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Original Research Article

Range expansion of an already widespread bee under climate change

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ABSTRACT

Climate change is a key threat to pollination networks and has already caused shifts in the distribution and phenology of many bee species. Predictions based on species distribution models forecast that most bee species will continue to decline as climate change progresses, the few exceptions to this being common, widespread species with large dispersal capabilities. Most of the bees studied so far are temperate or tropical species but many ecosystems are predicted to experience increased aridification under climate change. Therefore, we need to understand how pollinator species are likely to respond. Here we present species distribution models for the arid-adapted Australian small carpenter bee, *Ceratina australensis* Perkins, 1912 (Apidae: Xylocopinae) under Intergovernmental Panel on Climate Change (IPCC) climate change conditions predicted for 2070 (Representative Carbon Pathway 8.5). We applied Maximum Entropy, Generalized Linear Models, Generalized Additive Models and Random Forest methods. Overall, our models predict that this bee will have an increased area of suitable habitat as climate change progresses, including an increased range within protected areas. However, its potential range will shift further into coastal areas, that are highly human populated and urbanised. Our results suggest that wild bee taxa may be able to cope with the predicted scale of future aridification under climate change. Finally, this species is predicted to increase in urban environments, which highlights the need for city planning, suitable habitats and green spaces to support wild bee species.

1. Introduction

Wild bees are often under-recognised but essential pollinators of natural, urban and agricultural environments. They are crucial to agricultural production (Breeze et al., 2011) and this service is further boosted by increased wild bee diversity (Winfree et al., 2018). However, there is substantial evidence that wild bees are at risk from a variety of human-induced pressures, a key threat being climate change (Aguirre-Gutiérrez et al., 2017; Kerr et al., 2015; Potts et al., 2010; Vanbergen and Garratt, 2013).

Studies based on museum collections across the last 200 years have identified that there have already been range shifts and localised losses of species due to ongoing human-induced climate change (Aguirre-Gutiérrez et al., 2016; Bedford et al.,

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2012; Hegland et al., 2009; Kerr et al., 2015; Parmesan et al., 1999). Though not all species have or will suffer from reduced climate suitability, the most at risk species tending to be rare specialist species with limited dispersal capabilities (Casey et al., 2015; Rasmont et al., 2015; Silva et al., 2015). Another consideration is whether climate change will spatially separate, or desynchronise the phenology of, angiosperms and pollinators (Corlett and Westcott, 2013; Settele et al., 2016). And indeed, some phenological and spatial shifts due to climate change have already been documented. Some communities are shifting in unison at least for now (Bartomeus et al., 2011; Gorostiague et al., 2018), while others demonstrate corresponding declines between bees and flowers, likely indicating phenological mismatches (Biesmeijer et al., 2006; Burkle et al., 2013; Schweiger et al., 2012). However, the long-term museum collections that these types of studies rely on are rare, effectively limiting these studies to small areas of the globe and traditionally highly collected groups (Graham et al., 2004; Newbold, 2010).

Another way to investigate the effects of climate change on bees, without requiring long-term museum collections, is to model how species have responded to historical climate change events, using coalescent phylogenetic methods. A number of studies have modelled the historical demography of bee species, by calculating the change in effective population size (N_e), calibrated with a molecular clock, to show changes in N_e over time. Such studies have been performed on orchid bees (Euglossini; López-Uribe et al., 2014), sweat bees (Groom et al., 2014, Halictini; 2013), bumble bees (Bombini; Dellicour et al., 2014) and small carpenter bees (Ceratinini; Dew et al., 2016; Shell and Rehan, 2016). These groups commonly show strong increases in N_e, in response to historical global warming events, linked to the dispersal of species from refugia during arid glacial periods (López-Uribe et al., 2014). However, there are limitations to this approach (Grant, 2015), and while these studies are indicative of future trends, they lack the predictive power to help guide conservation approaches.

One method that does offer a predictive approach is species distribution modelling. This method correlates data from climate change models with the known current occurrence records of species, to determine the area that will be climatically suitable for that species in the future. Many species distribution models on bees have focussed on members of the genus *Bombus*, numerous species of which already have declining populations due to climate changes (Cameron et al., 2011; Jacobson et al., 2018; Kerr et al., 2015). In North America, species distribution modelling found that *Bombus* species diversity is likely to decrease in southern regions in the future, with northern areas becoming more climatically suitable (Sirois-Delisle and Kerr, 2018). However, the authors predict that the bees will be unable to disperse northward quickly enough to avoid species declines. Likewise across Europe, the vast majority of *Bombus* species are predicted to lose climate suitable area, even if they are capable of dispersal (Rasmont et al., 2015). A further study restricted to the UK also predicted declines, though inclusion of land-use management or biotic interactions into these models gave less severe predictions, possibly indicating that considering climate alone may over estimate responses (Giannini et al., 2013b; Marshall et al., 2018). Of course, all these studies are focussed on one largely temperate, cold-adapted genus in the Northern hemisphere, so are not necessarily indicative of bee responses worldwide.

The majority of the literature outside of *Bombus* has focussed on tropical biomes. Almost all of these studies were conducted within Brazil, which has a predominantly tropical climate with some semi-arid regions (Olson et al., 2001). Many bee species in Brazil are likely to have more restricted distributions with ongoing climate changes (Faleiro et al., 2018; Giannini et al., 2013a, 2012). Other species show shifts in the location of suitable habitat but will maintain or gain in overall area of distribution (Martins et al., 2015; Nemésio et al., 2016; Silva et al., 2015; Teixeira et al., 2018). However, the extreme deforestation in some areas of Brazil may prevent successful dispersal (Nemésio et al., 2016), and other species are likely to move towards the coast, possibly limiting future dispersals (Teixeira et al., 2018). These changes in bee distributions have been predicted to impact the pollination of crops in Brazil, especially guava, tomato, and coffee (Elias et al., 2017; Giannini et al., 2017a, 2013b). Together these studies suggest that many tropical pollination networks are at risk through bee species declines and spatial mismatch.

There has been, to our knowledge, only three studies of bees in xeric zones. This is a surprising oversight given that climate change is predicted to lead to increased aridification in many parts of the world (D'Odorico et al., 2013; Dai, 2013). Giannini et al. (2017b) looked at a *Melipona* species in a semi-arid region of Brazil, finding this species would gain in distribution with climate change, but risks losing connectivity and gene flow through the middle of its range. An orchid bee found widely across both tropical and semi-arid regions of Brazil was also predicted to expand in distribution with climate change (Silva et al., 2015). Correspondingly, an Australia arid zone allodapine bee is predicted to increase in distribution, as will the two species of trees that it is reliant on for nesting sites (Silva et al., 2018). These studies suggest that arid adaptation may be beneficial for these species in coping with climate change. Given that xeric regions are thought to host the greatest diversity of bee taxa (Michener, 2007) it is important to understand how diverse species are likely to respond to climate change in arid-zones worldwide.

The small carpenter bee genus, *Ceratina*, has a global distribution encompassing many biomes, including arid zones (Rehan and Schwarz, 2015; Rehan et al., 2010). The Australia small carpenter bee, *Ceratina* (*Neoceratina*) *australensis* Perkins, 1912 (Apidae: Xylocopinae), is a common bee species that nests in a variety of plants, including weedy stems found in both urban and agricultural landscapes. It is widespread across the south-east of mainland Australia and found in subtropical, temperate and semi-arid regions (Dew et al., 2016; Oppenheimer et al., 2018). As an arid-adapted bee, our aim was to predict the range of this species under climate change using species distribution modelling. Based on the previous literature we hypothesised that *C. australensis*, as a common and widespread species with a generalist diet and pre-adaptations to arid biomes, would expand its distribution as climate change progresses.

2. Methods

2.1. Occurrence data

In total, 812 occurrence records were compiled for *Ceratina australensis* (Fig. 1). There were 757 records from 30 unique collection localities downloaded from the Atlas of Living Australia database (www.ala.org.au; Supplementary Table 1). The Global Biodiversity Information Facility database was also checked but had no additional records (GBIF, 2019). We only included records from the mainland of Australia, with GPS coordinates with an uncertainty of 100 m or less. Records lacking a measure of GPS uncertainty were included if regarded as valid based on the accompanying metadata. A further 53 unique collection localities were attained from field collections conducted from January 2014 to 2018 (Supplementary Table 2). Two additional occurrence records were obtained from specimens present in the South Australian Museum collection. All occurrences used in our modelling procedures are shown in Fig. 1.

2.2. Occurrences partitioning, modelling methods, and evaluation

For modelling the distribution of *C. australensis* under the current climate scenario, we gathered 19 climatic variables available in the Worldclim website (Hijmans et al., 2005) at 2.5 min resolution (cell size of 0.041° at the equator), comprising the middle-eastern portion of the Australian continent. Then, we z-transformed the variables we used (mean equal to zero, variance equal to $|1|$) in order to avoid any of them having unequal effects upon the modelling process. Following this, we performed a principal components analysis (PCA hereafter) on the transformed variables to produce orthogonal and spatialized principal components (PCs hereon) to be used to predict the distribution of *C. australensis* in the current climate scenario. The selected PCs accounted for ~95% of the raw environmental variables. This method of using orthogonal variables as predictors of a species distribution range has previously been shown to be effective in decreasing model overfitting while increasing model reliability (De Marco and Nóbrega, 2018; Dormann et al., 2013, 2012).

We also gathered the same 19 climatic variables from 17 Atmosphere-Ocean Global Circulation Models (AOGCMs hereon) available in Worldclim for 2070 (*Representative Carbon Pathway* - RCP 8.5) from the latest Intergovernmental Panel on Climate Change (IPCC) report (IPCC, 2013). In this scenario, the carbon emissions are expected to continue to rise, as land use changes and governmental policies to decrease carbon emissions remain ineffective, while the human population increases steadily up to 12 billion people. In this baseline scenario, global temperatures may rise, on average, 3.7 °C, with a range of 2.6° to 4.8 °C until 2100 (IPCC, 2013; Taylor et al., 2012). This is the RCP with the greatest potential climatic impact upon the planet's biodiversity, corresponding to a business as usual scenario, where the human population continues to grow and there are no technological improvements that allow for a decrease in carbon dioxide emissions. As recent studies have shown that the projected scenarios for climate change may have been severely underestimated (Fischer et al., 2018; e.g. Steffen et al., 2018) we opted to model our species considering this emission scenario. We also z-transformed these variables from the 17 AOGCMs, projected upon each one of them the PCA's linear coefficients obtained for the present-day scenario, and then performed new PCA analyses, one for each of the future 17 AOGCMs, in order to have orthogonal and spatialized variables, that are related to the current scenario, for each of these potential future scenarios as well.

In our modelling procedures we considered four modelling methods: Maximum Entropy (Phillips et al., 2017, 2006; Phillips and Dudík, 2008), General Linear Models (Guisan et al., 2002), Generalized Additive Models (Guisan et al., 2002;

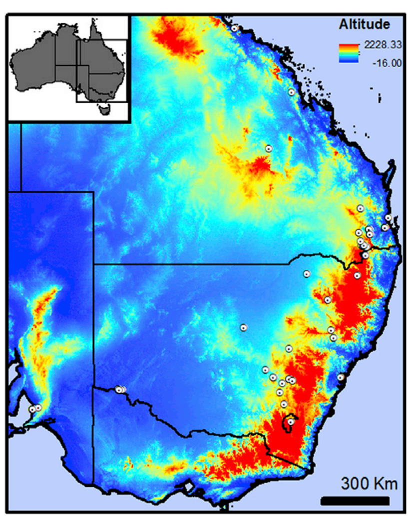

Fig. 1. Occurrences of *Ceratina australensis* in mainland Australia. Map showing altitude in metres (Geoscience Australia, 2011).

Hastie and Tibshirani, 1986), and Random Forest (Breiman, 2001). While GAM, GLM, and RDF are statistical methods, MAX is a machine learning method.

We made use of a bioclimatic envelope model (Nix, 1986) to create a multivariate space that was used to constrain the allocation of pseudoabsences used in our modelling procedures. Pseudoabsences were allocated outside of the bioclimatic conditions of the multivariate space, which were then laid upon the corresponding geographic space. This pseudoabsence allocation method significantly improves the results of the modelling procedure, as it compares the climatic conditions of the known occurrences of the target species with those of the pseudoabsences (Lobo and Tognelli, 2011; VanDerWal et al., 2009).

Regarding the available occurrences for *C. australensis*, we partitioned them following a checkerboard method (Muscarella et al., 2014; Roberts et al., 2017). This partition method is spatially structured, and the occurrence data is separated into two independent subsets, one used to predict the species distribution and the other used to evaluate the produced range. Later, the subset that was used initially to evaluate the first produced range is used to produce a second distribution range for the species, which is then evaluated by the subset of occurrences that was used to predict the first distribution range for the species. We produced the final maps to represent the species distribution under every single scenario using a threshold that balances both omission and commission errors and maximizes specificity + sensitivity of our models to cut the suitability maps for *C. australensis* into presence/absence maps (Jiménez-Valverde and Lobo, 2007, 2006).

To evaluate our models, we considered the true skill statistic (TSS hereon; Allouche et al., 2006), which varies from −1 to +1 and is a threshold-dependent metric. In this metric, negative and around zero values correspond to range predictions produced at random, minimum values of 0.5 are acceptable and those equal or higher than 0.7 are considered reliable. We performed all the modelling procedures in R environment (R Development Core Team, 2019) using a script developed by Andrade et al. (in prep; https://github.com/andrefaa).

To produce the final ranges for *C. australensis* in each one of the current and future climatic scenarios considered, we produced an ensemble (Araújo and New, 2007; Marmion et al., 2009) considering the distribution ranges with TSS values higher than the mean of all models we produced. We also produced a separate single ensemble for the future scenario, to evaluate the potential distribution range of the species in comparison to the ensemble distribution produced for the present scenario. Finally, considering the ensembles that we obtained for both the present and future scenarios, we downloaded the shapefile of the protected areas network for Australia from the Protected Planet website (http://www.protectedplanet.net/) to evaluate how much of the predicted range of *C. australensis* is/will be protected considering its predicted range. In this analysis, we only considered the restricted protected areas according to IUCN categories I to IV.

3. Results

Our models reached acceptable TSS values (0.57 ± 0.059; mean ± standard deviation). In the present scenario, our models predicted suitable areas for *C. australensis* along the whole east Australian coast, and some areas in the centre of the study extent. Nonetheless, there were some areas in subalpine and alpine regions of the Snowy Mountains in New South Wales and the Victorian Alps that were predicted as unsuitable for the species in the current scenario, according to all modelling methods (Fig. 2A–D). For the future scenario, all modelling methods, except GLM, showed a range increase for *C. australensis* in Australia. The GLM method showed a decrease in the amount of suitable areas for the species in the future.

Considering the final ensemble distribution for *C. australensis* in the present and future scenarios (Fig. 3), the same overall pattern was maintained across the different modelling methods, and the species' range is expected to increase in the future.

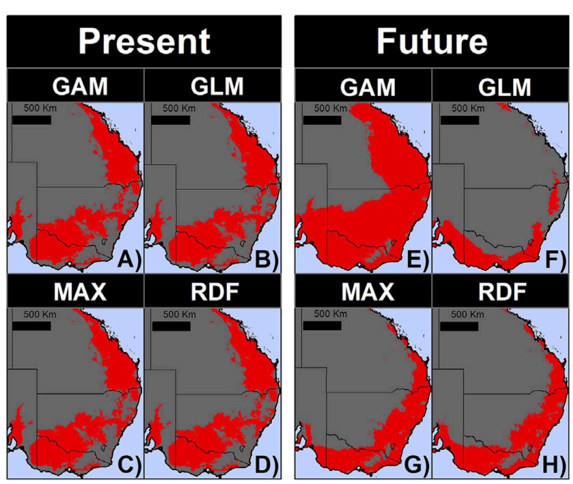

Fig. 2. Range predictions for *Ceratina australensis* in the current and future scenarios considering all algorithms we employed. Red corresponds to the presence of the species. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

As a result of this predicted range increase, the area of protected habitat for *C. australensis* is expected to also increase in the future, going from ~8.9% of its range, to a total of ~12.2%.

4. Discussion

Ceratina australensis is predicted to have an overall increased range with progressing climate change, with a shift towards more coastal areas (Fig. 3). The individual models exhibited some variation in the extent of the range into central and northern parts of Australia but the gain in coastal habitat is consistent (Fig. 2). There will be a continued absence of suitable habitat in central Australia and in the subalpine and alpine regions of the Snowy Mountains and the Victorian Alps (Fig. 3). Of its predicted future range ~12.2% will be within protected land, an increase from the ~8.9% of the present day. These results corroborate predictions based on the historical demography of this species, which indicated an increase in the effective population size of *C. australensis* during the period of global warming following the last glacial maxima (Dew et al., 2016). However, climate suitability alone will not determine this species' distribution in the future and below we discuss other relevant factors governing the future of this species.

Overall, our models suggest that *C. australensis* will have an increase in potential habitat with climate change, and this corresponds to previous research. All of the arid adapted bee species studied so far are predicted to have increased distributions under future climate change (Giannini et al., 2017a; Silva et al., 2018, 2015). Seventy percent of the Australian continent is arid, and it is predicted to undergo increased aridification as climate change progresses (Byrne et al., 2008; D'Odorico et al., 2013; Dai, 2013; Park et al., 2018). Hence species with arid adaptation may have an advantage in coping with the rapid pace of modern-day climate change. Being a habitat generalist across temperate, subtropical and semi-arid regions also has advantages for plasticity to climate change and dispersal capability (Rasmont et al., 2015; Silva et al., 2015). Additionally, *C. australensis* has a broad polylectic diet (McFrederick and Rehan, 2019), so it is less constrained by changes in floral communities spatially or phenologically. However, *C. australensis* is not predicted to occupy the most arid regions of Australia, which could lead to restrictions in distribution if aridification continues beyond the extent of our current model.

As well as the arid interior of Australia, *C. australensis* is not suited to subalpine to alpine regions and will not retreat into these high elevation areas with climate change. In the Northern hemisphere studies, the most commonly report shifts in taxa are to cooler regions; either northwards or up in elevation (Aguirre-Gutiérrez et al., 2016; Jacobson et al., 2018; Kerr et al., 2015; Parmesan et al., 1999; Ploquin et al., 2013; Rasmont et al., 2015). We generally see this shift to cooler clines for *C. australensis* with a shift to more temperate coastal regions (Fig. 3). However, the highest areas of elevation in the Snowy Mountains and Victorian Alps will remain unsuitable for this species. It is possible that these alpine areas may serve as areas of refugia for non-arid adapted bee species and species distribution models under future climate change are needed for alpine specialist and temperate Australian bees in this region.

While *C. australensis* will increase its potential range, including in protected areas, there are many other human induced factors that may limit its actual distribution. Its future distribution will encompass the most human populated area of Australia, with just the state capital cities in this region accounting for over half of Australia's population (Australian Bureau of Statistics, 2018). Therefore, this species will encounter increased urbanisation and agricultural land use. However, *C. australensis* is currently found in urban and agricultural areas that have historically undergone large scale disturbance and changes in vegetation (Oppenheimer et al., 2018), so this may not necessarily lead to population declines. Comparison of bee functional guilds in Australia found that bees with broad generalist diets, like *C. australensis*, are strongly associated with treeless roadside landscapes (Hall et al., 2019). They also found that stem-nesting bees were foraging in areas further away from remnant vegetation. Relatively open habitats appear, somewhat counterintuitively, to be beneficial for some bee species (Carper et al., 2014; Hall et al., 2019; Roberts et al., 2017; Silva et al., 2015). Again, these are commonly populous generalist

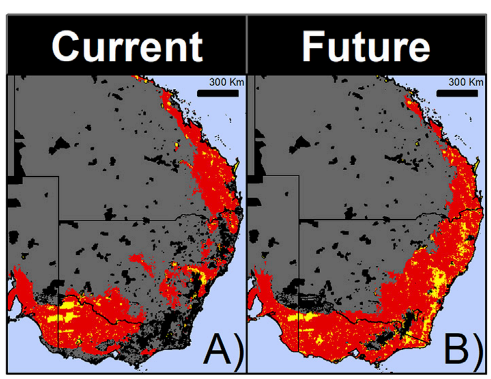

Fig. 3. Final ensembles for the range predictions of *Ceratina australensis* for the current and future climatic scenarios, considering the available network of restricted protected areas. Red corresponds to the presence of the species, yellow the predicted range in each scenario within PAs (~8.9% of the total range in current scenario and ~12.2% the total range in the future). Black areas, PAs where the species range was not predicted as suitable. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

species, with rare specialist species relying more on native vegetative patches (Hall et al., 2019). For stem-nesting bees the availability of nest sites can also be an important constraint on distribution (Dew and Schwarz, 2013; Silva et al., 2018), however, *C. australensis* utilises many different plants for nesting substrate, including common weedy plants found along roadsides and in empty lots. Therefore, nest availability may not be a large concern for this species, if these urban patches continue to persist or if communities put in place urban gardens to provide forage and nest sites (Baldock et al., 2019; Hall et al., 2017; Heneberg et al., 2017).

Overall, our study supports the notion that common, widespread bees with generalist habitat and dietary niches are likely to cope with ongoing climate change. Arid-adaptation may give some species resilience to climate change in regions such as Australia and this is particularly important given the predicted aridification in biomes worldwide. However, there is still uncertainty on the future of this bee, and whether it will continue to expand its range into increasingly urban environments. While it is predicted to have a larger range within protected areas, it will also shift in distribution towards the coast which is highly urbanised in Australia. Further studies are needed to model how urban factors may impact bee distributions. It is possible that generalist species such as *C. australensis* may be able to compensate for pollination losses as other species decline. Further studies combining museum records and genetic data would offer useful comparisons to determine historical distribution changes of arid species and better inform future predictions.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00584.

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