus forecast (Araújo and New, 2007). The trend reversals were not driven by a certain future climatic scenario or due to the choice of a particular classification threshold.

A possible reason for these changes in the trend of range expansions/contractions is that changes in the different climatic
variables are not always correlated. For example, in some areas where temperatures rise, humidity increases, while in others humidity decreases (GIEC, 2007). Change in rainfall patterns and temperature rises are not predicted to happen at the same temporal scale across different regions of the world (Walther et al., 2002). Consequently, it is possible that some areas will become suitable at first due to changes in certain variables, increasing the total suitable area. But later in the future, other places may decrease in suitability for the species. Another, non-exclusive possibility is that the same area can first be suitable and then unsuitable for the species because a parameter optimum (e.g., temperature), has been reached and then exceeded. The fitness of ants has been shown to follow this pattern (Abril et al., 2008). Furthermore, purely “geographic” reasons may also play a role in explaining trend reversals. For example, as species niches shift in space, the total area that corresponds to the climatic conditions under which the species can thrive may be present in a smaller amount of landmass on Earth (i.e., constrained by geographical barriers), thereby decreasing the potential habitat of the species. As the niche shifts further in space due to the changing climate so the area characterised by this set of conditions may increase again.

Previous studies using projections for several points in the future have shown data that support trend reversals in the impacts of climate change on species ranges over time (Fitzpatrick et al., 2008; O’Donnell et al., 2011). However, these studies have not explicitly pointed out that for some of the species considered a trend reversal occurred and have not discussed the potentially far-reaching consequences of these findings. For example, in the case of a threatened species, conservation decisions depend on projections of areas that will be suitable for a focal species. Similarly, management decisions for invasive species may have to be revised if trend reversals occur. It is essential to make assessments

![Fig. 4. Quantitative changes in potential habitat relative to the species’ current potential range for 3 dates in the future (2020, 2050, 2080) for the six species showing trend reversals.](image-url)
Quantification of the importance of the trend changes, for the six species showing change over time, for the three indices: (a) Magnitude of the trend reversal (dark red bars), expressed in % of the species current potential range. The light red bars represent the magnitude of the impact of climate change on the species potential range by 2080. (b) Reversal percentage and (c) Compensation Index. See text for explanations of the indices. In the case where two trend reversals occurred, we calculated the indices based on the trend reversal that had the greatest magnitude. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

at several points in time because critical patterns might otherwise be overlooked.

For example, an invasive species might decrease substantially in 2050 but increase subsequently in 2080, reaching even a net increase in potential habitat (pattern observed in M. rubra in this study). If a management decision were based on a single projection in 2050, it would seem reasonable to decrease efforts of controlling the species (at least in the areas that it is not predicted to be able to invade) and direct them towards other invasive species, or other areas. However, if the decision were based on a projection in 2080, the opposite conclusion would be reached.

We also caution against the tempting conclusion that management decisions could simply be based on a single projection in the far future (e.g., 2080). First, climatic projections for the far future (2080–2100) are considered more uncertain than medium-term projection (e.g., 2050). In addition, the successive trends of the distribution range change may be relevant. If an invasive species is predicted to decrease in 2080 but had increased in the meantime, it is possible that the impacts of the initial increase could override the subsequent decrease. Therefore, the invasive species, which has benefited from climate change at an earlier date, may still persist in 2080. Consequently, the species may still pose a greater threat compared to today – even though the model for 2080 has predicted a decline.

Similarly, a species that would be predicted to increase by 2080, might have decreased dramatically in the meantime – which could be sufficient to prevent it from occupying its increased potential distribution several decades later. A similar pattern was observed to some extent in M. rubra and S. invicta. It would be extremely worrying in the case of threatened species that could seem to be unaffected by climate change – or even benefit from it – in 2080. Indeed, an initial decrease in potential range, when it concerns an endangered species, can equate to dangerously low population sizes, or even to extinction. That the potential range subsequently increases may therefore not reflect the true impact of climate change on that species, which could be severe and underestimated.

Species distribution models have a number of limitations (Guisan and Thuiller, 2005; Sinclair et al., 2010). For example, they are based solely on climatic variables. Although climate is the most important factor determining the distribution of ants at a global scale, other variables such as biotic interactions, habitat structure and local dispersal limitations become important at a local scale (Roura-Pascual et al., 2011). In particular, it has been shown that even if climate is suitable for an invasive ant species, there is a higher chance that it invades highly disturbed sites (e.g., adjacent to roads, buildings and landscaped areas) (Fitzgerald and Gordon, 2012). Future studies on potential distributions of invasive ants may consider including these factors to get a more precise estimation of suitable areas for the species, but these forecasts will necessarily be carried out at a local scale. In this study, we have used invasive ants as a model system to demonstrate that trend reversals are a frequent phenomenon when using widely used modelling tools. Descriptive information on their spatial distributions was not the focus of this study.

It has been strongly advocated to move beyond theoretical analyses and to implement model predictions in order to protect biodiversity (Dawson et al., 2011). Notably, several hotly debated issues in conservation biology, such as assisted colonisation (Hewitt et al., 2011), triage-base assessments (Bottrill et al., 2008; Millar et al., 2007), prioritization of protected areas (Heller and Zavaleta, 2009; Summers et al., 2012) require consequential decisions if we want to mitigate the impacts of climate change on biodiversity. Although many model pitfalls have been highlighted (Sinclair et al., 2010), “trend reversals” do not seem to be recognised as a potential problem. However, it should be stressed that making predictions for additional dates (instead of a single projection in the future) comes at a marginal time cost for the modeller now that climatic projections are available. Yet, it can lead to a substantially better understanding and could even prevent disastrous consequences, if the model is to be applied for conservation or management decisions. To improve the understanding of the response of a particular species to climate change, it is even possible to choose more than three dates as there are now climate scenarios available for every decade (GIEC, 2007). This would allow quantifying the rate of trend reversal, leading to a better understanding of the response of a focal species to climate change. This will likely be superfluous in those species for which a continuous trends is observed with time, but we have shown here with a sample of 15
species of restricted taxonomy and ecology breadth that many species could be incorrectly assessed with only one date in the future.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bioccon.2013.07.038.

References


