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LETTER

Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change

Alex Bush,[1]* Karel Mokany,[1] Renee Catullo,[1,2,3] Ary Hoffmann,[4] Vanessa Kellermann,[5] Carla Sgrò,[5] Shane McEvey[6] and Simon Ferrier[1]

[1]CSIRO Land and Water Canberra, Australia [2]Biological Sciences Macquarie University Sydney, Australia [3]School of Science and Health Western Sydney University Australia, [4]Melbourne University Melbourne, Australia [5]Monash University Melbourne, Australia [6]Australian Museum Sydney, Australia

**Correspondence: E-mail: alexalbush@gmail.com*

Abstract

Based on the sensitivity of species to ongoing climate change, and numerous challenges they face tracking suitable conditions, there is growing interest in species' capacity to adapt to climatic stress. Here, we develop and apply a new generic modelling approach (*AdaptR*) that incorporates adaptive capacity through physiological limits, phenotypic plasticity, evolutionary adaptation and dispersal into a species distribution modelling framework. Using *AdaptR* to predict change in the distribution of 17 species of Australian fruit flies (Drosophilidae), we show that accounting for adaptive capacity reduces projected range losses by up to 33% by 2105. We identify where local adaptation is likely to occur and apply sensitivity analyses to identify the critical factors of interest when parameters are uncertain. Our study suggests some species could be less vulnerable than previously thought, and indicates that spatiotemporal adaptive models could help improve management interventions that support increased species' resilience to climate change.

Keywords

Drosophila, niche model, phenotypic plasticity, physiological tolerances, thermal tolerance.

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INTRODUCTION

Evidence that biodiversity is reacting to ongoing climate change has driven a sustained surge in the demand for ecologists to improve predictions of future outcomes (Thomas *et al.* 2004; IPBES 2016). A key component in understanding species' vulnerability is their capacity to adapt to future climates through evolutionary and plastic responses. While the rate of projected change is expected to exceed the capacity of many species to adapt (Etterson & Shaw 2001; Quintero & Wiens 2013), rapid evolutionary responses have already been observed in many taxa (Franks *et al.* 2007; Skelly *et al.* 2007; Sinclair *et al.* 2012; Krehenwinkel *et al.* 2015). However, the correlative biodiversity models upon which so many predictions rely are conceptually disconnected from the theory of niche evolution (Peterson *et al.* 1999; Soberon & Peterson 2005), and assume species' distributions are at equilibrium with their environment and niches are conserved over time; assumptions widely acknowledged as flawed (Wiens *et al.* 2009; Araújo & Peterson 2012).

Lack of consideration of evolutionary adaptation in species distribution models (SDM) is due in part to the absence of relevant information on fitness traits and their heritability, which is needed to estimate species responses to selection from climate change (Huey *et al.* 2012). However, new genomic and experimental data offer the opportunity to characterise species' responses in greater detail (Hoffmann & Sgrò 2011). As more information on adaptive capacity becomes available, including through phylogenetics, genomics and functional approaches, new methods are required to incorporate this knowledge in predicting where and when adaptive capacity could affect species persistence under climate change (Lavergne *et al.* 2010; Catullo *et al.* 2015; Wade *et al.* 2016).

To identify the potential for species to adapt under climate change, a variety of new approaches have emerged based on evolutionary theory (Thuiller *et al.* 2013). Many studies have examined the precise dynamics involved in evolutionary changes, and the importance of factors such as genetic variance, plasticity, admixture, dispersal and range margins (Dytham *et al.* 2014; DeLong & Gibert 2016; Rees & Ellner 2016). However, the detailed evolutionary processes considered by these models typically restrict their application to simple scenarios of hypothetical or simulated environments (Bocedi *et al.* 2014; Schiffers & Travis 2014). Other studies have modified environmental tolerances of species within applied models (Lozier & Mills 2011; Hill *et al.* 2014), but have based estimates on observed range expansions, rather than emerging from an evolutionary process. To date, only Kearney *et al.* (2009) have integrated evolution, dispersal and abiotic constraints into a spatially explicit SDM, however this application involved a detailed physiological model customised to a focal species (the *Aedes aegypti* mosquito).

Given the urgent need to assess vulnerability of many taxa to climate change (Huey *et al.* 2012), methods that incorporate evolutionary adaptation will only be tractable if they remain flexible to data availability (Thuiller *et al.* 2013). To help environmental managers understand when and where actions could improve species' resilience to climate change, models must also be spatiotemporally explicit (Sgrò *et al.* 2011; Hoffmann *et al.* 2015). Building upon a framework for assessing species' adaptive capacity using direct and indirect sources of genetic, physiological and ecological information (Catullo *et al.* 2015), we demonstrate a new generic approach that considers the effects of evolutionary adaptation on species' distributions, called *AdaptR*. The approach couples an SDM with information on physiological tolerances, dispersal and genetic variation to predict range shifts that allow for adaptation under environmental change. Code to run AdaptR is available as an R package through the GitHub repository (https://github.com/KarelMokany/AdaptR). We assess the extent to which explicit consideration of evolutionary adaptation alters our understanding of vulnerability to climate change by applying this new modelling approach to 17 species of Drosophilidae in Australia.

METHODS

AdaptR

To be widely applicable, the *AdaptR* modelling framework was designed to incorporate evolutionary adaptation within SDMs with minimal additional data. The model (Fig. 1) allows adaptation of physiological traits within a spatiotemporal context, implementing the conceptual framework of species' adaptive capacity outlined by Catullo *et al*. (2015). To account for fluctuating environmental conditions, the model proceeds temporally through time steps, hereafter referred to as generations. For populations within each grid cell, the selection pressure of each generation is based on their accumulated exposure to extremes for the environmental attribute of interest. Dispersal allows for colonisation of unoccupied cells with suitable conditions, and for admixture of physiological tolerances among occupied locations experiencing different degrees of evolution (Figs 1 and 2). In addition to the environmental layers and occurrence records required to fit an SDM, the model uses eight parameters, described below (see also Appendix S1), to dictate evolutionary responses for a given trait, as well as a dispersal kernel and admixture probabilities. Although for many species not all parameters will be directly available, various indirect approaches can be used to estimate values (Catullo *et al*. 2015), and sensitivity analysis can be employed to assess the importance of missing values.

There are four key sets of inputs to the *AdaptR* model: (1) the eight parameters describing adaptive capacity and dispersal probability (described below and in Appendix S1); (2) the initial distribution (presence/absence) of the focal species within the region of interest and for each generation, (3) spatial layers of environment conditions for target variables under selection and (4) spatial layers of environmental conditions for non-target variables or of predicted suitable habitat derived from an SDM, conditional on target variables. The model predicts the distribution (presence/absence) of the species at each generation over time, given its distribution in the previous generation, relevant environmental changes and specified species attributes. Species can persist in (or colonise) cells if environmental conditions are suitable. If the environment of a cell becomes unsuitable, the species will go locally extinct (if occupied) or be unable to colonise that location (if unoccupied) (Fig. 2).

AdaptR is a hybrid SDM approach, spanning the divide between purely correlative and mechanistic models (Kearney & Porter 2009). Users can define fundamental limits (as opposed to observed, realised limits) using physiological thresholds for all environmental variables in the model, or use statistical SDMs to dictate habitat suitability. While it is the addition of adaptation that most strongly differentiates *AdaptR* from other hybrid SDM approaches, the inclusion of dispersal dynamics are also a significant improvement on most SDM applications because they control fluctuation of range shifts to changing climate conditions (Brotons *et al*. 2012).

For a target environmental variable (e) in which the species' upper or lower tolerance threshold (Te) is undergoing evolutionary adaptation, a standard quantitative genetic model (Falconer & MacKay 1996) is used to calculate the evolutionary response (R) equating to the change in environmental tolerance for a population in a grid cell following a selection event, similar to Kearney *et al*. (2009):

$$R = ih_e^2\sigma_{Pe} \tag{1}$$

where i is the intensity of selection, h_e^2 is the narrow sense heritability of the environmental tolerance threshold for that species and σ_{Pe} is the standard deviation of the tolerance threshold value within the local population (Fig. 1). The new environmental tolerance threshold at time Te_{t+1} is then simply the sum of the previous value (Te_t) and the evolutionary response ($Te_{t+1} = Te_t + R$). The environmental tolerance threshold is assumed to have a normal distribution within the local population/grid cell (mean = Te; SD = σ_{Pe}), and the

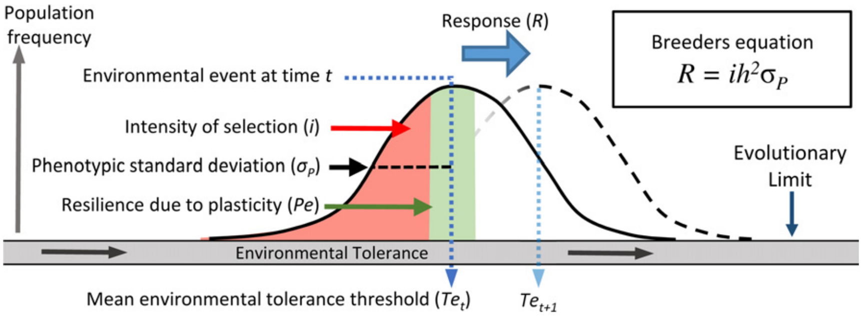

Figure 1 *AdaptR* framework illustrating how evolutionary adaptation is modelled within each cell. To begin with, physiological measurements are used to define Te, the species' mean environmental tolerance threshold (fundamental limit). Individual tolerance within a local population is normally distributed, described by the phenotypic standard deviation (σ_{Pe}; black dotted line). During a given generation at time t, the intensity of selection (i; proportion in pink) is determined by the proportion of the population whose threshold exceed after plasticity (Pe; proportion in green) is deducted from the environmental event (blue arrow) for that time. The resulting response (R) is calculated using the Breeder's equation and leads to a shift in the population mean threshold (Te_{t+1}). Further shifts may occur in subsequent generations until thresholds are capped at the evolutionary limit.

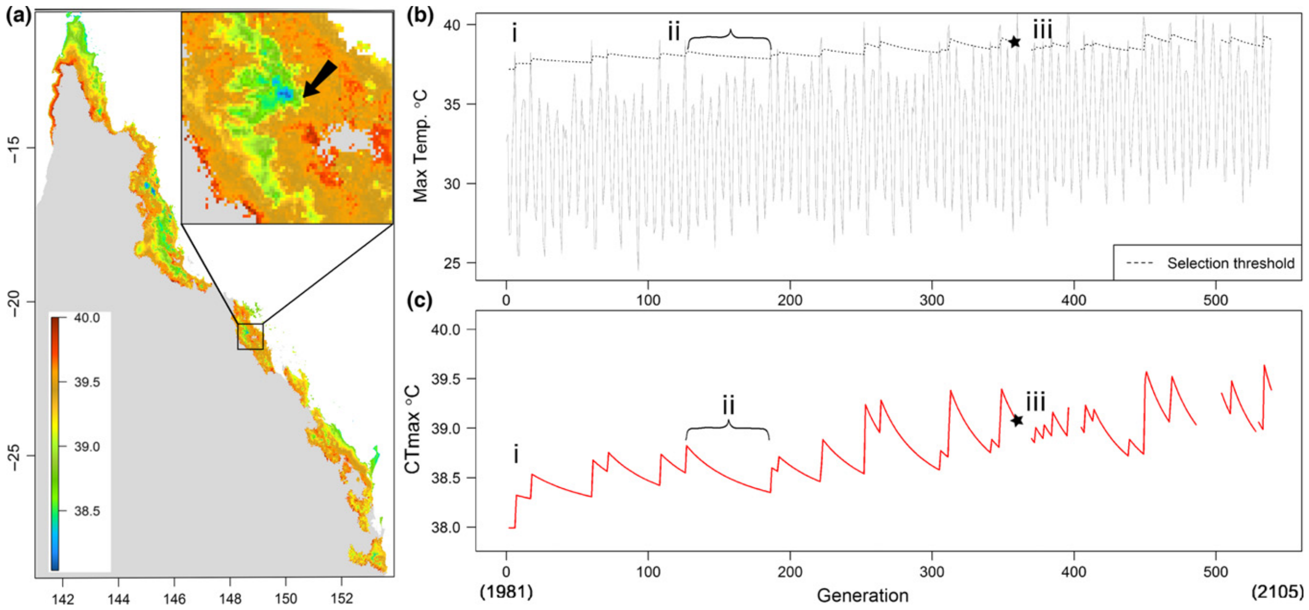

Figure 2 (a) Map showing an example of local adaptation of the CT_{max} (critical thermal maximum temperature tolerance threshold) in *Drosophila jambulina* under climate change (scenario CanESM2). Arrow in inset map marks the location of the grid cell in which displayed temperature and CT_{max} were recorded. (b) The changes in maximum temperature and the threshold for selection to occur, and (c) the CT_{max} of the species for a single run, as it evolves over time. Key characteristics of the model dynamics shown include evolutionary adaptation (i), stabilising selection due to fitness costs of adaptation (ii) and local extinction due to high maximum temperature event (iii).

intensity of a selection event is approximated as in Kearney *et al.* (2009), using a polynomial function based on the proportion of the population with tolerance traits exceeding the environmental event, and hence surviving this event (S) (Falconer & MacKay 1996):

$$i = a + bS + cS^2 + dS^3 \tag{2}$$

where $a = 2.2014$, $b = -0.0488$, $c = 0.00058$ and $d = -0.0000029$.

We have included the influence of plasticity on S by allowing the survival of additional individuals not genetically adapted to the environmental conditions, using a specified value of environmental plasticity (Pe). This value was assumed fixed and independent of the value of the environment (Kellett *et al.* 2005). The environmental exposure is effectively reduced when plasticity is present, increasing the proportion of the population in the grid cell that survives (S) and hence decreasing selection intensity (i) (Fig. 1). Following high-intensity selection events, populations are at high risk of local extinction due to demographic stochasticity and are also likely to suffer losses of genetic diversity (Willi *et al.* 2006). Therefore, local extinction occurs only if S is < 5%. Similarly, very weak selection is unlikely to drive substantial evolution, hence a response (R) is generated only if S is < 95%.

Under continued selection pressure, over multiple generations, an environmental threshold trait can continue to shift until values in the population reach the specified evolutionary limit (Catullo *et al.* 2015). Further shifts in the environmental threshold trait would result in a proportion of the population under a normal distribution falling beyond this limit; that proportion is assigned to the evolutionary limit, reducing σ_{Pe}.

Both theory and empirical evidence suggest that fitness costs are often incurred when a population undergoes evolutionary adaptation, especially when adaptation is rapid (Falconer & MacKay 1996; Jansen *et al.* 2015). We account for costs by increasing the strength of stabilising selection as the current threshold trait value (Te_{tx}) deviates from the original threshold trait value (Te_{t0}). In this case, we apply eqn 1 using the same heritability (h_e^2) and phenotypic standard deviation (σ_{Ptx}) of the trait in the grid cell population at the current generation (time = x). Intensity of (stabilising) selection (i) increases linearly with the squared deviation of Te_{tx} from the original value in that population (Te_{t0}), with a specified constant slope parameter [m; i.e. $i = m(Te_{t0} - Te_{tx})^2$] (see Falconer & MacKay 1996) (Fig. 2).

Dispersal in *AdaptR* occurs at each time step (generation) through a user-specified set of probabilities of successful dispersal (P_{ij}) to each grid cell (j) in a specified radius around an occupied grid cell (i), allowing complete flexibility in incorporating dispersal. The probability (P_j) of an unoccupied cell (j) with suitable environmental conditions being colonised through dispersal from one or more occupied cells ($n = k$) is therefore:

$$P_j = 1 - \prod_{i=1}^{k} \left(1 - P_{ij}\right) \tag{3}$$

with a colonisation event based on a random draw of probability P_j. In the case of an unoccupied cell becoming occupied, the value of any environmental threshold traits undergoing evolutionary adaptation for the newly occupied grid cell (Te_j) are determined by taking the average of the environmental threshold traits of all k occupied grid cells (Te_i) within the dispersal radius, weighted by the dispersal probability from those cells:

$$T_{ej} = \frac{\sum_{i=1}^{k} \left(T_{ei} . P_{ij}\right)}{\sum_{i=1}^{k} P_{ij}} \tag{4}$$

Likewise, the phenotypic standard deviation of a newly colonised grid cell (σ_{Pj}) is determined from the average of k occupied cells, weighted by dispersal probability. The same process is also used to account for change in the environmental threshold traits (Te_i) and the phenotypic standard deviation (σ_{Pi}) of occupied cells due to admixture from surrounding populations. In the case of admixture, however, we add a weighting parameter (w) ≥ 1 to the focal grid cell (i) to account for the likely larger size of a local population relative to gene flow from other locations.

Case study: Australian drosophilids

We used *AdaptR* to project the distributions of 17 Australian drosophilids with significant variation in their genetic diversity related to climate tolerance (Hoffmann *et al.* 2003). We considered evolutionary adaptation only for a species' critical thermal maximum (CT_{max}), with responses to other environmental variables fixed at their current realised limits. Methods are described here in brief, but details are provided in Appendix S1. Genetic variances for heat resistance were estimated in 10 species through a full-sib–half-sib study design, and inferred from closely related species for the remaining seven (Kellermann *et al.* 2012). Values for CT_{max} were taken from previous studies (Kellermann *et al.* 2012; Blackburn *et al.* 2014).

Climate data

Environmental conditions are naturally highly variable, and the interyear variation in temperature globally has been as great as the rise in mean temperature over 30 years (Huntingford *et al.* 2013). The frequency, magnitude and spatial extent of these events all play a role in defining species range boundaries, as well as determining the intensity of exposure to which taxa must adapt. The interval over which extremes are defined in our approach is based on generation time, which varies among drosophilids between 6 and 9 weeks, but for simplicity was set to 2 months. The distributions of Australian drosophilids correspond strongly to climatic extremes, in particular of temperature (Kellermann *et al.* 2009, 2012; Overgaard *et al.* 2014). We assembled six climate variables at approximately ~ 1 km (0.01°) resolution across the Australian continent between 1981 and 2010 (Hutchinson *et al.* 2014). Daily values were then aggregated to extremes within each generation (see Appendix S1). Future climate scenarios were drawn from AWAP projections (Jones *et al.* 2009) and the forecasts of two GCMs (Teng *et al.* 2012), GFDL-ESM2M and CanESM2, which predict moderate (2–3 °C) and high (4 °C) increases in maximum temperature, respectively, in eastern Australia. These projections were overlaid on the historic climate record to forecast conditions from 2016 to 2105 (90 years, 540 generations), from which 100 alternative timelines were generated, randomly varying the order in which extreme events occurred.

Species distribution models

If enough physiological data are available, *AdaptR* can operate as a purely mechanistic model by limiting species distributions using specified upper and lower environmental tolerances (Kearney & Porter 2009). However, for many species, a more tractable approach will be to predict habitat suitability as a static function of multiple environmental variables using a correlative SDM. To demonstrate *AdaptR*, this study used the popular correlative SDM approach Maxent (Phillips *et al.* 2006), but could have used any SDM method. Given that short-term environmental extremes are not comparable to long-term averages, model fitting and threshold selection were calibrated across historical generations (30 years, 180 generations) (Maiorano *et al.* 2013). Options for further model validation are discussed in Appendix S1. Finally, as *AdaptR* identifies the exposure of a population to maximum temperature separately to other variables, the layers of suitable habitat were made conditional on the effect of maximum temperature by projecting suitability using optimum values of temperature (i.e. temperature that maximises the response function while all other variables are held fixed).

Dispersal

To identify the probabilities of dispersal (P_{ij}) for drosophilids, we used stochastic simulations based on observed movement distances for *Drosophila* (Dobzhansky & Wright 1943; Spencer-Johnston & Heed 1976; Taylor 1978), with the resulting dispersal probabilities approximated by a two-dimensional negative square power-law model (Mokany *et al.* 2014) with median dispersal distance (λ) = 1 and scaling factor (K) = 1. This kernel has a 'fat tail', making it suitable for representing rare long-distance passive dispersal events. We assumed a maximum possible dispersal distance of 5 km from the focal cell in a single generation. Dispersal between two occupied cells also provides the opportunity for genetic admixture, the effect of which is parameterised as the number of resident individuals per immigrant (w), applied as 1 per 1000 (i.e. $w = 1000$).

Fitness costs of adaptation

Heatwaves in Australia's recent past could have driven evolution of CT_{max} to higher limits than currently observed. Without considering the cost of adaptation to these events, CT_{max} can evolve unchecked and remain high. Furthermore, admixture then gradually transfers the elevated CT_{max} from range margins to the core. To select the cost slope parameter (m), we ran *AdaptR* for 1500 years under historical conditions, and chose the lowest value that kept the species CT_{max} to within 0.1 °C of its starting CT_{max} value in > 90% of runs. Based on the consistency of results across species, a single value of 0.05 was used for m in all species.

Analysis

The inclusion of dispersal dynamics meant that little benefit would be gained from a direct comparison between *AdaptR* and a standard SDM application. Therefore, to identify whether physiological tolerances and adaptation have a significant effect on a species' predicted range size under future climate scenarios, we used three types of projections: (1) the 'Basic Hybrid SDM' added dispersal dynamics to the original SDM predictions; (2) the 'Fixed Threshold' model added physiological data on known CT_{max}, but did not vary spatially or allow for adaptation (plasticity, phenotypic variance and heritability reduced to zero) and (3) the 'Adaptation' model allowed genetic adaptation of CT_{max}. In each case, the model was run 100 times using differing time series of environmental conditions as described above, replicated under a no climate change scenario and climate change scenarios based on forecasts by GFDL-ESM2M and CanESM2. To test the overall model results, a mixed-effects linear model was fitted using the *lme4* R package (Bates *et al*. 2012), treating percentage change in a species' starting range as a function of the modelling approach used and climate scenario, with the species and environmental time series included as random effects.

RESULTS

In general, range size was projected to decline as a result of climate change, although outcomes varied widely among species and simulation runs. In response to the rapid climate change under the CanESM2 scenario, *Drosophila simulans* went extinct in 70% of runs, irrespective of adaptation of CT_{max}, because other environmental factors were more influential (Appendix Table S1.4). One of the more striking outcomes of the *AdaptR* projections were the spatial patterns of local adaptation for CT_{max}, evident in widespread species under current climatic conditions and in all species after selection pressure from climate change was introduced (Appendix S2). In *Drosophila jambulina*, for example, CT_{max} in 2085 (averaged across 100 runs) was highest at the range edges, and closer to its original value near the coast and at high elevations (Fig. 2a). Model output from a single grid cell in a single simulation run highlights the key processes occurring as maximum temperature fluctuates within and between years, but gradually rises under climate change (Fig. 2b). In this particular run there are multiple temperature extremes early on, and rapid adaptation in response (Fig. 2c *i*), but during long intervals between such events, CT_{max} begins to decrease due to stabilising selection (Fig. 2c *ii*). As the climate warms further, heatwaves exceed the 95th percentile of the population's CT_{max} and drive the population locally extinct (Fig. 2c *iii*). The site is subsequently recolonised either from refugia in which the CT_{max} had remained low or from other adapted parts of the range. Variation in other environmental variables could also cause more frequent local extinction but was not an issue at this particular site.

The 'Adaptation' models offset many declines in range size that occurred if thermal tolerance was fixed, regardless of a species' current distribution (Fig. 3). Although only small increases in the average CT_{max} were necessary to reduce range losses (Fig. 3d), this often conceals the high spatial variation in adaptation, which increased the probability of persistence at range margins (Fig. 2 and Appendix S2). For example, under climate change, the distribution of *Drosophila ironensis* contracts to high altitude and coastal refugia, but with adaptation of CT_{max} range losses were reduced as the species had a much greater likelihood of persisting in each of the three regional populations, including lowland environments (Fig. 4).

Final range size was highly variable depending on the sequence of environmental extremes and time for recovery that preceded 2105 (Fig. 3), but after accounting for variation among species and runs there were clear effects of adaptation

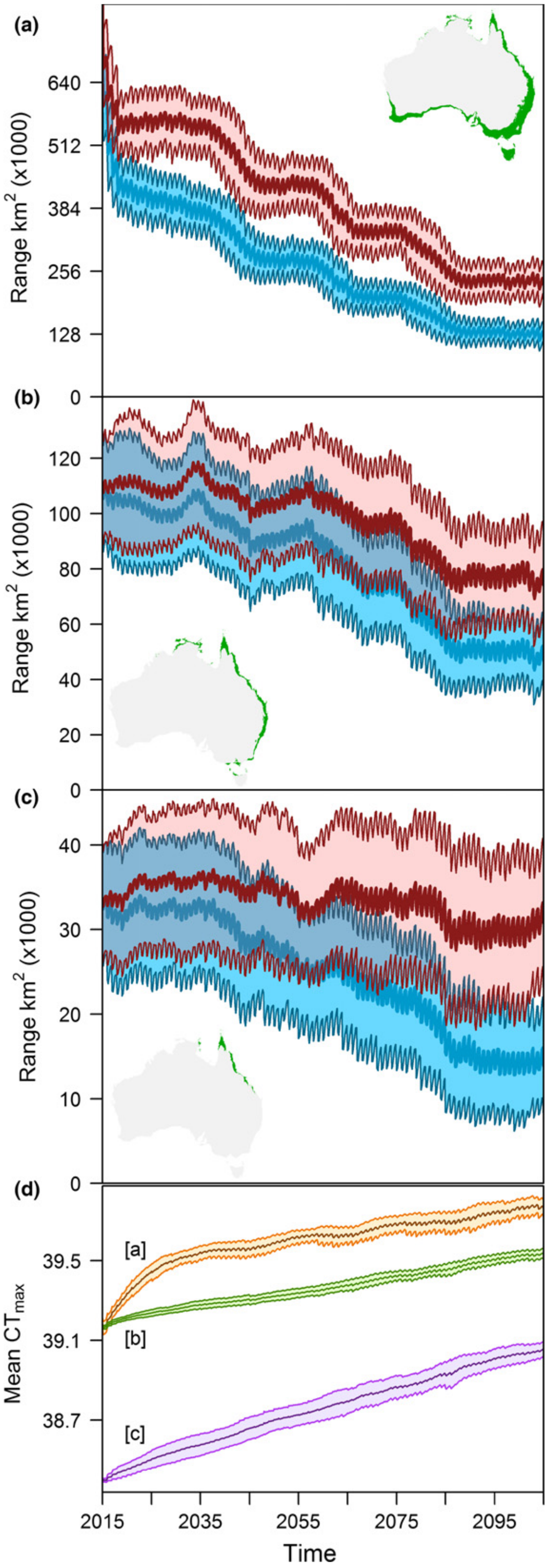

Figure 3 Timeline of changes in range size of (a) *Drosophila melanogaster* (continental distribution), (b) *D. simulans* (east coast) and (c) *D. rubida* (Wet Tropics) under the CanESM2 climate change projections. Each plot shows timelines for projections in which CT_{max} is held fixed (blue), and when plasticity and genetic adaptation are included (red) (mean ± 1 SD of 100 runs). For runs with adaptation, panel (d) shows each species mean CT_{max} (± 1 SD) (°C); a–c, respectively, over time.

(Fig. 5). Without climate change, persistence in more exposed range margins meant projections incorporating plasticity and evolution ('Adaptation') allowed species to occupy approximately 7% more area than if CT_{max} were held fixed ('Fixed Threshold'). Under climate change, the Adaptation projections were on average 15% (GFDL-ESM2M) and 30% (CanESM2) higher than the Fixed Threshold models. There was a poor relationship between the 'Basic Hybrid SDM' approach and the Fixed Threshold model (Fig. 5). Suitable habitat extent is typically underestimated by the Basic Hybrid SDM because relationships with maximum temperature begin to decline at higher values, dropping below the binary threshold earlier than they would using the known CT_{max}. Without specifying CT_{max}, the default approach allows species to persist in some instances under severe scenarios that exceed thermal tolerances in the threshold or adaptation model runs.

Drosophilids were chosen because we were confident in the parameters necessary to run *AdaptR*, but in circumstances where parameter estimates are missing or uncertain (e.g. for less well studied species), it can be useful to explore the sensitivity of results to their variation. Figure 6 shows the differences in mean range size and CT_{max} of *Drosophila sulfurigaster* if heritability is increased (combined with greater phenotypic variance). For *D. sulfurigaster*, sensitivity of mean range size and CT_{max} to climate change decreases rapidly as capacity to adapt is introduced, but at higher heritability values these benefits plateau because other factors become limiting (other environmental variables or the balance with fitness costs) (Fig. 6). In comparison, range size and mean CT_{max} increase almost linearly with plasticity (Appendix S3). Dispersal kernels affect species' capacity to recolonise after extreme events and therefore significantly influence average range size, but not CT_{max}. Conversely final range and CT_{max} appeared to be insensitive to changes in admixture.

DISCUSSION

We demonstrate that accounting for evolutionary adaptation in response to climate change can substantially alter projected species' distributions (Williams *et al.* 2008). Broader tolerances will naturally improve species persistence, but given the empirical basis of the parameters we apply (Kellermann *et al.* 2012), *AdaptR* demonstrates that drosophilids, and potentially other organisms with appropriate attributes, have the capacity to adapt under realistic scenarios of climate change (Skelly *et al.* 2007; Sgrò *et al.* 2011). The *AdaptR* framework provides a generic approach to estimating the influence of adaptation on the distribution of species for which we can approximate basic physiological and genetic parameters (Catullo *et al.* 2015). Physiological tolerances, plasticity and heritability are being characterised for an increasing range of wild and laboratory populations (Hansen *et al.* 2011; Araújo *et al.* 2013; Seebacher *et al.* 2015; García-Robledo & Kuprewicz 2016), as well as their trade-offs in populations of livestock (Hoffmann *et al.* 2016). Furthermore, if some parameters are uncertain, sensitivity analyses provide a simple basis for identifying possible outcomes (Fig. 6), and directing attention to critical evolutionary factors affecting species-specific vulnerability (Hoffmann & Sgrò 2011).

Outlook for drosophilids

Given drosophilids, like many insects, appear to have become locally adapted to their thermal environments (Hoffmann *et al.* 2013; García-Robledo & Kuprewicz 2016), the perception has been that they have little additional capacity to tolerate change (Kellermann *et al.* 2012), and will therefore experience significant declines under climate change (Overgaard *et al.* 2014). However, the discrepancy between the

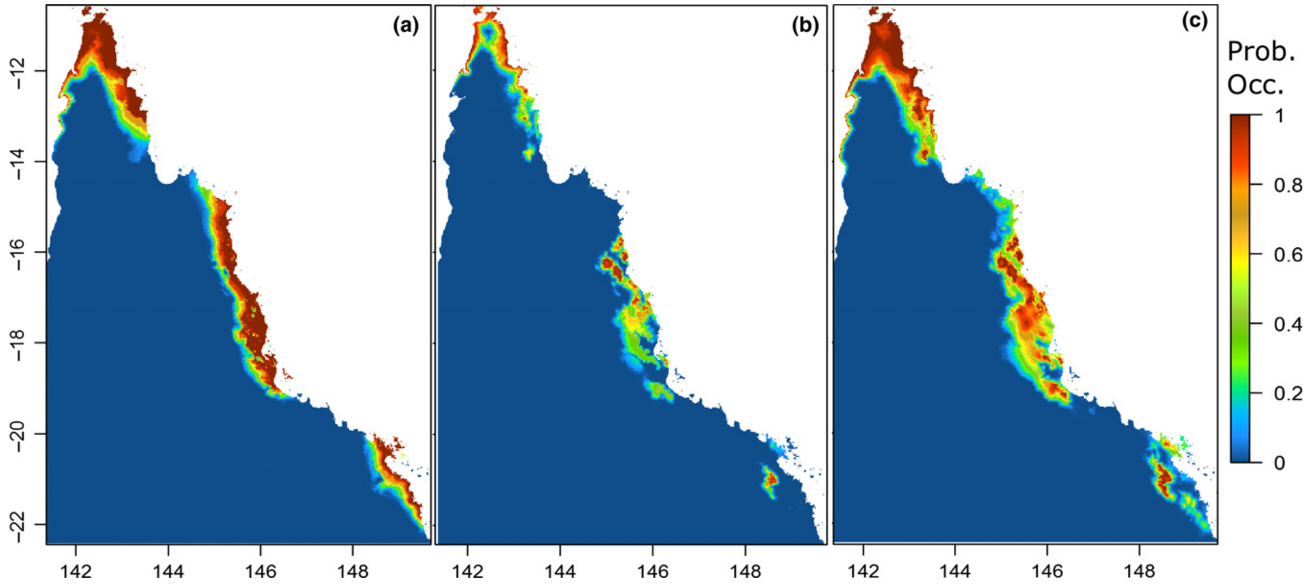

Figure 4 Probability of occurrence of *Drosophila ironensis* in 2105 based on (a) a fixed CT_{max} and no climate change and under climate change (CanESM2) with either (b) a fixed CT_{max} or (c) including adaptation of CT_{max} (plasticity and evolution). Probability of occurrence was derived from the proportion of model runs in which each grid cell was predicted to be occupied after the final generation.

'Basic Hybrid SDM' and 'Fixed Threshold' projections highlights the errors that can be made transferring spatially fitted SDMs to future projections (Wiens *et al*. 2009; Araújo & Peterson 2012). After including adaptation of fundamental limits in response to realistic rates of climate change (van Heerwaarden & Sgrò 2014), the majority of species studied (with the possible exception of *D. simulans*) could persist in a large proportion of their current range. Even tropical species with low heritability like *D. ironensis* are expected to persist in multiple locations, although with greatest confidence in high-altitude refugia. Although persistence was typically high in southern latitudes like Tasmania, our results do not generally suggest a latitudinal trend in range shifts, but rather indicate that species' ranges along the east coast of Australia will become increasingly fragmented, retracting towards coastal and high-altitude refugia.

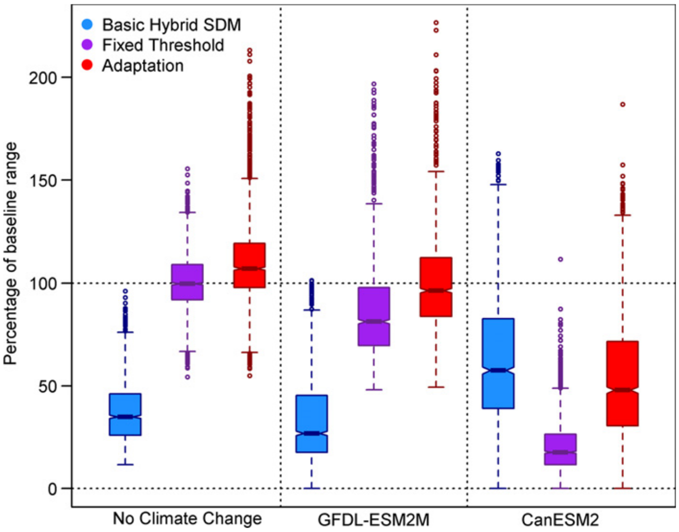

Figure 5 Boxplot of average per cent differences in the projected range of 17 species of drosophilids. Differences were calculated relative to the mean of Fixed Threshold projections without climate change. Projections were based on the naïve SDM projections ('Basic Hybrid SDM') in which both existing CT_{max} and adaptation are omitted, a 'Fixed Threshold' model that accounts for CT_{max} and the 'Adaptation' projections that include plasticity and allow evolution of CT_{max}. Changes in range.

Previous studies demonstrated latitudinal clines in knockdown temperature for *Drosophila melanogaster* (Hoffmann *et al*. 2002), and a southerly shift in the alcohol dehydrogenase polymorphism linked to climate adaptation (Umina *et al*. 2005). Although *AdaptR* did not reproduce the same latitudinal clines, the CT_{max} of continental species like *Drosophila busckii* and *Drosophila repleta* under current conditions showed clear increases of 1–2 °C at their inland range margins. However, this may be difficult to validate because the model also indicates a rise in local extinction risk, both as a result of hotter heatwaves that drive selection pressure for higher CT_{max}, and due to other climatic factors that make habitat suitability more marginal. Habitat suitability of rainforest species like *Drosophila birchii* fell more sharply with declines in rainfall and vapour pressure, and as a result the average distribution of CT_{max} under climate change reflected the expansion from coastal or altitudinal refugia. Despite such constraints by additional factors like precipitation, adaptation of CT_{max} still led to a significant reduction in the level of

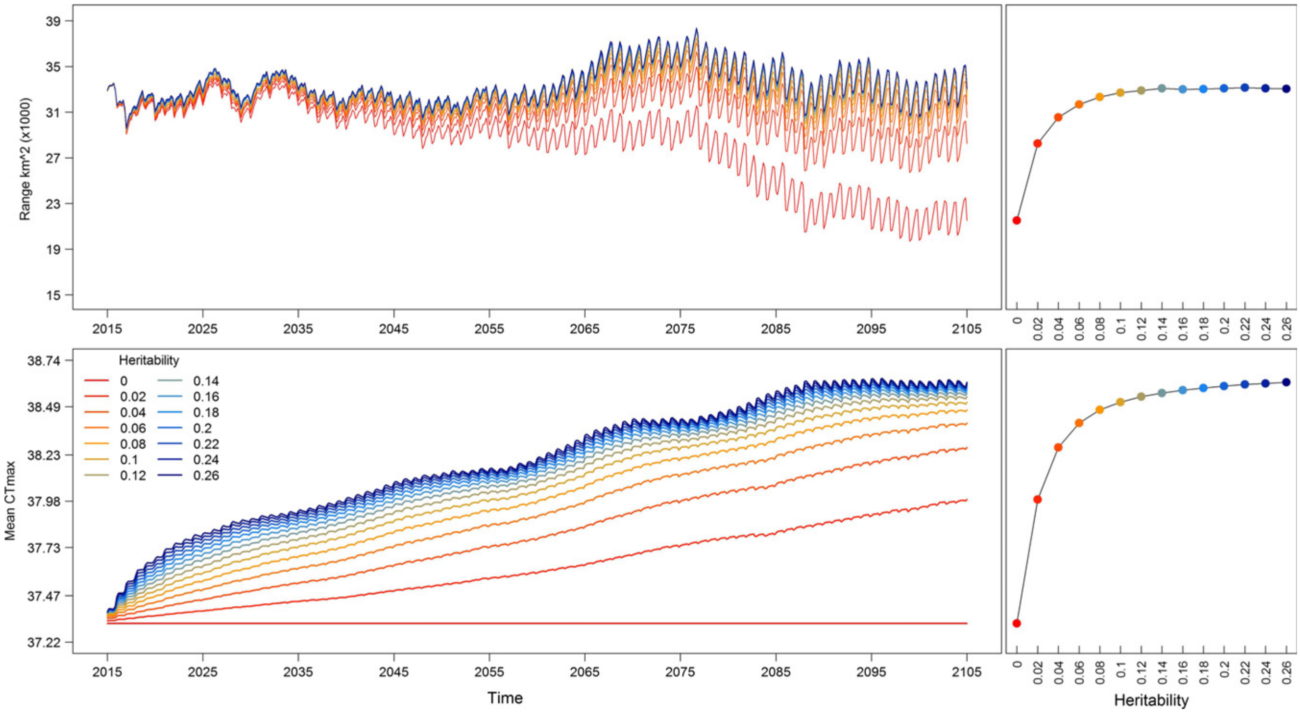

Figure 6 Variation in the timeline and final value of range and CT_{max} for *Drosophila sulfurigaster* in response to changes in heritability. All runs follow the same sequence of climatic extremes under the CanESM2 climate change scenario.

range contraction expected for all species under climate change, although the sensitivity analyses demonstrated the diminishing returns adaptation of CT_{max} can make to reducing vulnerability (Fig. 6). While generation length naturally moderates the necessary heritability for trait evolution (Davis *et al.* 2005), our study suggests adaptation could still be important to species thought to have low adaptive capacity, and therefore strategic management of existing adaptive genetic variation could play a significant role in their resilience to climate change (Sgrò *et al.* 2011).

Challenges and assumptions

Including all current understanding of eco-evolutionary dynamics in a comprehensive modelling framework would bring few practical benefits, as assumptions and uncertainties would quickly escalate and reduce the number of species to which it could be applied (Thuiller *et al.* 2013). To manage this trade-off, we use a basic framework that includes important features such as phenotypic limits and variance, plasticity and admixture, with the option to include more advanced processes if data become available (Catullo *et al.* 2015). As a result, the requirements for running *AdaptR* are modest in comparison to mechanistic SDMs or individual-based evolutionary models (Kearney *et al.* 2009; Bocedi *et al.* 2014; Schiffers & Travis 2014), with potential application to any species with occurrence data to support SDM, and data that directly or indirectly inform estimation of adaptive capacity (Catullo *et al.* 2015). Nonetheless, where *AdaptR* is applied in association with correlative SDMs, it is important that users apply the same quality control, checks for biases, and understanding of modelling assumptions as they would when fitting and validating a standard SDM (Wiens *et al.* 2009; Araújo & Peterson 2012).

Notwithstanding the paucity of genetic information, biodiversity models are frequently limited to predicting occurrence rather than local abundance (VanDerWal *et al.* 2009). This inherently limits the form of evolutionary response that can be considered (Hoffmann & Sgrò 2011), and requires a number of assumptions regarding population size, demography and dispersal probability. Gomulkiewicz & Holt (1995) concluded that even populations with the genetic wherewithal to persist in a novel environment may often fail to do so due to demographic stochasticity. Nonetheless, if appropriate data were available, the *AdaptR* model could easily be modified to account for more complex dynamics (e.g. Fordham *et al.* 2013). For example, modelling of selection on a trait like CT_{max} could be expanded to consider optima on thermal performance curves or tolerance landscapes (Rezende *et al.* 2014); phenotypic variance could respond more realistically to selection, mutation and drift (DeLong & Gibert 2016); and the model could consider potential trade-offs with other fitness traits or selection pressures (Mellard *et al.* 2015), particularly outside laboratory conditions (Sinclair *et al.* 2012). Although no trade-offs were found between heat tolerance and other traits in *D. melanogaster* (Williams *et al.* 2012), antagonistic relationships can severely constrain adaptive responses (Etterson & Shaw 2001). *AdaptR* should therefore be considered a starting point for understanding climate change adaptation. After the evolutionary outcomes of the model have been validated [e.g. by comparing current patterns of local adaptation or niche shifts during expansion by invasive species (Appendix S1)], further refinements and more complex analyses of a species' adaptive capacity could be incorporated (Thuiller *et al.* 2013).

In addition to gaps in information on evolutionary processes, there are also some technical challenges in generating environmental layers that match relevant physiological traits of organisms. To map the exposure, and hence intensity of selection experienced by an organism requires the variation in microclimate outside meteorological stations be considered (Kaspari *et al.* 2015). Consequently, the capacity for organisms to adapt their behaviour and improve thermoregulation or to avoid hostile conditions in different life-cycle stages may be important (Kingsolver *et al.* 2011; Huey *et al.* 2012). These issues are particularly important when considering which physiological parameters to use and how they are measured (Mitchell & Hoffmann 2010; Andersen *et al.* 2015). Mapping micro-climate has been one of the main challenges to applying mechanistic SDMs in the past (Kearney & Porter 2009). However, additional data collection during fieldwork could define the statistical relationships for downscaling coarse environmental layers (Storlie *et al.* 2013). Furthermore, new tools are now available to scale thermal conditions in a variety of microhabitats (Kearney *et al.* 2014).

CONCLUSIONS

The interest in species' evolutionary potential under climate change is not just critical to conservation of biodiversity; genetic adaptation could also prove vital to carbon sequestration (Padfield *et al.* 2016), agriculture (Lobell *et al.* 2015), biosecurity risk analysis (Shearer *et al.* 2016), fisheries (Muñoz *et al.* 2014) and human welfare (Kearney *et al.* 2009). Many species, particularly those that have short generations, could have substantial capacity to adapt under climate change and therefore previous estimates of sensitivity may have been overestimated. Here, we have applied a new, and relatively simple, framework to characterise niche limits and adaptive capacity (Catullo *et al.* 2015), which can be informed either directly by empirical studies (Hangartner *et al.* 2015) or indirectly using the wide variety of trait and phylogenetic data sources now available for many species (Jarošík *et al.* 2011; Kellermann *et al.* 2012). In coming years, genomics will increase our ability to identify distinct lineages, detect gene flow, characterise patterns of adaptation across landscapes and quantify levels of genetic variation relevant to adaptive capacity under climate change (Sgrò *et al.* 2011; Hoffmann *et al.* 2015). To build on this foundation, spatiotemporal models like *AdaptR* are needed to identify whether there is capacity to adapt to climate change, and where management intervention should occur. *AdaptR* could also inform where to source genetically diverse and pre-adapted communities for restoration (Prober *et al.* 2015), increase the efficiency of translocation, identify refugia that allow for migration and/or increase genetic connectivity and population sizes (Sgrò *et al.* 2011). Finally the flexible basic structure of *AdaptR* will hopefully encourage further research into how we model evolutionary processes realistically.

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AB, KM, RC, AH and SF designed the study and modelling framework; AH, VK, SM and CS collected and contributed drosophilid data; KM and AB developed the model; all authors contributed to revisions of the manuscript (AB wrote first draft).

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