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Climate change in Australian tropical rainforests: an impending environmental catastrophe

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It is now widely accepted that global climate change is affecting many ecosystems around the globe and that its impact is increasing rapidly. Many studies predict that impacts will consist largely of shifts in latitudinal and altitudinal distributions. However, we demonstrate that the impacts of global climate change in the tropical rainforests of northeastern Australia have the potential to result in many extinctions. We develop bioclimatic models of spatial distribution for the regionally endemic rainforest vertebrates and use these models to predict the effects of climate warming on species distributions. Increasing temperature is predicted to result in significant reduction or complete loss of the core environment of all regionally endemic vertebrates. Extinction rates caused by the complete loss of core environments are likely to be severe, nonlinear, with losses increasing rapidly beyond an increase of 2 °C, and compounded by other climate-related impacts. Mountain ecosystems around the world, such as the Australian Wet Tropics bioregion, are very diverse, often with high levels of restricted endemism, and are therefore important areas of biodiversity. The results presented here suggest that these systems are severely threatened by climate change.

Keywords: biodiversity; climate change; extinction; range size; montane; rainforest

1. INTRODUCTION

Globally, average temperatures have already risen *ca.* 0.6 °C and they are continuing to increase (Houghton *et al.* 2001). Over the remainder of this century we will experience an increase in average temperatures of between 1.4 °C and 5.8 °C combined with large increases in atmospheric CO_2 concentrations and significant changes in rainfall patterns (Houghton *et al.* 2001). Although the effects on rainfall patterns are more uncertain, it is predicted that rainfall variability and dry-season severity will increase (Walsh & Ryan 2000). That is, rainfall will be more variable from month to month, with longer dry spells and possibly with an increased frequency of disturbance events such as flooding rains and cyclones (Easterling *et al.* 2000; Walsh & Ryan 2000; Milly *et al.* 2002; Palmer & Raianen 2002). Additionally, a rise in the average basal altitude of the orographic cloud layer is expected (Pounds *et al.* 1999; Still *et al.* 1999). A reduction in cloud-moisture capture from this cloud layer will exacerbate the effects of longer and more variable dry seasons (Still *et al.* 1999). Climate change has already produced significant and measurable impacts on almost all ecosystems, taxa and ecological processes, including changes in species distributions, phenology of biological behaviours, assemblage compositions, ecological interactions and community dynamics (Hughes 2000; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003).

Rainforests in the Wet Tropics bioregion were listed as a World Heritage Area in 1988 primarily because of the high biodiversity values of a unique regional biota. Although the area of rainforest within the region is small on a global scale (*ca.* 10 000 km²), there are 65 species

of rainforest vertebrate that are regionally endemic. On a regional scale, patterns of biodiversity have been largely shaped by Pleistocene contractions in rainforest area and subsequent expansion episodes (Winter 1988; Williams & Pearson 1997). The contraction of rainforests to cool moist upland refugia probably imposed an extinction filter resulting in most of the remaining regionally endemic species being cool-adapted upland species (Williams & Pearson 1997; Schneider *et al.* 1998). These factors have predisposed the fauna to being particularly vulnerable to global climate change for two reasons: (i) the biogeographic history has resulted in an endemic fauna that is adapted to a cool, wet and relatively aseasonal environment; and (ii) the impacts of increasing temperatures should be most noticeable across altitudinal gradients and, in this region, the altitudinal gradient and associated complex topography dominate the biogeography of the region (Nix & Switzer 1991; Williams *et al.* 1996). In fact, the altitudinal gradient is the most significant gradient determining species composition and patterns of biodiversity in the region (Williams *et al.* 1996; Williams 1997; Williams & Pearson 1997; Williams & Hero 2001). The total spatial extent of upland forest types in the Wet Tropics bioregion is also predicted to shrink significantly under expected climate-change scenarios (Hilbert *et al.* 2001).

2. MATERIAL AND METHODS

Distributional data on all terrestrial vertebrates were collected during intensive field surveys across the region and by collating all available sources from the literature and institutional databases. Realistic distribution models require good coverage of the range of environments present within the distribution of each species. Therefore, the regional coverage of both geographical and environmental space was analysed and additional standardized surveys were carried out to fill gaps in both geographi-

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cal and environmental space as much as possible. Total survey effort across the bioregion consisted of 652 bird surveys, 546 reptile surveys, 249 spotlighting transects, *ca.* 50 000 trap nights for small mammals, 111 stream frog surveys, 231 microhylid frog surveys and a further 6373 miscellaneous records collected during the fieldwork. Other major sources of data included the *Birds Australia* database and the Queensland Parks and Wildlife Service 'WildNet' fauna database. This produced a database containing 92 967 spatially referenced records of 622 terrestrial vertebrate species. Each record was checked for both positional and taxonomic reliability and only records of high reliability were retained in the analyses. The analyses presented here used a subset of these data consisting of 7123 non-duplicate records of the 65 species of regionally endemic rainforest vertebrates.

The modelling program we used was BIOCLIM, a part of the ANUCLIM 5.1 package (Houlder *et al.* 2000). The digital elevation model used for the region had a pixel resolution of 80 m × 80 m. BIOCLIM generates up to 35 climatic parameters based on maximum temperature, minimum temperature, rainfall, radiation and evaporation; however, the unrestricted use of so many variables in a climatic envelope method results in over parameterization and loss of predictive power of the models. Therefore, we restricted the environmental variables to 10 parameters that had previously demonstrated significance in explaining biological patterns of diversity within the region. The parameters chosen were the mean annual temperature, intra-annual variability of monthly mean temperature, maximum temperature of the warmest quarter, minimum temperature of the coldest quarter, mean annual precipitation, intra-annual variability of monthly mean precipitation, precipitation of the wettest quarter, precipitation of the driest quarter, mean annual radiation and intra-annual variability of monthly mean radiation. Core environmental distribution was defined as the areas where the climatic parameters fall between the 5th and 95th percentiles of the values of the parameters in the species profile.

Bioclimatic envelope methods such as BIOCLIM will generally overestimate distribution area. Current distribution models were evaluated by experts and by comparison with known patterns of subregional occurrence (Williams *et al.* 1996). Out of the 65 species modelled, the distribution areas of 17 species were significantly overestimated. These were corrected by removal of over-predicted areas where we were highly confident that the species does not occur, thereby providing accurate models for 51 species (78%). There were 11 species for which the models possibly underestimate distribution area owing to a low number of records; however, expert evaluation of these models suggested that they were reasonable given current knowledge.

We chose a range of temperature-increase scenarios to encompass the predicted range (1.4–5.8 °C; Houghton *et al.* 2001), including temperature increases of 1, 3.5, 5 and 7 °C. These increases were applied to each of the three temperature variables uniformly across the region. We used the bioclimatic models based on current species distribution to predict distributional changes with increasing temperature and subsequent changes to regional patterns of biodiversity. The area of core environment remaining under the different temperature scenarios formed the basis of the analyses. Species-richness maps were produced by overlaying species-distribution models within each climate-change scenario.

3. RESULTS

The changes in the pattern of geographical species richness are complex and dramatic on inspection (figure 1).

They are significant even with a 1 °C increase in global temperature, a change that is considered inevitable within the next few decades. The major areas of high diversity in the uplands remain relatively unscathed and in some areas diversity may increase slightly; however, significant declines in local species richness occur across the lowlands and in mid-altitudinal areas (figure 1). The loss of biodiversity with a 3.5 °C increase is obvious. There are no areas with high species richness remaining (greater than 30 species) and all endemics have disappeared from the low- and mid-elevation regions. There are only four refugial areas remaining that support a reasonable level of species richness. Beyond this temperature the losses are essentially complete: small areas of refugia for a few species survive at +5 °C but the entire ranges of all 65 species are gone at +7 °C.

We predict that even a 1 °C increase will cause significant declines in range size in almost every species of regionally endemic vertebrate in the Wet Tropics bioregion. Out of the 65 species modelled, the area of core environment significantly declines in 63 species (figure 2; paired t-test: d.f. = 63 with one missing value at 1 °C, $t = 10.735$, $p < 0.001$) to an across-species mean of 63% of current area (figure 3). One species may go extinct with a complete loss of core environment (*Cophixalus* sp. nov., found only at Thornton Peak). With an increase of 3.5 °C, all 65 species are predicted to undergo dramatic declines in distribution, with 30 of these species completely losing their core environment (figure 2). The mean remaining area of core environment for the surviving 35 species is only 11.4% of their current distribution (figure 3). A more severe increase of 5 °C will completely remove the core environments of 57 species and the remaining eight species will be left with an average of only 3% of their current core area. None of the 65 regionally endemic species is predicted to have any core environment remaining at the more extreme possibility of a 7 °C increase in temperature. If we assume that the complete loss of its core environment will result in the extinction of a species, we can predict the number of likely extinctions as a function of the increase in temperature (figure 4). The relationship between increase in temperature and predicted extinctions was best fitted by an S-curve ($r^2 = 0.997$, $p = 0.001$). The arrow on figure 4, indicating the range of predicted increases in temperature, highlights the difference in impacts between the minimum and maximum predictions, *ca.* 6% and 96% extinction of endemics, respectively.

4. DISCUSSION

Globally, mountain systems are hotspots of biodiversity and endemism owing to the compression of climatic zones over the elevational gradient (Körner 2002). It is precisely this dependence on orographic gradients that makes these systems vulnerable to climate change. Many studies have predicted that climate-change impacts will largely consist of shifts in latitudinal and altitudinal species distributions with concomitant complex changes in assemblage structure (Parmesan 1996; Hill *et al.* 2002; Peterson *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003). In the Australian Wet Tropics, and in most montane systems, the dispersal distances involved in moving up with a moving climate are relatively small; however, we are facing the
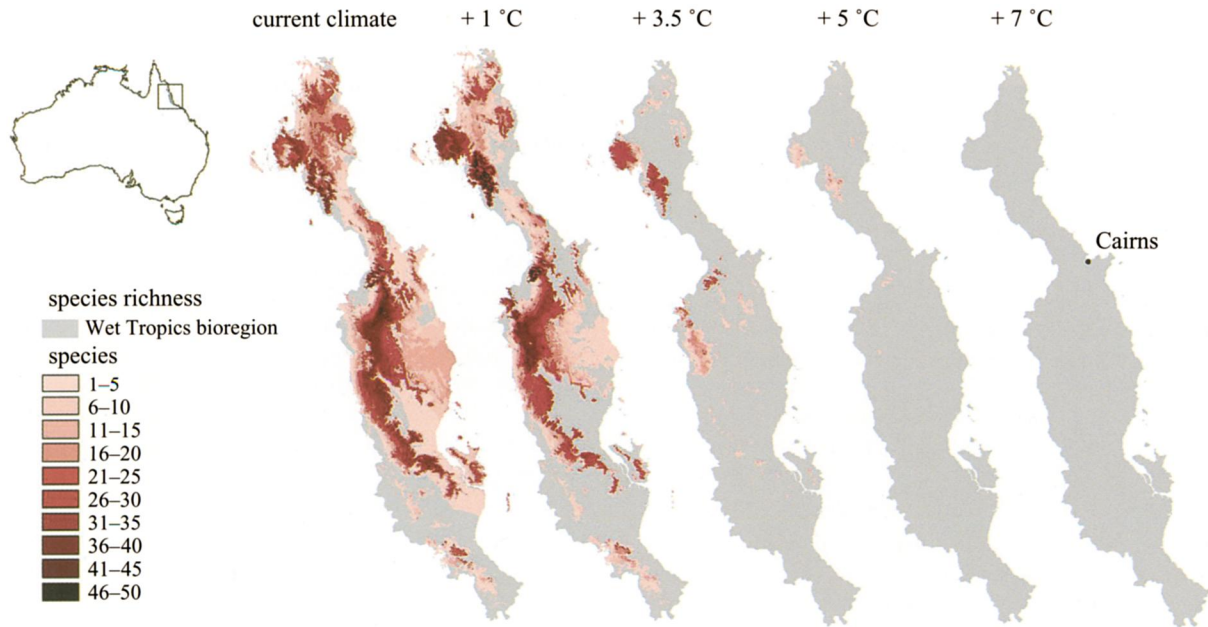
Figure 1. Geographical pattern of species richness of regionally endemic rainforest vertebrates at each temperature scenario. Species richness is produced by overlaying all species-distribution models at each temperature scenario.
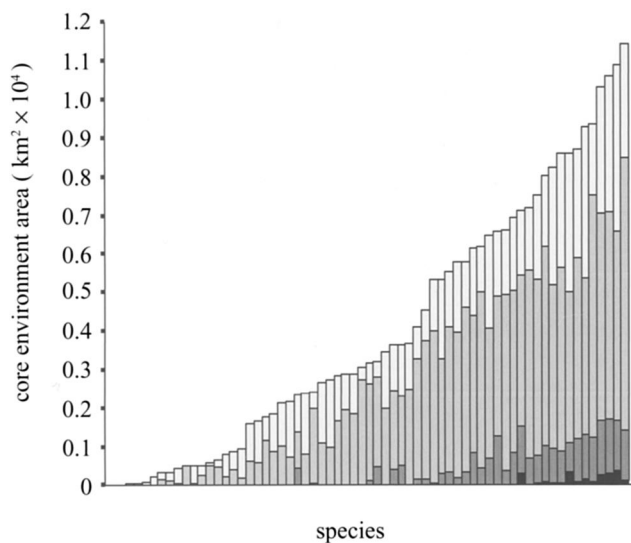

Figure 2. Core-environment area for each of the 65 regionally endemic species of rainforest vertebrate modelled for each temperature scenario and ranked in increasing order of area of current distribution. The predicted distribution area for each species under each temperature scenario is overlaid to show the reduction in core area for each species at each temperature-increase scenario. Light grey represents the loss caused by a 1 °C increase, mid-grey the additional loss caused by a 3.5 °C increase, dark grey a 5 °C increase and black a 7 °C increase.

complete disappearance of specific environmental types combined with a low possibility of natural dispersal to other suitable habitats. An analogous study of the impacts of climate change on Mexican fauna predicted relatively few extinctions or drastic range reductions (Peterson *et al.* 2002). By contrast, our results suggest that we may be facing an unprecedented loss of biodiversity in any montane biota, an environmental catastrophe of global significance.
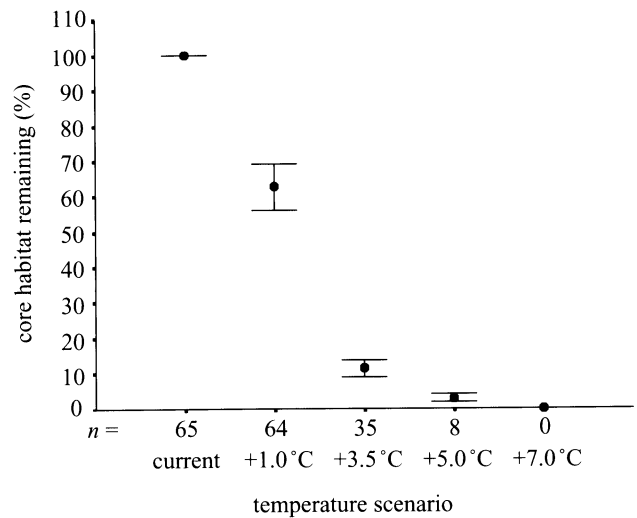

Figure 3. Across-species mean of the decline in area of core environment for each species of regionally endemic rainforest vertebrate expressed as a percentage of current core-environment area (± 95% confidence interval) for each temperature scenario examined.

We have shown that, despite formal and enforced protection of the rainforests of the Australian Wet Tropics World Heritage Area, most of the endemic vertebrates are severely threatened by predicted climate changes over the remainder of this century. The results presented here suggest that, even with an extremely conservative increase of only 1 °C, one species will completely lose its core environment and almost all other species will face significant decreases in distribution. The predicted decreases in range size with climatic change rely on the assumption that distribution and environment are inextricably linked, an assumption that is generally accepted in ecology (Lawton 1995). There will surely be significant variation between species with respect to the validity of this assump-
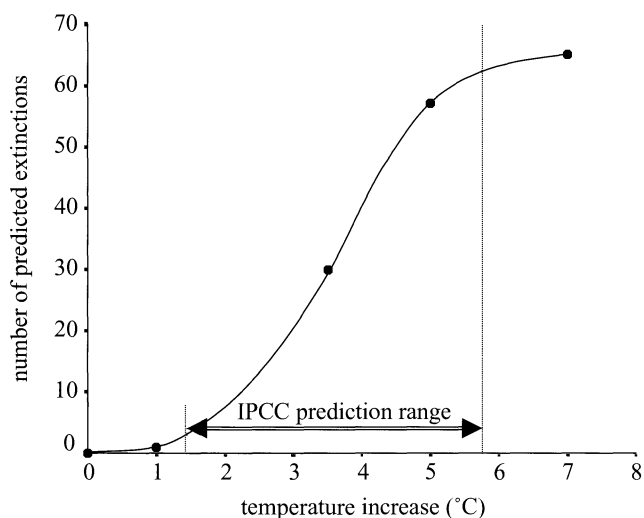
Figure 4. Relationship between increasing temperature and the number of predicted extinctions of regionally endemic rainforest vertebrates resulting from the predicted complete loss of their core environments. Arrow shows the range of the possible increase in temperature during this century, as predicted by the Intergovernmental Panel on Climate Change (IPCC) (Houghton *et al.* 2001). S-curve fit: adj. $r^2 = 0.997$, $p = 0.001$.

tion. However, we expect that there will be both species that suffer less than predicted owing to greater than expected environmental tolerances and species that decline faster than expected owing to the disruption of other ecological interactions. Additionally, predictions based on a climatic envelope method such as BIOCLIM will generally be conservative; therefore the predictions presented here may in fact be a best-case scenario.

The power of the overall pattern lies in the broad taxonomic and ecological generality of the results and in the strength of the altitudinal gradient in this ecosystem. The geographical contraction of species' ranges has implications beyond the loss of species richness. Based on known patterns of vertebrate phylogeography and population-level genetic diversity in the region (Moritz 2002), the geographical pattern of population extinctions (figure 1) represents a significant loss of genetic diversity and an associated reduction in evolutionary potential within the region.

Although the complete loss of its core environment may not unequivocally cause a species to go extinct, it will certainly make the species extremely vulnerable. At worst, the predicted extinction curve will be an underestimate of the extinction rate owing to the compounding effects of other impacts and disrupted processes. However, at best it describes the increase in the number of species that will become severely threatened as they lose their core environments. The low number of points on the curve in figure 4 means that the predictive power of the relationship is reduced; however, the shape of the curve is precisely what would be expected theoretically. Assuming that the relative extinction proneness of species is normally distributed with respect to a given threatening process (in this case increasing temperature) then we would expect the extinction curve to be an S-curve. Initially, the extinction rate would increase slowly, affecting only a few sensitive species; this would be followed by a period of rapidly increas-

ing extinction rates through the modal region of the curve before the rate slows down when only a few hardy species remain. This is exactly the pattern demonstrated here (figure 4). An important point to note is the prediction that impacts will not increase linearly: they may be quite slow initially but the rate will increase rapidly. This is a significant point with respect to conservation management: it would be completely inappropriate to define thresholds for management action on the basis of monitoring the increase in temperature. It is probable that once the lower inflection point is reached on the S-curve there will be massive and rapid increases in the impacts with relatively small increases in temperature. It is imperative to keep the temperature increase below this inflection point of *ca.* 2–2.5 °C to minimize impacts.

Several other independent lines of evidence support the predictions presented here. Hilbert *et al.* (2001) used neural-net models to predict the magnitude of vegetation changes in the region with strikingly similar results to those presented here for vertebrate distributions. A generalized linear model predicted a very similar pattern of decline for the golden bowerbird (*Prionodura newtoniana*), although at a slightly faster rate than the equivalent BIOCLIM model presented here (Hilbert *et al.* 2003). There is also experimental and anecdotal evidence to support the predictions. It has previously been suggested that the limited altitudinal ranges of many species of mammalian folivores are determined by thermal tolerances (Winter 1997; Kanowski *et al.* 2001). Laboratory studies confirm that one species, the green ringtail possum (*Pseudochirops archeri*), is intolerant to high temperatures, with body temperature increasing linearly with time when the ambient temperature is above 30 °C, leading to the possibility of lethal effects after only 4–5 h (A. Krockenberger, personal communication). There have also been anecdotal reports of unusual mortality in arboreal folivores within the region following recent periods of record maximum temperatures. As most models of climate change predict not only rising mean temperatures, but also more frequent periods of extreme temperatures, it is likely that the marsupial folivores will be particularly sensitive to predicted climate changes.

In the distribution models discussed here, only the effects of increasing temperature have been considered. The impacts of climate change on the region will conceivably be much more severe owing to a range of compounding factors. Increased CO_2 levels will reduce the nutritional value, increase the toughness and increase the concentration of some defence compounds of foliage (Lawler *et al.* 1997; Kanowski 2001). This will have significant detrimental effects on folivore abundance (particularly affecting endemic ringtail possums, tree kangaroos and many insects). Furthermore, the predicted changes in geographical distribution will move species from nutrient-rich basaltic soils to increasingly poorer granitic soils at higher elevations. Rainforests on these poorer soils support lower densities of arboreal folivores (Kanowski *et al.* 2001). A lifting cloud bank (Still *et al.* 1999), directly resulting in a reduction in critical inputs of mist and water at high altitude, has been linked with synchronous declines of amphibians and altitudinal shifts in the distributions of birds in the cloud forests of Monteverde, Costa Rica (Pounds *et al.* 1999). These impacts are

particularly relevant to the frogs of the family Microhylidae (a diverse group of restricted regional endemics), where species richness is limited by low rainfall in the dry season (Williams & Hero 2001). A raised orographic cloud base will potentially affect many taxa requiring high and consistent moisture levels (e.g. microhylid frogs, litter skinks, soil invertebrate faunas, microbes), thereby indirectly affecting most litter-feeding insectivores (many species of birds, skinks, microhylid frogs, dasyurid mammals, bandicoots, etc.) and litter processes (nutrient cycling, decomposition, etc.). Increasingly unpredictable rainfall may also have significant negative impacts (Knapp et al. 2002; McLaughlin et al. 2002). The intra-annual variability in rainfall was the most significant variable explaining regional patterns of bird abundance in the Wet Tropics bioregion, particularly for insectivores and frugivores (Williams 2003). Basically, population size is negatively related to rainfall seasonality, a factor that is predicted to increase under climate-change scenarios. Short periods of dry weather have been shown to limit insect biomass (Frith & Frith 1985) and probably fruit biomass, providing a plausible mechanism explaining these patterns, namely, that short bottlenecks in available resources limit local abundances (Williams 2003). Habitat fragmentation has previously been shown to increase the extinction proneness of many species within the Wet Tropics bioregion (Laurance 1991, 1994). Fragmentation has two implications in the context of the analyses presented here: (i) current habitat fragmentation will impede climate-induced shifts in faunal distributions; and (ii) as species' ranges contract further up the mountains, distributions will become more fragmented, thereby exacerbating the impacts of reduced range size. All of these factors are likely to compound the impacts of increased temperature and may act to increase the slope and decrease the position of the lower inflection point predicted in figure 4.

Ultimately, the impacts of global climate change will depend on two factors: first, the final realized degree of change and, second, the resilience of the ecosystem in question. The first factor needs to be addressed globally and at a governmental level by reducing global greenhouse-gas emissions. The second issue, of resilience, can be addressed locally and immediately. Resilience refers to the ability of a system to withstand and/or recover from perturbation and is a key management concept in dealing with an unpredictable future (Walker et al. 2002). To maximize ecosystem resilience, it is imperative that we maintain ecological processes and minimize any action that may damage the inherent resilience of the ecosystem, such as habitat fragmentation, feral animals, weeds and diseases. Conservation management can increase the probability of ecosystem survival and/or recovery by focusing on the protection of ecosystem resilience. We need to acquire a greater understanding of the interacting processes that maintain resilience and the factors that currently limit the distribution of species, especially physiological and environmental factors, and develop sophisticated predictive tools that incorporate the multifaceted impacts of global climate change. Only then will it be possible to plan and implement realistic conservation strategies to minimize the damage to these unique biota and ecosystems.

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