

# Beyond the model: expert knowledge improves predictions of species' fates under climate change

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**Abstract.** The need to proactively manage landscapes and species to aid their adaptation to climate change is widely acknowledged. Current approaches to prioritizing investment in species conservation generally rely on correlative models, which predict the likely fate of species under different climate change scenarios. Yet, while model statistics can be improved by refining modeling techniques, gaps remain in understanding the relationship between model performance and ecological reality. To investigate this, we compared standard correlative species distribution models to highly accurate, fine-scale, distribution models. We critically assessed the ecological realism of each species' model, using expert knowledge of the geography and habitat in the study area and the biology of the study species. Using interactive software and an iterative vetting with experts, we identified seven general principles that explain why the distribution modeling under- or overestimated habitat suitability, under both current and predicted future climates. Importantly, we found that, while temperature estimates can be dramatically improved through better climate downscaling, many models still inaccurately reflected moisture availability. Furthermore, the correlative models did not account for biotic factors, such as disease or competitor species, and were unable to account for the likely presence of micro refugia. Under-performing current models resulted in widely divergent future projections of species' distributions. Expert vetting identified regions that were likely to contain micro refugia, even where the fine-scale future projections of species distributions predicted population losses. Based on the results, we identify four priority conservation actions required for more effective climate change adaptation responses. This approach to improving the ecological realism of correlative models to understand climate change impacts on species can be applied broadly to improve the evidence base underpinning management responses.

**Key words:** climate change impact; endemic species; expert knowledge; fine-scale data; Maxent; rainforest; refugia; species distribution modeling.

## INTRODUCTION

The global scale of climate change impacts on species distribution and abundance has demanded its increased consideration in management, planning and conservation (Jones et al. 2016, Reside et al. 2018). Detailed behavioral, physiological, and ecological data sufficient for detailed mechanistic models are available for some species (Kearney and Porter 2009). For the vast majority of species, however, predicting the impact of climate change has involved correlative modeling and trait-based vulnerability assessments (Bellard et al. 2012, Foden et al. 2013, Reside et al. 2016). Evidence suggests that the correlative modeling approach can provide useful insights into the ways that species might be impacted by, or respond to, changing climate (Tingley et al. 2009).

However, correlative modeling is widely criticized, particularly where species biology and ecology are not taken into account, and because the correlative approach is highly influenced by data quality, resolution, model algorithm, and model parameters (Seo et al. 2009, Reside et al. 2011, Warren and Seifert 2011). Substantial advances continue to be made in this field, resulting in ever-improving standards for best practice. Yet, given the velocity, magnitude, and uncertainty of the expected changes, further examination is required to determine whether correlative models accurately reflect species presence, and particularly the environmental and ecological reasons for why they do not.

Like all techniques used to aid practical action, species distribution models and their future projections should be scrutinized for ecological realism. In particular, inaccurate models should be examined to elucidate the factors that affect model performance but are not accommodated by the correlative modeling process. For example, standard correlative species distribution models do not accurately reflect species interactions (but see Pollock et al. 2014 for advanced

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techniques of co-occurrence), and the spatial resolution of predictor data can vastly influence the climate projections of species (Reside et al. 2011). Model performance is further influenced by biogeographic context (Luoto et al. 2005), baseline climate data (Baker et al. 2016), species adaptive capacity (Bush et al. 2016), other traits (Santini et al. 2016), species responses to extreme weather events (Morán-Ordóñez et al. 2017), and fire events (Regos et al. 2017). In many cases, model evaluation is difficult: model quality as determined by statistical scores can improve without necessarily increasing ecological realism. The problem is exacerbated with studies of future climate change impacts, which assume a species' current distribution represents the full range of its climatic tolerances (Araújo and Pearson 2005, De Marco et al. 2008).

Gaps in data are a key challenge for conservation science generally and distribution modeling specifically, particularly for under-studied species. Expert knowledge to inform understanding and to guide management is increasingly used where decisions need to be made but empirical data are insufficient (Martin et al. 2012). Expert knowledge is particularly useful for predicting the impact of climate change and prioritizing management actions (Foden et al. 2013, Firn et al. 2015, Javeline et al. 2015). Methods have been developed to minimize bias and uncertainty inherent in expert knowledge, and to account for wide variances in knowledge (Martin et al. 2012). Further development of methods enables shrewd and transparent judgement of the best conservation actions, which help circumvent the tendency of scientists and managers to delay action because knowledge is incomplete (Nicol et al. 2018). In a case where many species require assessment but detailed information about each species is lacking, the combination of expert knowledge and empirical and predictive models can produce better results than either approach used alone (Burgman et al. 2011).

We investigate the effect of these data gaps by taking a regional assemblage of species identified as highly vulnerable to climate change (Williams et al. 2003) and scrutinizing in detail each species' prospects under a business-as-usual climate change scenario in 2085. Our aim was to resolve where the models underperform and derive guidelines for using ecological principles to improve these models. We compare the model projections for species using (1) 1-km resolution climate predictor data, (2) 250-m resolution "Accuclim" climate data (Storlie et al. 2013), and (3) the Accuclim models refined by expert vetting. From these projections, we quantify the extent and location of spatial differences between the three model outputs and examine the factors that are missed by the first two modeling approaches. We use the final expert-refined model outputs to predict the areas likely to harbor important micro refugia in areas where the models predict widespread loss of suitable climate and infer key refugial areas for multiple species.

## METHODS

### *Study area*

The Australian Wet Tropics (AWT) in northeastern Australia (Fig. 1) consists of mixed tropical forests and extends

from coastal lowlands to an elevation of 1,620 m (Williams et al. 2009). Most of the rainforests of the region are within the Wet Tropics World Heritage Area. The rainforest is home to 65 endemic vertebrate species, which are predominantly confined to cooler, wetter rainforest that occurs at higher elevations (Williams et al. 2009, 2010). Most of these higher elevation species (97%) are predicted to be severely impacted by even moderate climate change (Williams et al. 2003).

### *Study species*

We focused on 17 rainforest vertebrates (eight frog and nine bird species) endemic to the AWT. We chose the species to achieve a broad representation of the different ecological contexts and modeling issues found in the region.

### *1-km models*

The 1-km (0.01°) resolution species distribution models were fitted with Maxent (Phillips et al. 2006) incorporating baseline climate (1976–2005) sourced from Australian Water Availability Project (Jones et al. 2007, Grant et al. 2008). Bioclimatic predictor variables were derived using the "climates" package in R (VanDerWal et al. 2011a): annual mean temperature, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation seasonality, precipitation of wettest quarter, and precipitation of driest quarter. Species occurrence data were accessed from Atlas of Living Australia, Queensland Museum, and the Centre for Tropical Biodiversity and Climate Change database (Williams et al. 2010, Reside et al. 2013, 2017a). A "target-group background" (Phillips and Dudik 2008) consisting of the occurrences of all the species in the same class was used to account for any spatial bias in the occurrence records. Future climate projections from the Tyndall Centre (<https://www.tyndall.ac.uk/>) consisted of 18 general circulation models (GCMs), and the business-as-usual scenario RCP8.5 (also considered a "severe" climate change scenario) for the year 2085. The median of modeled climate suitability across the 18 GCMs for each year was calculated, and areas beyond a reasonable dispersal distance from species' current distribution were removed for more realistic estimates of future distributions (Warren et al. 2013). Details of the species data and modeling process are described in full detail in previous work (Reside et al. 2013, 2017a).

### *Accuclim models*

Species distributions modeled using fine-resolution "Accuclim" climate data were sourced from Storlie et al. (2013), so the methods are described here only in brief. Species occurrence data were obtained from the Centre for Tropical Biodiversity and Climate Change database and have been carefully vetted for accuracy (Williams et al. 2010). The climate data were from Australian Water Availability Project, downscaled from 5-km resolution to 250-m resolution (detailed methods in Williams et al. 2010). The temperature consisted of daily  $T_{\max}$  and daily  $T_{\min}$ ,

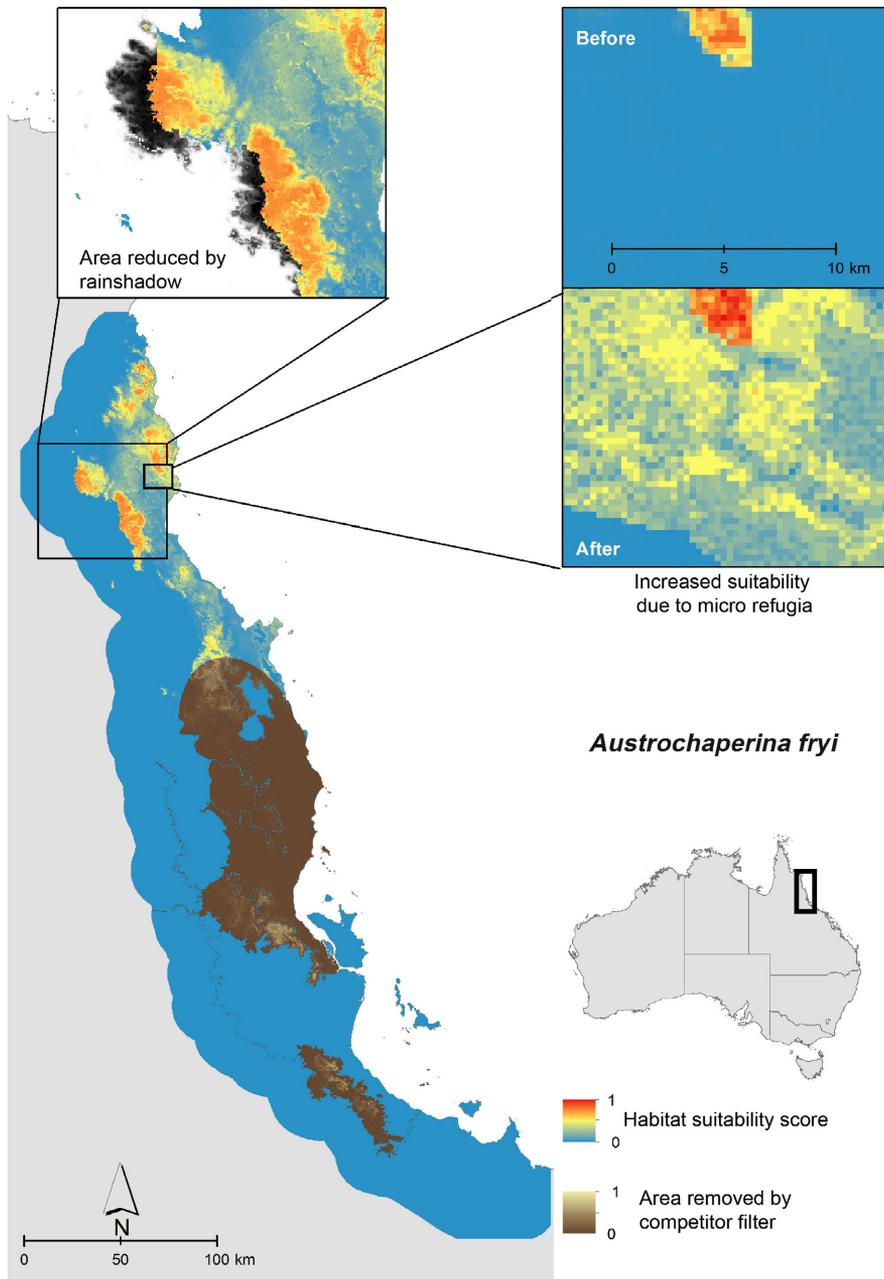


FIG. 1. An example of a current distribution model for a species, *Austrochaperina fryi*, in the Australian Wet Tropics region. We use this species to demonstrate three general principles and their filters on models: rain shadow (top left insert; black shows areas masked out because there is a sharp transition to dry forest that the distribution model did not reflect), micro refugia (top right inserts), and competition (brown area has been masked out because the species does not occur there due to probable interspecific competition from the parapatric species *Austrochaperina robusta*).

downscaled using 10 topographic, weather, and environmental variables resulting in accurate and vetted temperature surfaces at 250-m resolution, referred to as “Accuclim” (Storlie et al. 2013). Spatial layers of mean annual temperature, temperature seasonality, mean maximum temperature of the warmest month, and mean minimum temperature of the coldest month were created from the Accuclim data. Rainfall data were the downscaled Australian Water Availability Project spatial layers of mean annual precipitation, precipitation seasonality, precipitation of the wettest month, and precipitation of the driest month. Spatial surfaces were

created using the “climates” package (VanDerWal et al. 2011a).

Future climate scenarios were created by subtracting the downscaled Accuclim climate layers from Anuclim climate layers to generate an “anomaly” layer describing the spatial pattern of difference between the two (Storlie et al. 2014). This anomaly can then be applied to the future climate scenarios from the Tyndall Centre, producing downscaled future climate estimates that accounted for topographic and environmental factors known to decouple climatic processes from broad to fine resolution. Accuclim species distribution

models for current and projected future were fitted using Maxent, further described in Storlie et al. (2014).

#### Post-processing

A threshold was applied to both the 1-km and Accuclim species distribution models to delineate between where the species was likely to be present and where it was likely to be absent. Below the threshold, the habitat suitability was zero and above the threshold was the continuous habitat suitability score. For the 1-km models, the appropriate Maxent-derived threshold was individually selected for each species to give the best representation of the species' ranges as part of a previous study (details described in Reside et al. 2013). The Accuclim models all had the Maxent-derived "Balance training omission predicted area and threshold value" logistic threshold because it was the most accurate for these species modeled at this resolution (VanDerWal et al. 2009). For all models, distribution area was calculated in R (R Core Team 2014) using the "ClassStat" function within the package SDMTools (VanDerWal et al. 2011b).

#### Expert workshop

Eight individuals with expert knowledge of the ecology, biology, and distribution of the study species and the Wet Tropics bioregion participated in the workshop. Workshop participants represented a variety of backgrounds and perspectives including government scientists, university researchers, an environment officer from a regional council group, and a scientist from the Wet Tropics Management

Authority. The Accuclim species distribution models were converted to kml files and overlaid onto Google Earth, then were projected with an Epson EB-595Wi (Seiko Epson Corporation, Suwa, Japan) interactive projector onto a table. Using tabletop computing software and Epson Easy Interactive Pens, the experts made graphical annotations on the projected map that were saved as a png file (Mathieson 2016). The Google Earth background allowed zooming in to fine resolution to examine the terrain, forest cover of areas, and distances between forest patches. The experts first assessed the current distribution of each species to verify the current models, or to find areas that over- or underestimated habitat suitability, roughly guided by predefined questions (Appendix S1). Next, the experts inspected the projected future distribution of the species and discussed the areas that were likely to have suitability over- or underestimated, given the resolution of the data and knowledge of the species' ecology. We did not use a structured elicitation process, because we had a small group of people with broadly differing expertise, and found instead that exploratory discussion of the context and issues surrounding each species proved very useful. Through discussion and close examination of the models, the experts developed a set of general principles that describe the conditions under which the models consistently gave inaccurate estimations, and the species to which each of the general principles applied (Table 1). These are likely to be applicable for many more species within similar contexts, such as mountainous rainforest regions. At the end of the workshop, there was a thorough discussion of the conservation priorities required to maintain the persistence of the focal species in the face of climate change.

TABLE 1. General principles that describe models' under- or overestimating habitat suitability.

Principle	Example region	Example species
1. Rain shadow†. Models did not reflect the sharp transitions from rainforest to drier forest, particularly along the western edge of the uplands	Windsor Tableland, Carbine Tableland	<i>Acanthiza katherina</i>
2. Micro refugia†. High topographic ruggedness, southerly aspect and gullies are likely to maintain cooler areas, but the models predict regional climate to become unsuitable	Bellenden Ker Range, Thornton Uplands	<i>Cophixalus neglectus</i> , <i>Ptiloris victoriae</i>
3. Upper temperature tolerance unknown. The upper temperature tolerance is unknown because the lowland range is bound by ocean or represented by few records because of extensive land modification. Models predict species will disappear from the lowlands but likely they can survive hotter temperatures than estimated	Mission Beach	<i>Orthonyx spaldingii</i>
4. Geographical barriers†. Species do not exist where habitat modeled to be suitable exists, presumably because of existing geographic barriers to dispersal. It is assumed these geographic barriers will continue to be barriers to dispersal into the future, so species' suitability masked out of the areas they are unlikely to be able to disperse. This includes over-predictions to islands where species does not occur	Black Mountain Corridor, Seaview Range, Hinchinbrook Island, Palm Islands, Goold Island	<i>Litoria dayi</i> , <i>Austrochaperina pluvialis</i> , <i>Lichenostomus frenatus</i>
5. Competitor species†. Species distribution restricted by competitor species, despite suitable modeled climate.	Northern Atherton Tablelands, Lamb Range	<i>Austrochaperina fryi</i> limited by the presence of <i>Austrochaperina robusta</i>
6. Disease†. Frog species are absent from upland areas of modeled range due to chytrid (fungus pathogen causing local and global amphibian extinctions).	Paluma Range, Carbine Tableland	<i>Litoria lorica</i> , <i>L. nannotis</i> , <i>L. dayi</i>
7. Sparse locality data. Inaccurate models due to paucity of records in parts of range or species total range very small.	Lowland coastal areas, mountain top endemics	<i>O. spaldingii</i> ; records artificially biased to uplands <i>Cophixalus exiguus</i>

Note: Example regions are illustrated in Appendix S1: Fig. S1.

†Spatial filters were applied to improve the fine-resolution Accuclim models.

### *Post-workshop model refining*

Where possible, we used spatial filters to correct under- and over-prediction of the current and future species distribution models using ArcGIS v10.2 (ESRI, Redlands, CA, USA) based on the general principles outlining the model limitations (Table 1). The filters were designed according to expert knowledge of the landscape and species. Brief methods are outlined below for the spatial filters described as “rain shadow,” “micro refugia,” “geographical barriers,” “competitor species,” and “disease.” Details of these filters can be found in the Appendix S1.

*Micro refugia.*—We combined aspect and topographic position to create a fine-resolution (1 arc second,  $\sim 30 \times 30$  m) spatial layer of the areas most likely to harbor cool, moist microclimates that decouple from regional climate (termed “micro refugia” in Rull 2009). To incorporate aspect, we used the Aspect tool (ArcGIS; ESRI) with a 1 arc second digital elevation model from Geoscience Australia (2011). The aspect layer shows the facing direction of any slope in the study area. It was reclassified into three classes: coolest (southeast to south facing,  $90^\circ$ – $225^\circ$ ), warmest (north facing,  $315^\circ$ – $225^\circ$ ), and moderate (all remaining orientations). These orientations were chosen based on the primary direction of the sun at the central latitude of the study area. North-facing slopes receive direct sun for most of the year, decreasing their suitability for providing refuge from climate warming. Although south-facing slopes experience direct radiation for a small portion of the year, this occurs in the summer wet season when a large number of days are overcast. Therefore, for this study, it was deemed the north-facing slopes would have a substantially higher number of days with direct sun.

We used the topographic position index (TPI), created by Jenness (2006), to further categorize the landscape for micro refugia suitability. The TPI uses a neighborhood function to classify the target cell in relation to its surroundings. Using the topography toolbox created for ESRI, ArcGIS (Dilts 2015), we used a neighborhood size of  $100 \times 100$  cells ( $\sim 3,000$  m window) to gain optimal resolution of features in the landscape. This resulted in a range of values from 274 (high peak) to  $-229$  (low valley). The TPI values were classified into five classes of micro refugia suitability: suitable (TPI  $< -150$ ), somewhat suitable ( $-150$  to  $-20$ ), moderate ( $-20$  to  $20$ ), somewhat unsuitable ( $20$ – $150$ ), and unsuitable ( $>150$ ). The class boundaries were chosen based on the distribution of values.

The values of the aspect and TPI suitability layers were added together to create a combined micro refugia suitability. This combination created six classes, with the highest value being the most suitable (Appendix S1: Table S1). The experts identified parts of the species’ distributions that micro refugia were likely to exist, but were not reflected in the distribution models. In many cases, experts believed that the micro refugia would only persist above a certain elevation. In the expert-identified areas, the micro refugia filter was applied to the species distribution model, and the habitat suitability score was increased incrementally according to the TPI score (Appendix S1: Table S1). For example, where the TPI score was six (highly suitable), the habitat suitability score was increased by 0.6 (to a maximum of one). The species-specific

elevation thresholds identified by the experts are listed in Appendix S1: Tables S2 (birds), S3 (frogs).

*Rain shadow.*—The experts indicated that many of the models over-predicted the suitability of parts of the study area (Fig. 1) because they did not reflect the very steep gradients in moisture availability and vegetation cover associated with the rainforest–sclerophyll boundary. This sharp boundary occurs predominantly along the western edge of the upland rainforests and is determined by fire, based on a complex interplay between moisture, aspect, topography, substrate, and soil (Ash 1988). To address this, the boundary of the extent of rainforest along the western side of study area was defined using the Queensland Government’s Regional Ecosystems data (version 8.0 published November 2013; Accad and Neldner 2015) to identify non-rainforest vegetation types (all of which are subject to fire). Regional Ecosystem maps are presented at 1:50,000 scale, and the map units are accurate to  $\sim 1$  ha. We created a mask using the non-rainforest vegetation types to exclude the over-predicted species distributions in the west.

*Geographical barriers.*—The models often predicted suitability of habitat in places where the experts were confident that the species does not occur, and these locations were often remote from the species current distributions and beyond presumably insurmountable geographical barriers such as the ocean or inhospitable vegetation types (e.g., non-rainforest). The most common over-predictions of suitability were to islands where species did not occur. Given these species are not occupying this habitat now, presumably as a result of dispersal limitations, they are unlikely to in future even if habitat suitability increases. The areas beyond the geographical barriers where species were absent, particularly the islands, were therefore masked out of the study area for these species.

*Disease.*—Chytridiomycosis disease, caused by the “chytrid” fungus (*Batrachochytrium dendrobatidis*), has caused large losses to the populations of some frog species within the study area, so that they no longer occur in parts of their former ranges (Puschendorf et al. 2011). Chytrid is present throughout the Wet Tropics but only impacts populations of susceptible species in cooler mid and upland rainforest (Puschendorf et al. 2011, Scheele et al. 2017). Hotter temperatures are less optimal for chytrid: temperatures above  $26^\circ\text{C}$  significantly slow growth, with a lethal thermal maximum at  $28$ – $29^\circ\text{C}$  for Queensland-derived chytrid (Stevenson et al. 2013). For chytrid-impacted species, the experts identified the current upper elevation limits imposed by chytrid, which were not reflected in the distribution models. Using the mean temperature of every grid cell at the current upper elevation limit ( $\pm 1$  m) for each affected species, we calculated the mean elevation in which the upper elevation limit would likely be in 2085 under the severe climate change future. For each species, we masked out the modeled areas that were above the elevation limit for both current and the predicted future elevation limit. In some cases, the chytrid fungus has extirpated isolated populations, and in these cases, the population was removed from the model by reducing the probability in the affected areas to zero. There is evidence that some of the affected species are moving back into

areas they had disappeared from due to chytrid (McKnight et al. 2017, Scheele et al. 2017), and it is likely that in the future they will continue to recolonize up the elevation gradient. However, we could not build this into the models due to a lack of data on the rate or potential ultimate extent of this recolonization.

*Competitor species.*—For some species, the models over-predicted the distribution into areas occupied by ecologically very similar species. Such species pairs were generally known to be sister species from genetic analyses and deemed by the experts to have highly congruent ecological niches. For example, *Austrochaperina robusta* occupies the southern half of the Wet Tropics region and *Austrochaperina fryi* occupies the northern Wet Tropics. The two species abut in a narrow contact zone through the central Wet Tropics where there is limited hybridization (Hoskin 2004). These species appear to be ecologically equivalent and hence strong competitors. In cases like this, where the experts could make a strong case for competitive exclusion, the spatial extent of a competitor was masked out from the potential distribution.

#### *Sum of species*

We summed the models to estimate the number of our 17 vertebrate species predicted to occur in each cell across the study area. This was to help identify problematic areas that could consistently be over- or under-estimated in importance and to identify areas that are likely to be highly important. We created binary suitable/not suitable model outputs using the same species-specific Maxent thresholds as described above, but instead of a continuous suitability above the threshold, suitable areas were scored as “1.” For each of the three modeling approaches, 1 km, Accuclim and expert-refined Accuclim, and for current and future, we summed the binary distribution models to achieve a sum of species estimate.

## RESULTS

### *Workshop*

The distributions of eight bird and nine frog species were examined in detail by the experts during the workshop, chosen from the pool of 65 endemic birds and frogs modeled in the study area to represent the different ecological contexts experienced by endemics in the region (Appendix S1: Table S1). The interactive tabletop computing software and projector were highly useful tools for visualizing and interacting with the areas and the models in fine detail. The technology enabled detailed communication of the ecological concepts underpinning actual vs. modeled distribution of species, which was important due to the diversity of expertise on the panel. The visualization tools were also useful for examining focal areas of the landscape and their influence on species and the model outcomes. The experts derived seven general principles that describe how the distribution modeling under- or overestimated habitat suitability (Table 1). The inability of the models to accurately reflect fine-scale, moist, cool, rainforest conditions was the biggest issue across all species. For rainforest endemics, high

moisture availability and cool conditions are important drivers of habitat suitability, and nuanced fine-scale moisture and temperature are difficult to model. The “rain shadow” general principle was established to account for the sharp transition between rainforest and drier forest to the west of the range, which was consistently poorly modeled (Table 1). There were two general principles required where models inaccurately represented response to temperature: “micro refugia” and “upper thermal tolerance unknown.” Micro refugia were missed by even the fine-resolution Accuclim models, resulting in likely over-projections of widespread range retraction in the future. Where the upper thermal tolerance was not adequately represented by the species’ current distribution model because hotter temperatures in the region do not currently exist, or the species distribution is bound by an ocean, future projections were likely to overstate range loss from climate warming. Additionally, the models did not always accurately reflect non-climatic limits

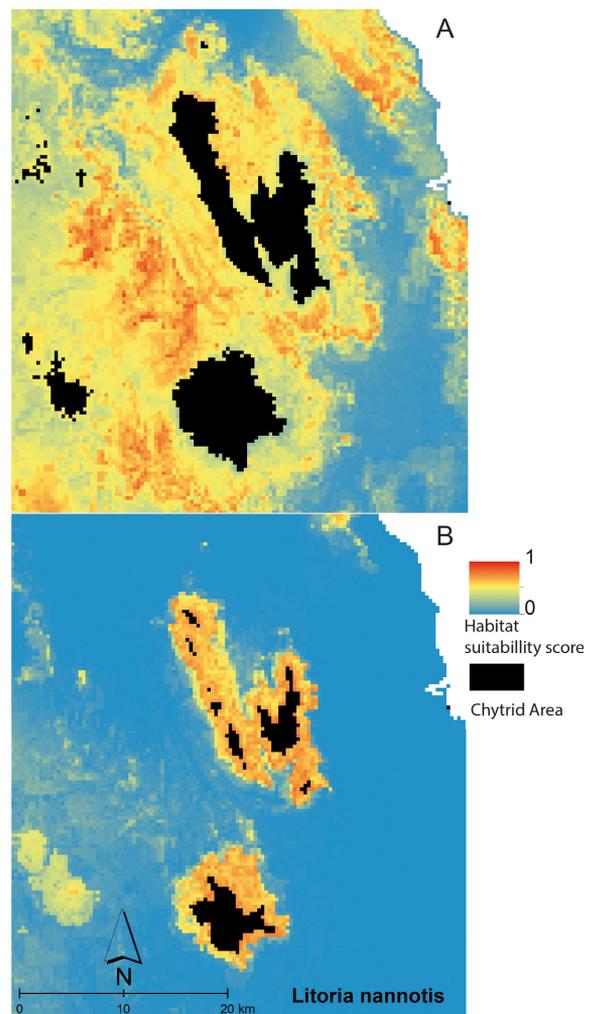


FIG. 2. Demonstration of the disease principle for over-prediction illustrated for *Litoria nannotis*. Areas in black have become unsuitable because of chytrid infection (A). These areas are predicted to retract by 2085 as the warmer conditions give the frog species competitive advantage (B). At the same time, other parts of the species’ range are predicted to become unsuitable due to the more direct effects of climate change.

to species distributions. Four general principles reflected limiting factors other than climate: “competitor species” (Fig. 1), “disease” (Fig. 2), “geographical barriers,” and “sparse locality data.” Of the seven general principles, spatial filters could be applied to account for five (Table 1).

#### *General principles related to climate*

Of the seven general principles behind under- and over-prediction, “rain shadow” was the most commonly applied (12 out of 17 species), reflecting how poorly the sharp transition to non-rainforest habitat was reflected in the models (Fig. 1). The Accuclim climate data, which refined the distribution models considerably from standard interpolated climate data (used for 1-km models), improved only the temperature predictions (Storlie et al. 2013), but used standard interpolated rainfall data. The current rainfall data did not accurately reflect the rain shadow areas and the drier western edges of the mountain ranges, or the magnitude of the orographic rainfall effect on the eastern side of some mountains (Appendix S1: Fig. S4). In some cases, species such as *Cophixalus bombiens* were under-predicted on the wetter, eastern edge of the mountains. The rain shadow principle was applied to the future distributions of five frogs (Fig. 3A) and all but one bird species (Fig. 3B). It also led to the largest proportional decreases in the amount of suitable area modeled for each species it was applied to, except for *Litoria nannotis*, which lost more area when the disease filter was applied.

Micro refugia were the second most commonly applied principle (11 species; Fig. 3) and relate to inaccurate estimates of water availability and temperature at micro (<250 × 250 m grid) scales. The experts identified regions that were likely to contain localized microclimates suitable for micro refugia, even where the future projections of species distributions predicted population losses. Micro refugia that occur within small creek lines, gullies, and rock piles could be missed at 250-m grid size, but were identifiable at the 30-m grid scale (the resolution of the digital elevation model used to create micro refugia filter). These types of micro refugia are likely to be suitable for all frogs in the family Microhylidae in our study: the species in the *Austrochaperina* and *Cophixalus* genera. The micro refugia areas were also likely to be suitable for some bird species: experts also reported seeing Bridled Honeyeater (*Lichenostomus frenatus*), Blue-faced Parrot-finch (*Erythrura trichroa*), Pied Monarch (*Arses kaupi*) and Victoria’s Riflebird (*Ptiloris victoriae*) along gullies and creek lines that traverse otherwise unsuitable habitat (e.g., drier forest, agricultural areas). The application of the micro refugia filter (Fig. 1) increased habitat suitability of some areas and led to small but potentially important increases in the overall suitable area available to the relevant species (Fig. 3A, B).

The principle “upper thermal tolerance unknown” was required because the upper temperature limit of some future distribution models was the same as the hottest temperature of the region where the species had been recorded. As a result, some models over-stated the importance of cooler upland habitats for some species, and experts believed that future distributions were overly constrained by high temperatures, as evidenced by severe contractions in future

projections of suitable climate. In some cases, the upper thermal tolerance of species was unknown because parts of the species’ likely former ranges (usually the lowland parts, which are hotter) have been lost to historic land conversion. In other cases, the upper temperature tolerance of species was unknown where species distributions were limited by the coastline, rather than unsuitable terrestrial conditions. There were other cases where locality data were missing from smaller patches of lowland forest where the species could potentially occur, which applied to the Chowchilla (*Orthonyx spaldingii*). Experts had seen Chowchillas in small lowland fragments, but these observations were not captured in the available locality data, and severe future climate change projections of this species’ range are believed to be an inaccurate reflection of its temperature tolerance. We were unable to create a spatial filter for this principle because more extensive field data collection would be required.

#### *General principles related to non-climatic factors*

Geographical barriers, which in this region include unsuitable vegetation, are likely to be a contributing factor determining species absence from areas modeled to be suitable. Where this was the case for our study species, we applied a “geographical barriers” filter that excluded parts of the species range where they were absent, presumably due to dispersal barriers. Dry, non-rainforest vegetation (mostly wet and dry sclerophyll forests) is a dispersal barrier to the smaller and often remote rainforest patches. In some cases, the Accuclim models improved on the 1-km models, with areas modeled as unsuitable where species were absent, but for others, areas modeled as suitable by Accuclim had to be removed with a geographical barriers filter.

There were five species for which suitable climate space was predicted for islands to the east of the region’s coastline, although the species had not been recorded on one or more of these islands. Over-prediction to islands is considered here a subset of the “geographical barriers” principle, where species could theoretically survive on the island but have been prevented from dispersing to or recolonizing the island after a local extinction. However, there could be other reasons for species’ absence on islands, which may function differently compared to climatically similar sites on the mainland due to local-scale processes and assemblages. It is unlikely that species with low dispersal capacity, such as most of the frogs, would be able to disperse to the islands in the future despite any modeled increase in habitat suitability. Altogether, the “geographical barriers” filter was applied to seven species, which removed only a small proportion of any species’ suitable modeled area (Fig. 3A, B).

Competitor species were the limiting factor for the distributions of three frog species in our study. For example, *A. fryi* was limited by the presence of *A. robusta*. In these cases, we used a “competitor species” filter to mask out the areas modeled as suitable where the target species did not occur because of its competitor.

The general principle “disease,” where species do not occur because disease resulted in local extinctions, was relevant to three of the frog species (*Litoria lorica*, *L. nannotis*, and *L. dayi*; Fig. 3A). These, and other frog species not included in this study, have become locally extinct in the

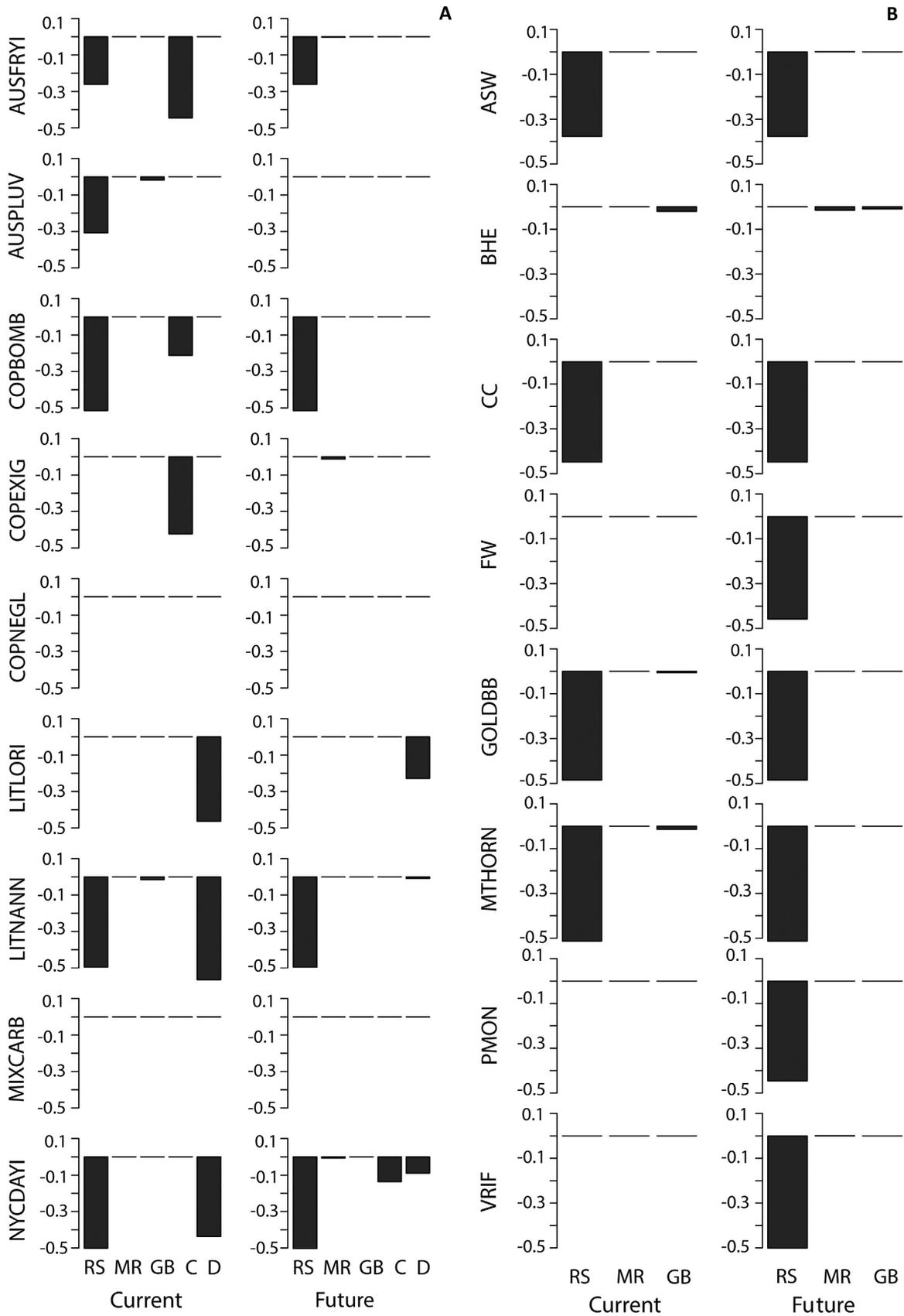


FIG. 3. The proportion of the species distribution that is gained or lost after applying the general principles to the Accuclim models, to produce the expert-refined Accuclim models, for (A) frogs and (B) birds. The principles are as follows: RS, rain shadow; MR, refugia; GB, geographical barriers; C, competition (frogs only); D, disease (frogs only). Species code names are defined in the Appendix S1: Table S1.

upper and cooler parts of their ranges due to infection by chytrid fungus. The presence of chytrid changes the optimal climate for the species, so that they are restricted to lower elevations. For these species, the upper elevations had to be removed from their ranges (Fig. 2).

The final general principle was “sparse locality data.” While this general principle contributes to others, such as “upper thermal tolerance unknown” and “disease” (through having outdated data), it is significant in its own right in constraining model accuracy for all species. We did not include a filter for this general principle, as it requires instead a specialized modeling approach, and ideally more field data.

Comparing the three modeling approaches, 1 km, Accuclim, and expert-refined Accuclim, revealed interesting distinctions for both current and future projections of species distributions (Fig. 4). This is shown in detail for the Golden Bowerbird (*Amblyornis newtonianus*), which had the rain shadow, micro refugia, and geographical barriers filters applied (Appendix S1: Table S1) to the Accuclim model to obtain the expert-refined Accuclim model (Fig. 4). The 1-km model for Golden Bowerbird over-predicted current suitability throughout the study region, particularly the lowlands, which then appears to result in proportionally greater area lost by 2085. The 1-km models did not accurately reflect the current level of natural and anthropogenic rainforest fragmentation, which could be the main driver of the over-prediction. The Accuclim and expert-refined Accuclim predicted smaller current distributions and proportionally smaller areas lost in the future. Therefore, the expert-refined Accuclim models predict a higher proportion of golden bowerbird’s range to remain suitable into the future.

The maps showing the sum of the 17 species in this study followed a similar pattern to that for the Golden Bowerbird, with substantial spatial differences in the modeling approaches (Fig. 5). The expert-refined Accuclim sum of species reveals a far more fragmented pattern of high richness than indicated by the 1 km or the Accuclim models. This fragmentation more accurately reflects the lack of corridors available for species to track their climate niche into the future. The expert-refined Accuclim sum of species highlights the importance of the Carbine and Windsor Uplands for the 17 species chosen for this study, particularly into the future (specific locations shown in Appendix S1: Figs. S1, S2). The expert-refined Accuclim sum of species shows that the Finnigan and Thornton Uplands are likely to have fewer of these species. This is also the case for Hinchinbrook Island and Mount Spec Uplands.

#### *Expert recommendations for conservation actions*

The experts discussed the conservation actions that they believed to be important for species persistence in the face of climate change. The consensus that emerged is summarized in the four points below.

- 1) Species governed by the rain shadow rule require fire management. The species occurring at the edge of the wet rainforest areas are vulnerable to degradation or loss of habitat due to fire, because of the drier, more flammable vegetation (such as monsoon forest, sclerophyll

forest, and savanna woodland) bordering their distributions. Climate change could likely exacerbate this (Stevens-Rumann et al. 2018).

- 2) Isolated peripheral populations of species are likely to be important and should not be ignored by management. While most conservation action focuses on larger, intact vegetation patches, isolated areas could retain populations of individuals that are pre-adapted to the climatic conditions likely to be more widespread in the future. In some cases, not connecting naturally isolated pockets of rainforest with other rainforested areas, maintaining their isolation, could help maintain evolutionary trajectories (Phillips et al. 2016). Individuals adapted to marginal conditions could be candidates for targeted gene flow translocations (Kelly and Phillips 2016).
- 3) Connectivity between core populations is important and should be enhanced and maintained where possible. However, connectivity should be investigated in a species-by-species context and not prioritized over protecting larger areas without full scrutiny of the trade-offs (Hodgson et al. 2011, Mair et al. 2014), particularly where naturally isolated pockets of rainforest could be important for local adaptation that house candidates for targeted gene flow translocations (Kelly and Phillips 2016).
- 4) Monitoring and evaluation are important for understanding many important aspects of conservation. Important information to collect includes (a) population trajectories (which could change rapidly); (b) whether, and where, the population is responding to changes in climate; (c) if species are responding to changes in climate, whether they are they responding at the predicted rate; and (d) the success of conservation actions.

## DISCUSSION

Accurate and comprehensive data, and robust predictions, are required for maximizing benefits from conservation action. This is especially challenging for climate change impact studies, where the uncertainty is high (Reside et al. 2018). This study demonstrated that spatially coarse or unrefined species distribution models can inflate the current suitability for species and subsequently inflate the predicted losses for species in response to severe climate change. Model over-predictions can lead to conservation resources being invested into areas that are suboptimal or even where species are absent, at the expense of areas that are crucial for species persistence. In this study, the Carbine and Windsor Uplands in the northwest of the study region (Appendix S1: Fig. S1) are likely to be crucial for the persistence of many of the 17 species in the face of climate change, whereas the Finnigan and Thornton Uplands are important for fewer species, a distinction not made with the standard Accuclim models.

This study highlights that even fine-scale models using ground-truthed and refined temperature data can harbor inaccuracies in habitat suitability for species. The most important inaccuracies result from the models’ inability to reflect fine-scale variability in moisture and temperature, and hence the presence of suitable micro refuges for rainforest-dependent taxa. While temperature data were able to be refined, this was not the case for rainfall data.

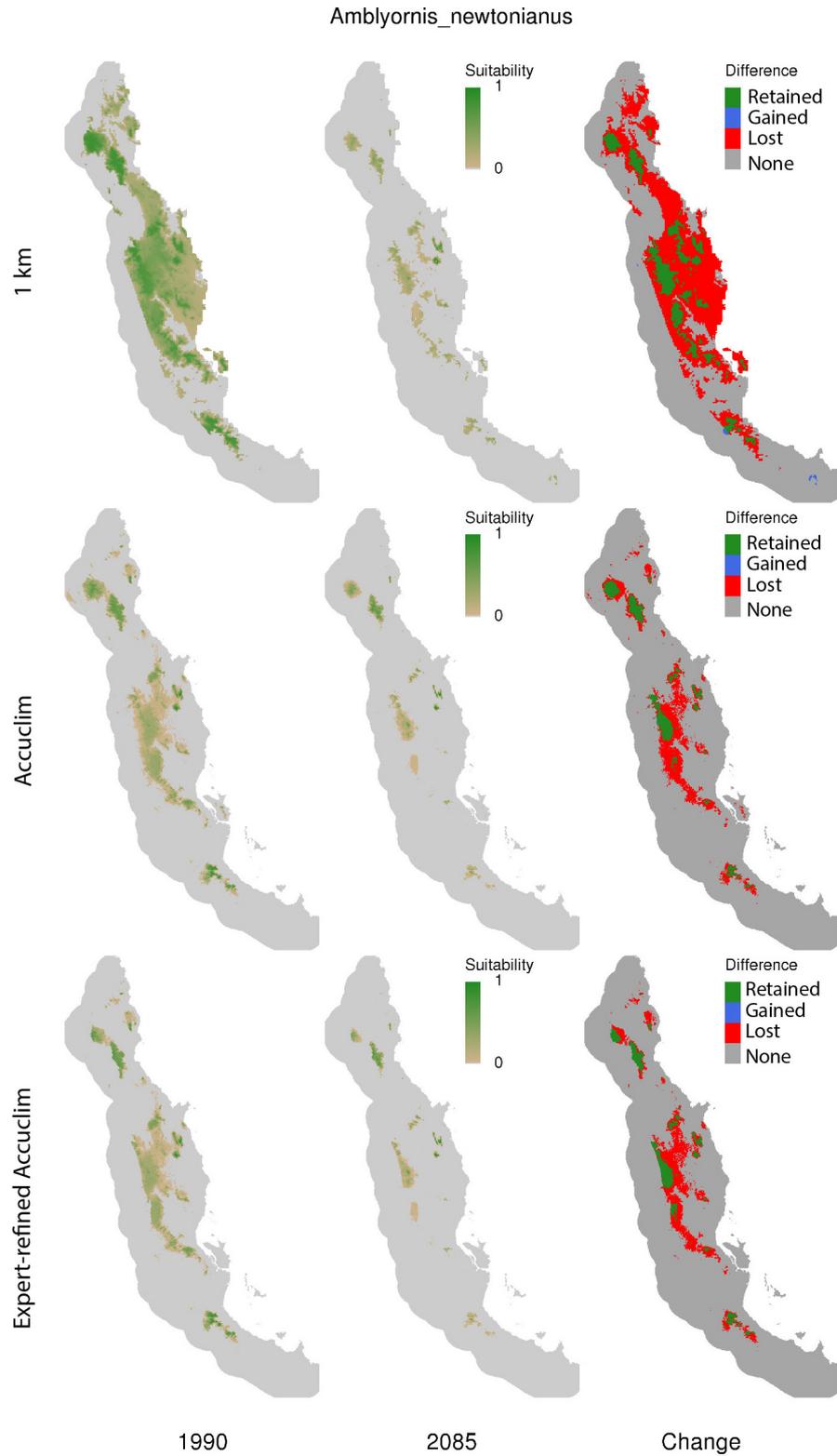


FIG. 4. Suitable climate for the Golden Bowerbird (*Amblyornis newtonianus*; species code: GOLDBB) predicted by the 1 km (top row), the Accuclim (middle row), and the expert-refined Accuclim (bottom row) models. The first and second columns show a continuous habitat suitability score; the third column shows the areas that are lost (red), gained (blue), and retained (green) from current to future for each of the modeling approaches, based on binary suitable/not suitable models.

Furthermore, moisture availability is further underestimated by missing orographic precipitation, reduced evaporation from cloud cover and rain shadow areas. These factors are

substantially more difficult to model and interpolate at the landscape scale. In the study area, this leads to an underestimation of moisture availability on the eastern side and

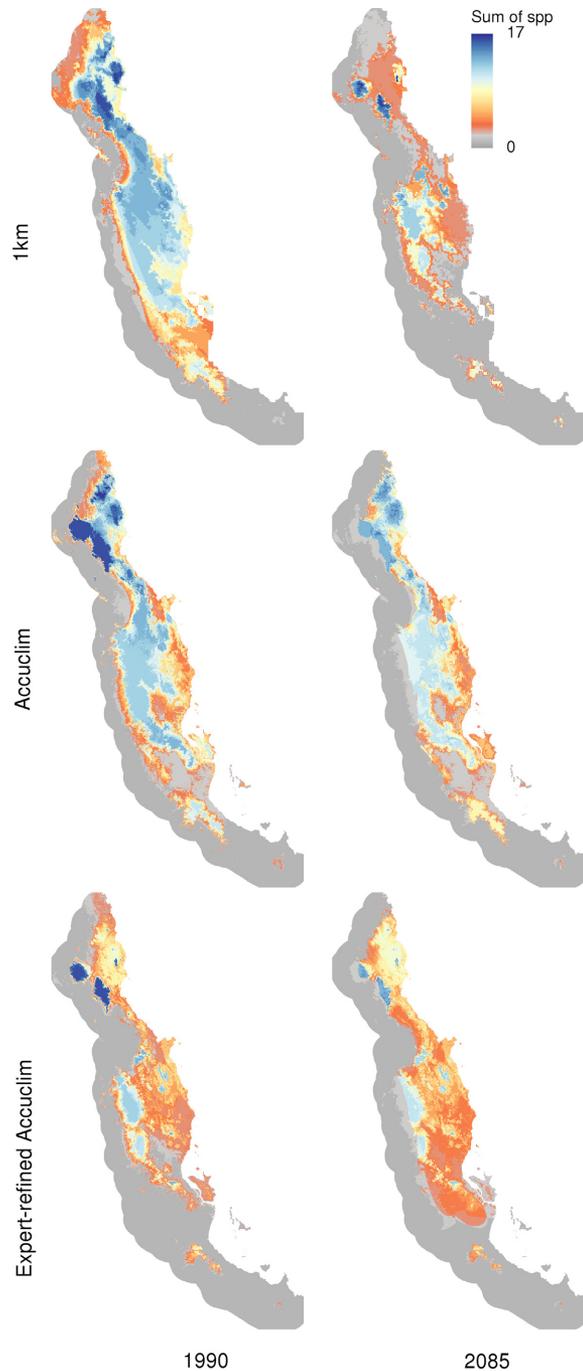


FIG. 5. Sum of the 17 species models, as predicted by the 1 km (top row), the Accuclim (middle row), and the expert-refined Accuclim (bottom row) models.

overestimation on the western side of mountain ranges. Other data, such as vegetation greenness indices (Mackey et al. 2012), can more accurately indicate moisture availability, but these data are generally unavailable for future predictions of evapotranspiration and rainfall.

Other aspects of prediction that are missed by even the fine-scale Accuclim models include species interactions, which have long been noted as important for accurately representing species distributions (Araújo and Luoto 2007, Bateman et al. 2012). In this study region, the important

interactions that are not captured by the unrefined Accuclim models include competitor species. This is relevant for the current models and likely to be highly influential into the future. For example, species such as *C. bombiens* and *Cophixalus ornatus* are probably currently limited by competitor *Cophixalus* frog species that occupy “core” upland areas. If their competitors are disadvantaged by climate change, these species may be able to expand their ranges into the vacated niche space. There have been some advances for incorporating species interactions, such as dominance among species, into correlative distribution modeling through joint species distribution models (Crase et al. 2015). Such interactions have been incorporated into frog distribution models (Pollock et al. 2014). However, the appropriateness of each technique is likely to differ depending on the specific and environmental contexts (Anderson 2017). Furthermore, understanding the full complexity of all biotic interactions, how these are driven by environmental conditions, and how they are likely to be altered is still beyond current scientific capacity, although there have been gains in this field (Walach et al. 2017). Our use of expert vetting attempted to partially fill some of the knowledge gaps for our region, by masking out suitable habitat occupied by a clear competitor or excluded by known disease impacts.

Climate change will exacerbate many of the factors that cause species declines. Planning for climate change adaptation will be optimized by drawing upon the field of systematic conservation planning (Schmitz et al. 2015, Reside et al. 2018). This involves setting specific objectives such as planning for species persistence, identifying the costs, benefits, and trade-offs for each relevant conservation action, and incorporating the uncertainty involved in each step (Reside et al. 2018). Innovative actions such as temporary reserves (Pressey et al. 2007) and targeted gene flow (Kelly and Phillips 2016) could be considered, while acknowledging their limitations (Moilanen et al. 2014). An adaptive management approach is required, as success will depend on review of the effectiveness of actions and adapting these as new information is available (McDonald-Madden et al. 2010b). This in turn will require ongoing monitoring to understand how species will respond to the changing conditions. Population monitoring is routinely underfunded and thus neglected, yet is a critical tool for determining population and distribution trajectories. Species models fitted for baseline climate make use of the pool of species data that have been collected often over many decades. To accurately detect impacts of climate change on species in relatively shorter time periods (i.e., within one decade), survey effort would need to be increased for many species. However, monitoring programs, like all conservation interventions, should be subject to rigorous cost-benefit analyses (McDonald-Madden et al. 2010a).

In most cases, the important habitat for most of our species is within the current protected area network, both currently and under future projections (Fig. 4). Key areas in the north-west are Windsor Tableland (Mount Windsor National Park) and Carbine Tableland (Mount Lewis, Mount Spurgeon, and Daintree National Parks, Appendix S1: Figs. S1, S2). For species in this region, maintaining habitat integrity within the national parks is important, including managing invasive species and fire (particularly at the western edge). Areas in the Atherton Uplands in the central part of the region are

currently lacking protection and have been identified as priorities for habitat restoration and land management compatible with conservation (Shoo et al. 2011). These areas have high potential for carbon sequestration and storage in addition to high conservation value, so should be considered for native carbon plantings (Reside et al. 2017b). Despite the protection of rainforest within vegetation legislation, “endangered” and “of concern” Regional Ecosystems within the Wet Tropics bioregion are being cleared faster on private land than “least concern” ecosystems (Rhodes et al. 2017). Therefore, regions identified herein as having high importance for the endemics should be evaluated for threat of habitat loss and considered for inclusion in any expansion of the protected area network.

### *Caveats*

We chose an informal elicitation process for this study, using exploratory discussion across the group, for several reasons. In particular, our experts had broad expertise: several knew the landscape and its management very well, but did not have strong knowledge of the species. Therefore, discussion among experts was helpful to elucidate the interactions between the nuance of the landscape and the likely species’ responses. While structured elicitation processes have been shown to be extremely useful (Martin et al. 2012, Firn et al. 2015), these require having a sufficient number of experts on these very restricted species that occur in a remote and unpopulated part of Australia. We recommend further studies endeavor to use the structured elicitation process wherever possible, and use the standard methods to quantify the uncertainty across experts.

Our study attempts to address the issue of achieving greater ecological realism of species models, beyond standard statistical validation techniques. For our study, the application of some of the general principles we identified could possibly lend themselves to statistical validation, such as “rain shadow,” “geographical barriers,” and “competitor species.” However, the application of several of our general principles does not lend themselves to standard validation techniques with the data that are currently available. For example, the likely areas of suitable “micro refugia” are relevant at a much finer scale than the models were run, and need field testing to understand whether these areas are useful to species, particularly in extreme weather conditions. Validation of the models where the “disease” filter was applied would require thorough resampling of the species presence and absence after the disease has caused local extinctions. The problem of “sparse locality data” plagues both the initial model runs and the ability to statistically validate the models. In all cases, validating the projections of the species models under climate change scenarios cannot be done, as the future is yet unknown. For this reason, the general principle “upper thermal tolerance unknown” is difficult to validate because the problem is only apparent for future projections, and understanding this parameter would require some physiological and, in some cases, behavioral data.

### CONCLUSIONS

Our study found that the absence of both fine-scale temperature and water availability data, and the addition of detailed

expert knowledge, resulted in divergent prioritizations of the important areas for species persistence under climate change. In many cases, fine-scale predictor data or accurate species data may not be available. These situations are likely to benefit even further from adopting a similar approach to that we have presented here, by taking species- and region-experts to examine the likely reality of model predictions and their flaws. The general principles outlined here should be a first step, particularly for other coastal, mountainous regions.

Although unable to accurately account for every nuance of species distributions, expert knowledge enabled critical evaluation of the model outputs and identified the conditions under which these deviated from reality. Modeling techniques need to be developed to specifically address some of the deficiencies identified in this study. Necessary improvements include (1) more accurate data on moisture availability across the landscape; (2) micro-habitat buffering associated with substrate, topography, and aspect; (3) disentangling thermal tolerances from artefacts of land use change or geography to explain species restriction to uplands; and (4) for frogs, better understanding of species range dynamics in the presence of chytrid fungus. Combined approaches of modeling and expert knowledge will be important for robust models and future predictions of species for most modeling studies.

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## SUPPORTING INFORMATION

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