

Golden bowerbird (*Prionodura newtonia*) habitat in past, present and future climates: predicted extinction of a vertebrate in tropical highlands due to global warming

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Abstract

A generalised linear model was used to predict climatically suitable habitat for the golden bowerbird (*Prionodura newtonia* De Vis), an endemic species of the Wet Tropics of North Queensland. Mean temperature of the coldest quarter and mean precipitation of the wettest quarter were found to be the best habitat predictors. For independent validation data, accuracy was 67% (Kappa statistic, $n=30$). Past, and future habitats suitable to the golden bowerbird were mapped by altering the temperature and precipitation input to the model. In the current climate, total potential habitat is estimated to be 1564 km², occurring as a number of separate patches with distinct bowerbird subpopulations. Past habitat was most limiting, 406 km², during the Holocene climatic optimum (c. 5000–3600 YBP, +2 °C and +50% rainfall relative to today). With future warming, assuming a 10% decrease in rainfall, potential habitat is reduced to 582 km² (1 °C warming), 163 km² (2 °C warming) and 37 km² (3 °C warming). Thus, global warming in the coming decades is likely to be a significant threat to the survival of this and similar upland and highland species in the tropics. Crown Copyright © 2003 Published by Elsevier Ltd. All rights reserved.

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1. Introduction

Forest clearing is generally thought to be the greatest threat to biodiversity in the tropics (Sala et al., 2000) and rates of clearing are certainly highest there, particularly in tropical Asia (Houghton, 1999). However, global warming may have a particularly strong impact on mountainous, tropical regions like the Wet Tropics World Heritage Area of north-eastern Australia where the peaks and higher tablelands can be thought of as cool-climate islands in a sea of warmer climates (Nix, 1991). These islands are separated from each other by the warmer valleys, which also support rainforest, and form a scattered archipelago of habitat for organisms that are heat intolerant. Of the Wet Tropics Region's 13 endemic bird species 10 are restricted to these cooler habitats and are not recorded from the lowlands

(Crome and Nix, 1991). These species are representative of a suite of cool-adapted fauna now restricted to higher altitudes in the tropics. The golden bowerbird (*Prionodura newtonia*), is a good example of such species. It inhabits cooler, upland and highland forests with bowers (indicating courting and breeding activity) recorded from approximately 700 to 1500 m a.s.l. The duration and degree of isolation of populations in the upland "islands" is indicated by the presence of population specific song dialects. These dialects are associated with continuous blocks of upland forest blocks and are sufficiently great as to result in song recognition failure (Westcott and Kroon, 2002). Whether these dialects are indicative of the degree of genetic isolation among subpopulations is unknown.

1.1. The wet tropics bioregion

The Wet Tropics Bioregion of North East Queensland (Sattler and Williams, 1999) lies roughly between 15 and 19° S, long. 145–146° 30' E (Fig. 1) and contains

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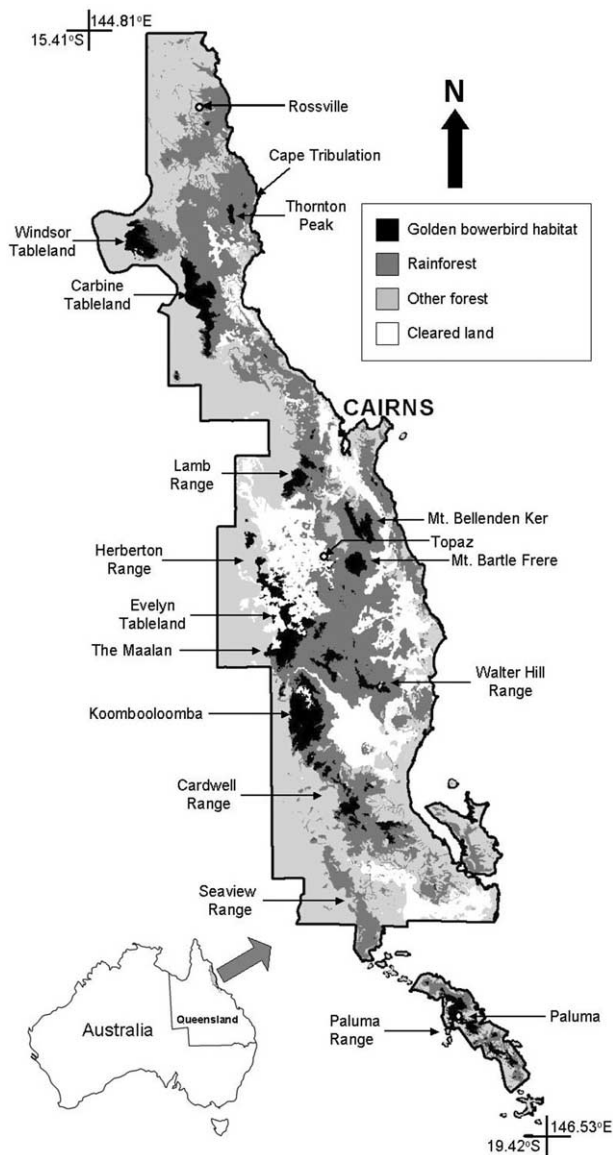


Fig. 1. The study area, the Wet Tropics of North Queensland (defined as the extent of a regional GIS containing data on terrain, climate, and vegetation mapping) and estimated habitat for the golden bowerbird (1564 km²) in today's climate. Note that vegetation mapping is incomplete south of the Seaview Range but contains all rainforests.

Australia's best developed tropical rainforests. The Wet Tropics is one of the most important biodiversity "hot spots" in Australia and is considered to be one of the most significant regional ecosystems in the world (Webb, 1984). Within an area of less than 2000 km², the region supports one third of all Australian terrestrial vertebrate species (741 species) including 85 endemic species (Wet Tropics Management Authority, 2002), 66 of which are restricted to rainforest (Williams et al., 1996). A majority of the regionally endemic species are restricted to the cooler uplands and highlands, often in a number of small disjunct patches of habitat. Plant species represent 65% of Australia's ferns, 37% of the conifers and 30% of both the

orchids and vascular plants (Wet Tropics Management Authority, 2002).

The region's complex topography (elevations ranging from sea level to 1615 m) produces steep gradients of temperature and rainfall (Nix, 1991). Mean annual precipitation varies from c. 600 mm to greater than 8000 mm with mean annual temperatures varying from above 25 °C to less than 17 °C at the highest elevations. The Wet Tropics' rainforests are known to have contracted considerably during the cooler and drier climate of the late Pleistocene when they were replaced by open forests and woodlands dominated by *Eucalyptus* spp. and other sclerophyll genera (Hopkins et al., 1993, 1996; Hilbert et al., 2001a). Rainforests expanded to their current extent during the warmer and wetter Holocene. By 1985, approximately 25% of the bioregion was cleared of natural vegetation with clearing concentrated on fertile, flat soils in the lowlands and uplands (Winter et al., 1987).

1.2. Past climate changes

It is now known that climate in the tropics changed significantly through the glacial cycles of the Pleistocene (Farrera et al., 1999). In the Wet Tropics, the climate during the last glacial maximum (LGM), c. 20–18 ka BP, was considerably colder and drier than at present. Near the Pleistocene/Holocene transition (PHT), c. 7.5–6 ka BP, the climate was cooler and wetter than today. Later, during the so called Holocene climatic optimum (HCO), c. 5–3.6 ka BP, global temperatures were significantly warmer than today and, locally, mean annual temperatures are estimated to have been 2 °C higher with 25% greater annual rainfall (Nix, 1991). This period is sometimes considered to be a good palaeo-model for near term, future climate change, at least in terms of temperature. Modelling of past forest environments (Hilbert and Ostendorf, 2001 and unpublished data) suggests that rainforests, especially complex mesophyll vine forests, could have had a larger extent in the Wet Tropics at that time. However, highland and upland rainforest types (Simple Notophyll and Simple Microphyll Vine Forests and Thickets) are likely to have been greatly restricted and more fragmented than in today's climate.

One motivation for the study of past climates is that the biogeographic distributions of a region's biota are often as dependent on the area's history as on the current environmental conditions. Thus, the study of past environments and distributions of taxa is essential in order to understand the present-day ecological patterns. Similarly, the analysis of past responses to climatic change provides important insights into the possible impacts of future alterations of climate.

1.3. Future climate change and its impacts

Elevated CO₂, methane and other greenhouse gasses already have had a measurable impact on mean global temperatures. Warming over land in the Southern Hemisphere from 1901 to 2000 is estimated to have been 0.52 ± 0.13 °C (Intergovernmental Panel on Climate Change, 2001). We appear to be headed for what some authors have termed a “super interglacial” with warmer conditions than Earth has experienced for millions of years. Recent projections for coastal north east Queensland, comparing five global circulation models (GCM), are approximately 1.4–5.8 °C by 2100 (i.e. one degree per degree of global warming), relative to 1990 with +4 to –10% changes in rainfall per degree of warming (Walsh et al., 2000). CSIRO’s Mark2 GCM predicts a more El Niño like mean state for the Pacific through this century (Walsh et al., 2000). Such conditions generally cause lower rainfall and longer dry seasons in the Wet Tropics Region.

Recent studies (Hilbert et al., 2001a,b; Ostendorf et al., 2001) found that the tropical forests of north Queensland are highly sensitive to climate change within the range expected early in this century. Large changes in the distribution of forest environments are likely with even minor climate change and the relative abundance of some rainforest types could decrease significantly. The area of lowland, Mesophyll Vine Forest environments increases with warming while upland, Complex Notophyll Vine Forest environments respond either positively or negatively to warming, depending on changes in rainfall. Highland rainforest environments (Simple Notophyll and Simple Microphyll Vine Fern Forests & Thickets) decrease by 50% with only a one degree warming. Cloud forests may be particularly sensitive to climate change (Foster, 2001). These analyses predict a great sensitivity of rainforest environments to climate change and suggest that it is imperative that we understand ecological patterns and processes over large spatial and temporal scales in the region and develop predictive tools to enable realistic conservation planning for the continued preservation of the unique biota and ecosystems of the Wet Tropics and other rainforests in Queensland. Because most of the region’s endemic vertebrates are distributed over areas with a very narrow range of annual mean temperatures, these species, key to the heritage values of the Wet Tropics World Heritage Area, may be under severe threat over the next few decades.

The lack of any climate change monitoring in the Wet Tropics makes it impossible to state whether warming over the past century has had an impact on its flora or fauna or ecosystem processes. However, monitoring in other parts of the world have identified a large number of ecological and biological changes due to recent climate change (Hughes, 2000; McCarty, 2001; Walther et

al., 2002). These include both latitudinal and altitudinal shifts in species ranges (Zalakevicius and Zalakeviciute, 2001) as well as changes in abundance and local extinctions. For example, a lifting cloud-base associated with increased sea surface temperatures has been implicated in the disappearance of 20 species of anurans in highland rainforests of Monteverde, Costa Rica (Pounds et al., 1999). Other observed effects include changes in phenology (Bradley et al., 1999; Menzel, 2000; Gibbs and Breisch, 2001); earlier flowering (Fitter and Fitter, 2002), emergence from hibernation (Masters et al., 1998; Inouye et al., 2000), migration and egg-laying in birds (Bergmann, 1999; Brown et al., 1999; Dunn and Winkler, 1999; Scharlemann, 2001; Zalakevicius and Zalakeviciute, 2001; Tryjanowski et al., 2002); and changes in morphological characteristics such as egg size (Jarvinen, 1994).

Here, we use spatial data in a regional geographic information system (GIS), detailed presence/absence surveys, generalized linear modeling and estimates of past and future climates to assess the role of climate in the potential distribution of the golden bowerbird. We show that the extent and spatial distribution of golden bowerbird habitat would have changed markedly in the past due to glacial cycles of cooling and warming. Several future climate change scenarios are considered, all of which indicate a large decline of potential, climatic habitat. We then discuss the implications of global warming for the long term survival of upland and highland vertebrates in the Wet Tropics Bioregion.

2. Methods

2.1. Spatial data

A regional GIS was utilised that covers the majority of the Wet tropics Bioregion. The data include vegetation mapping, a digital elevation model (DEM), and many climate layers derived from meteorological data and the DEM. Vegetation classes were mapped at 1:100 000 scale by Tracey and Webb (1975) from 1:80 000 aerial photos and field surveys. The forest classes are based on structure, not species compositions, and range from dry open woodlands to wet, coastal rainforests (Tracey, 1982). Estimated potential distributions of forests today and in the past climates come from an artificial neural network that models the suitability of environments (based on terrain, soil parent material and seven climate variables) for each of the region’s structural/physiognomic forest classes (Hilbert and van den Muyzenberg, 1999; Hilbert and Ostendorf, 2001; Hilbert et al., 2001a,b). Regional maps of past rainforest distributions, estimated from the artificial neural network model, are not yet published but a description of the method is given in Hilbert and Ostendorf (2001) and

Hilbert et al. (2001a). The predicted distributions of forest types are consistent with carbon-dated charcoal fragments found in rainforest soils that indicate the presence of sclerophyll forests at these locations in past climates (Hopkins et al., 1993, 1996, and unpublished data).

Climate variables were estimated spatially by the ANUCLIM software (Houlder et al., 1999) using a digital elevation model (AUSLIG, 1994), meteorological data from a large number of stations, and a thin-plate spline method to interpolate between observations.

2.2. Presence/absence data for the golden bowerbird

Presence and absence data were collected in rainforest from Paluma (19° 00' S) to Rossville (15° 40' S) between 1980 and 2002. Like most bowerbirds (Ptilonorhynchidae), golden bowerbird males build a structure, the bower, from which they display to attract potential mates (Borgia et al., 1985). While bowers are not used for nesting by females, they are required by males for obtaining matings and consequently their distribution is a good indicator of the breeding range of the species. Bowers were located during searches in which transects through rainforest were walked. Bowers were detected by direct encounters or by following sightings or vocalizations of males to the bower. Additional bower presence data for the Paluma area were obtained from Frith and Frith (2000) and elsewhere from field encounters by A. Ford and B. Grey (CSIRO). A total of 120 golden bowerbird bower locations were collected and entered into the GIS. To create the bower absence samples, transects and areas surveyed for bowers were entered into a GIS by digitising from 1:50 000 topographical maps. It was estimated that bowers could be detected within 75 m of a surveyor. Therefore, survey transects and areas were buffered by 75 m. As active bowers are separated by a minimum of approximately 150 m (Frith and Frith, 2000), the buffered areas were converted to a point coverage with points separated by 150 m. Absences within 75 m of a bowerbird sighting were removed. Thus, all absences come from areas that were intensively surveyed but in which bowers were not discovered. A total of 556 absence points were created of which 120 locations were selected at random for a total data set of 120 presences and 120 absences. These data were randomly assigned to a training set (105 presences and 105 absences) and a validation set (15 presences and 15 absences). The seven climatic variables were sampled from the GIS for each presence and absence location.

2.3. Habitat modelling

A generalized linear model (GLM) using a binomial distribution with a logit link function was developed for

predicting the presence of golden bowerbird bowers as a function of the seven climate variables we previously used for modeling forest distributions (Hilbert and van den Muyzenberg, 1999) as well as the square of each variable. The variables are: mean annual temperature; minimum temperature of the coldest period; mean temperature of the coldest quarter; mean temperature of the warmest quarter; mean annual precipitation, mean precipitation of the wettest quarter, and mean precipitation of the driest quarter. A forward-backward stepwise GLM procedure in S-plus (Insightful Corporation, 2001) was used to select the variables for the model.

The Kappa statistic (Hudson, 1987) was utilized to determine the optimal probability threshold for classifying habitat and assessing the overall model accuracy. Kappa was calculated at intervals of 0.1 (from 0.1 to 0.9) for predictions made with the training set and the threshold with the highest Kappa was selected for mapping and validation. Kappa measures proportional accuracy adjusted for chance agreement and is an effective and appropriate statistic for evaluating and comparing presence-absence models (Manel et al., 2001).

To map habitat, an ArcInfo program was written using the model, the optimum threshold and restricting the habitat prediction to rainforests. For current and future climate scenarios, rainforests mapped in the regional vegetation coverage (Tracey and Webb, 1975; M. Olsen, unpublished) were used. For past climate scenarios the modeled distribution of rainforests in these climates were used (Hilbert and Ostendorf, 2001; Hilbert et al., 2001a).

2.4. Climate scenarios

Palaeo-climate scenarios were developed from previously published estimates (Nix, 1991) and are presented in Table 1. These scenarios represent estimates of rainfall and temperature in three very different climates thought to have been present in the Wet Tropics since the late Pleistocene. The earliest period is the last glacial maximum (LGM) when the region was

Table 1

Changes to the climate variables used for the modelling in the three past climate scenarios: Last glacial maximum (LGM) (c. 20–18 ka BP), Pleistocene/Holocene transition (PHT) (c. 7.5–6 ka BP) and Holocene climatic optimum (HCO) (c. 5–3.6 ka BP)

Climate variable	Climate scenario		
	LGM	PHT	HCO
Mean annual temperature	−3.5 °C	−2.0 °C	+2.0 °C
Minimum temperature of coldest period	−3.5 °C	−2.0 °C	+2.0 °C
Mean temperature of warmest quarter	−3.5 °C	−2.0 °C	+2.0 °C
Mean temperature of coldest quarter	−3.5 °C	−2.0 °C	+2.0 °C
Mean annual precipitation	50%	120%	125%
Mean precipitation of wettest quarter	50%	120%	125%
Mean precipitation of driest quarter	50%	200%	150%

the driest and coolest during the last c. 100 000 years. During the Pleistocene/Holocene transition (PHT) the climate had warmed somewhat and is believed to have been wetter than today's climate. Following this, the Holocene "climatic optimum" (HCO) or "altithermal" was both warmer and wetter than present conditions. Future warming scenarios of one, two and three degrees Celsius are considered here. Because of the uncertainty in regional rainfall projections, we included four changes in rainfall (−10%, no change, +10% and +25%) combined with each of the three warming scenarios. For all scenarios, past and future, we added or subtracted the appropriate temperature change from the spatial estimates of today's climate variables that are stored in the regional GIS. No spatial variability in climate change is known or assumed. For rainfall variables, the appropriate percentage increase or reduction was calculated separately for each hectare in the current-climate data layers in the GIS. Thus, changes in rainfall are proportional to estimated, current values rather than additive, which is the case for temperature variables.

3. Results

3.1. Habitat estimation in today's climate

The forward-backward stepwise GLM procedure selected the model ($P < 0.005$)

$$g(P) = b_0 + b_1T + b_2R \quad (1)$$

where $g(P)$ is the logit function of the form $\ln(P/(1 - P))$, $b_0 = 22.98$, $b_1 = -1.64$, $b_2 = 0.0021$, T = mean temperature of the coldest quarter, and R = mean precipitation of the wettest quarter. Solving Eq. (1) for the habitat probability (P) gives

$$P = \frac{1}{e^{-(b_0 + b_1T + b_2R)} + 1} \quad (2)$$

The optimum threshold for classifying habitat, based on the training set, was 0.3. The resulting Kappa value for the validations set was 0.67 which, according to subjective guidelines suggested by Monserud and Lee-mans (1992), indicates good agreement with the data. Accuracy was 84% for the validation data and 93% for the training set (Kappa = 0.68).

Fig. 1 presents the extent and distribution of golden bowerbird habitat estimated by Eq. (2), a threshold P of 0.3 and the constraint that habitat is restricted to rain-forest. The total habitat comprises 1564 km² in a large number of separate patches. The largest of these occur on the Carbine Tableland and the Koomboooloomba region. The vast majority of predicted habitat patches are known to contain golden bowerbird populations, including relatively small and isolated patches such as occur on Mt Baldy in the north of the Herberton Range.

3.2. Habitat changes since last glacial maximum

Fig. 2 illustrates the contraction and expansion of golden bowerbird habitat that occurred as the result of past changes in climate from LGM to the present. While full glacial conditions (Fig. 2a) were quite dry, compared to the present, the forest model predicts fairly extensive patches of highland rainforest types at the highest elevations and the habitat model suggests that these would have provided suitable habitat (total area of 1512 km²) scattered throughout the region. The Windsor Tableland provided the largest habitat patch at this time. Aside from the Paluma Range, there was no habitat south of Koombooolooma. After the Pleistocene-Holocene transition (Fig. 2b), the cool and wet climate would have provided extensive areas (6102 km²) with environments suitable to golden bowerbirds. A large, mostly continuous, habitat patch was present in the central Wet Tropics, stretching from roughly west of Cairns in the north to the Walter Hill Range, inland from Cardwell, in the south. In the northern Wet Tropics, large areas of the Windsor and Carbine Tablelands would have provided habitat with smaller patches available in the highlands west of Cape Tribulation. Significant parts of the Seaview and Paluma Ranges had suitable habitat at this time. At HCO (Fig. 2c), further warming would have restricted golden bowerbird habitat (406 km²) to small and disjunct areas at the highest elevations. These small patches can be thought of as the interglacial refugia for golden bowerbirds for which habitat is more restricted by warmer climates, even if rainfall is quite high, than by cold and dry glacial conditions. The potential habitat in today's climate but before European settlement and extensive forest clearing is shown in Fig. 2d (1729 km²). With general cooling and drying since HCO, the refugial areas expanded and habitat again became available from Koomboooloomba to the Walter Hill Range. Comparing this with Fig. 1 shows that clearing has had only a minor, direct impact on habitat area and this is restricted to the southern and western Atherton Tablelands. Possible impacts of historic logging activities on habitat quality for golden bowerbirds throughout the uplands are unlikely to have been severe (Crome and Moore, 1989).

3.3. Future climate change scenarios

Changes in total habitat in the twelve future climate scenarios (four rainfall by three warming) are presented in Fig. 3. These results show that the extent of golden bowerbird environments is very sensitive to warming. Generally, the greatest absolute decrease occurs with the first degree of warming. To some extent, increases in rainfall can ameliorate the negative impact of warming. By three degrees of warming, however, uncertainties about future rainfall become insignificant. Clearly,

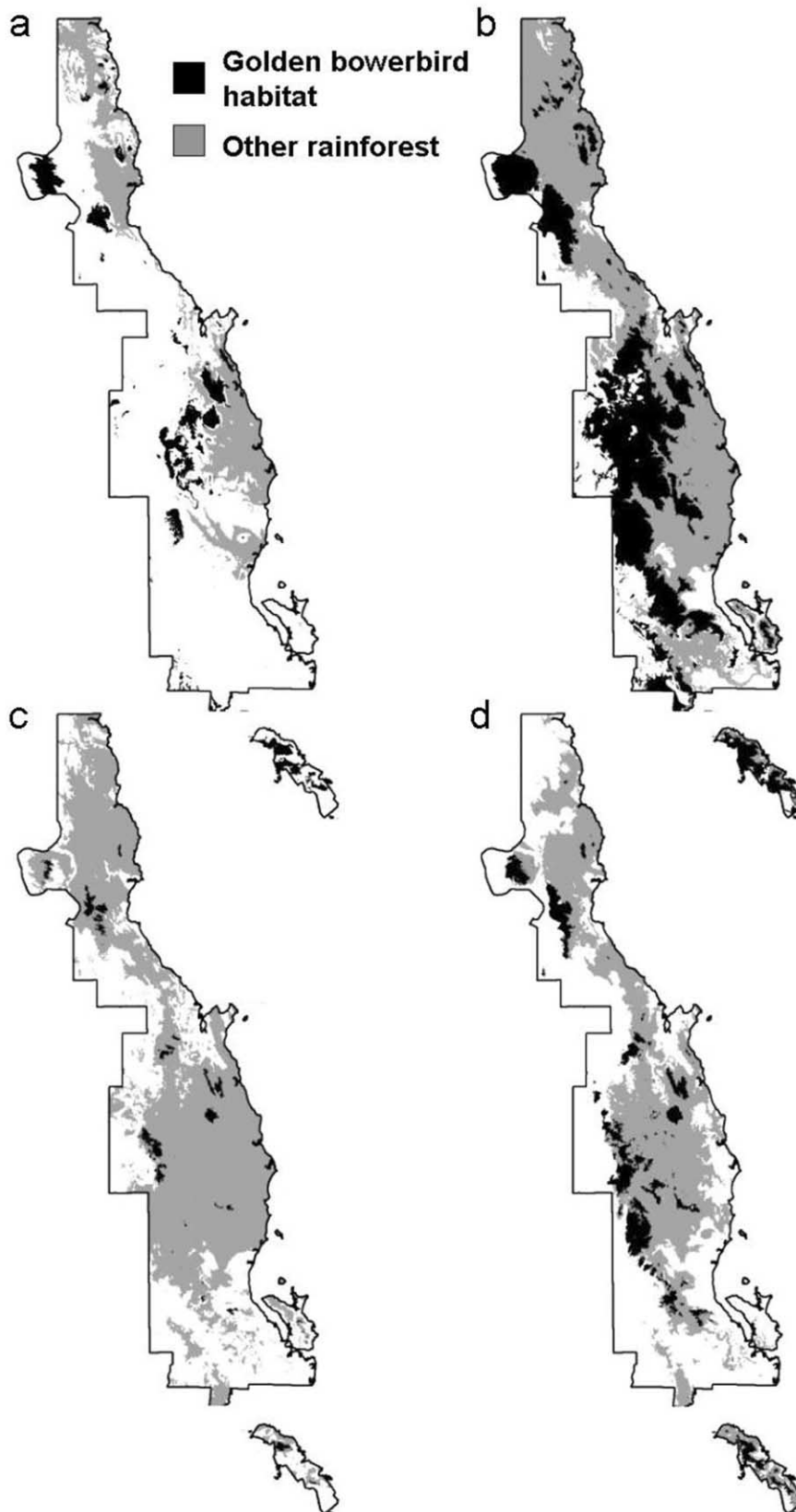


Fig. 2. Potential habitat for the golden bowerbird in four climates since last glacial maximum. (a) a cold, dry climate at last glacial maximum (c. 20–18 ka BP), 1512 km² of habitat; (b) a cool, wet climate after the Pleistocene/Holocene transition (c. 7.5–6 ka BP), 6102 km² of habitat; (c) a warm, wet climate at the Holocene climatic optimum (c. 5–3.6 ka BP), 406 km² of habitat; and (d) the potential distribution of forests and habitat in today's climate in the absence of clearing, 1729 km² of habitat.

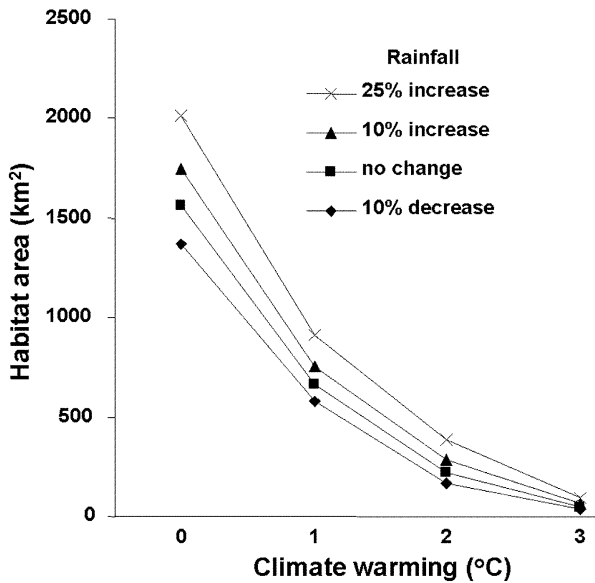


Fig. 3. Predicted area of golden bowerbird habitat in a number of future climate change scenarios including a range of changes in rainfall and from one to three degrees of warming.

there will be no climatically suitable habitat in the Wet Tropics at some point between three and four degrees of warming.

The spatial distributions of habitat in the three warming scenarios with a ten percent reduction in rainfall are mapped in Fig. 4. With one degree of warming (Fig. 4a, 582 km² of habitat), all habitat patches shrink and many of the smaller ones, especially south of The Maalan are lost. With two degrees of warming (Fig. 4b, 163 km²), no significant patches of habitat remain in the southern Wet Tropics, and in the north, most remaining patches are very small. This future scenario limits habitat more severely than our estimate for the warmest climate in more than 100 000 years (climatic optimum, Fig. 3c). With three degrees of warming (Fig. 4c, 37 km²), golden bowerbirds would be restricted to the two massifs, Bartle Frere and Bellenden Ker, Mt. Fisher on the Evelyn Tableland and very small patches at the top of peaks in the Lamb Range.

4. Discussion and conclusions

4.1. Modelling issues

For most species, the best or only information about their environmental constraints is geographic presence data. Much less frequently both presence and absence data are available. Consequently, correlative models such as we present here are an important and widely utilized tool in determining biotic responses to climate change. The availability of absence data along with

records of presence greatly expands the modelling techniques that can be utilized and allows the classification of habitat as we do here rather than the more limited “climatic envelope” approaches like BIOCLIM (Houlder et al., 1999). An important assumption of correlative models is that the species’ distribution is now in equilibrium with climate. For highly mobile vertebrates such as the golden bowerbird this assumption is reasonable. Applying a correlative model to altered climates requires the further assumption that the climate variables proximally constrain the species’ range or that the climate variables continue to be correlated with whatever unknown variables actually control the distribution. The degree to which the distribution of golden bowerbirds and other upland, endemic vertebrates is directly controlled by climate is unknown. Certainly, some vertebrates may be directly limited by temperature thresholds. Golden bowerbirds are only infrequently seen below c. 600 m and are not known to breed there. In the absence of detailed ecophysiological studies, the presence of rainforest and apparently suitable food sources at lower elevations and the strongest argument that climate *per se* restricts this species to the cooler uplands and highlands. Of the 40 tree species whose fruits are known to be eaten by golden bowerbirds, 21 are common in rainforest below 600 m (Westcott and Dennis, unpublished data) and many other tree species at lower elevations have fruit characteristics similar to those used by golden bowerbirds. Golden bowerbirds are known to use complex mesophyll vine forest above 600 m and this structural forest type is most common in the lowlands, so forest structural properties probably do not limit this species to higher elevations.

While it is possible that additional biotic factors (e.g., competition, predation and pathogens) may constrain golden bowerbirds to higher elevations we believe this is unlikely for a number of reasons. Competition seems an unlikely explanation as more potential frugivore competitors, including a greater number of bowerbird species, occur within golden bowerbird habitat than in the warmer, lower-elevation forests. A similar situation exists for likely predators which include some snakes, cats and raptors, however in this case there are no apparent altitudinal differences in their distribution. Finally, mid to high altitude distributions (above ca. 400 m a.s.l.) are relatively common amongst Wet Tropics vertebrates and occur across a broad taxonomic range including reptiles, amphibians, mammals and birds. A general effect such as climate must be viewed as the most parsimonious explanation for this pattern as each species and group would be expected to be influenced by very different sets of biotic factors. However, if biotic factors are in fact significant in determining the realised niche of these upland species, it would appear that these factors are probably themselves quite highly dependent on climate.

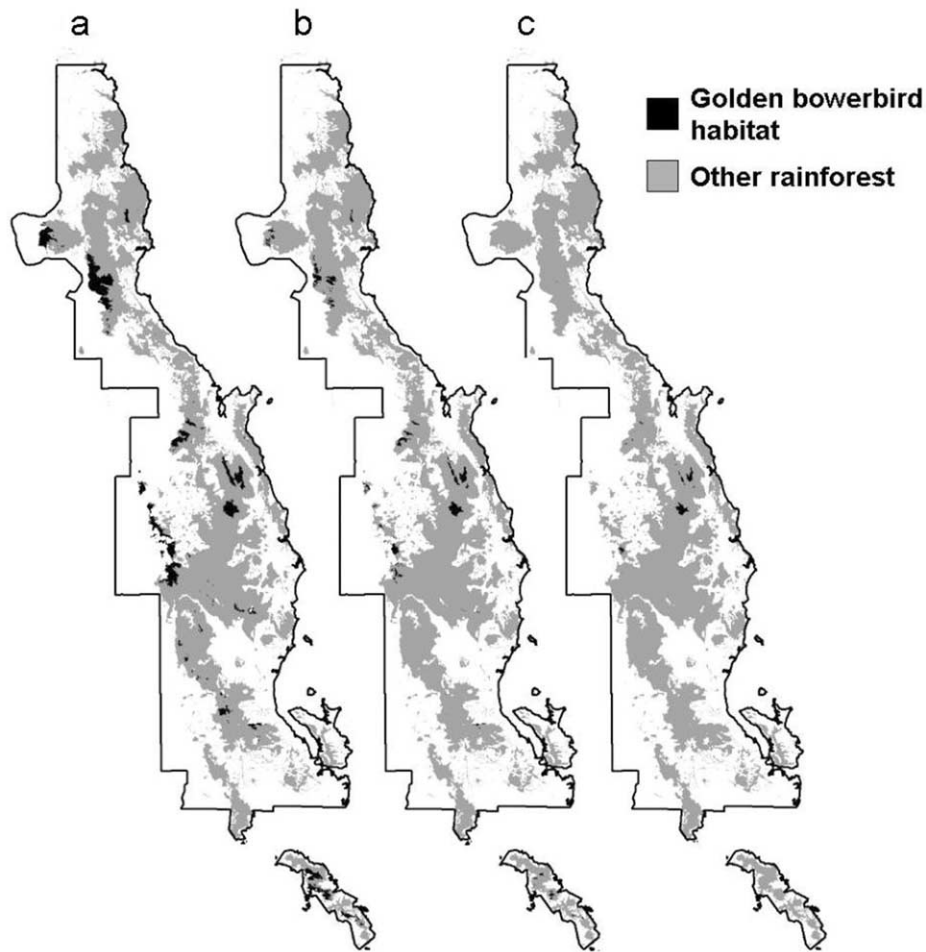


Fig. 4. Habitat for the golden bowerbird in three future climate change scenarios, all assuming a ten percent reduction in rainfall and that current rainforest distributions have not yet changed: (a) one degree of warming, 582 km² of habitat; (b) two degrees of warming, 163 km² of habitat; (c) three degrees of warming, 37 km² of habitat.

Correlative models have been criticised for ignoring range limitations due to dispersal and species interactions (which are often absent from mechanistic models as well). It is doubtful that dispersal is limiting for the golden bowerbird within the Wet Tropics. Populations now exist in many disjunct and small habitat patches within a relatively continuous matrix of upland and highland rainforest with no apparent barrier to dispersal. Furthermore, future warming leads to contraction of existing habitat patches for this species, not large geographic shifts in suitable habitat. Similarly, we would not expect species interactions to change radically since future habitat is a subset of the current distribution and the spatial relationships between habitats remain constant. Obviously, if the upper range of predicted warming for this century occurs (5.8 °C), no appropriate environments would remain within the Wet Tropics. Whether and where appropriate climates might come to exist further to the south is unknown. However, the closest rainforests to the south are far removed across significant habitat barriers from the Wet Tropics. Thus,

at continental scales, dispersal and species interactions are potentially significant (Hughes and Westoby, 1994).

4.2. Other threats to upland and highland rainforests

With the exception of the Atherton Tablelands, the rugged topography, relative inaccessibility and poor agricultural potential of upland and highland rainforests have protected them from the extensive clearing and fragmentation that occurred at lower elevations, despite extensive selective logging. From our estimates of potential habitat with and without known forest clearing (Fig. 2 and 2d, respectively) approximately 10% of golden bowerbird habitat may have been lost through clearing of rainforest. Because the higher elevation rainforests are largely intact and are protected by World Heritage listing, the biodiversity of these unique forests is often assumed to be largely secure. The loss of seven endemic stream-dwelling frog species from above 450 m, probably due to the fungus *Batrachochytrium dendrobatidis* (Berger et al., 1998; Wet Tropics

Management Authority, 2002), and forest dieback possibly due to the soil pathogen *Phytophthora cinnamomi* (Gadek et al., 2001) suggest that this assumption may overlook natural threatening processes. Much of the area affected by dieback lies within golden bowerbird habitat. This highlights the potential for existing threats, even in protected areas, to amplify and exacerbate the threat imposed by future climate change.

4.3. *Climate change impacts and golden bowerbirds*

Our analysis identifies two major impacts on golden bowerbirds. The first of these is the dramatic reduction in suitable breeding habitat within the region. Without some form of adaptive response on the part of golden bowerbirds this can only be assumed to lead to a significant reduction in population sizes. Irrespective, a reduction of approximately 50% of habitat area is predicted with just 1 °C of warming under the scenarios we considered. The second impact is on population structure. Currently, the golden bowerbird is distributed in numerous large and small sub-populations spread across the region (Fig. 1). Under all future scenarios considered here, golden bowerbird sub-populations are reduced to many fewer and much smaller populations (Fig. 4). Both these general categories of effect, decreases in habitat area or population size and increases in the degree of fragmentation of populations, are criteria recognised by the IUCN (IUCN, 2001) as indicative of endangerment. Climate change scenarios incorporating both kinds of changes do not bode well for the golden bowerbird.

Reduction in size and increased isolation of populations also has potential evolutionary impacts on a species (Futuyama, 1986). The loss of populations results in the loss of within species diversity and evolutionary potential (Moritz, 2002) as well as the potential of altering a species' evolutionary trajectory. Isolation of golden bowerbird populations in the past has resulted in population divergence in the signals associated with breeding (Westcott and Kroon, 2002). In other bowerbird species, divergence in breeding signals has resulted in divergence in female mate preferences between populations (Uy and Borgia, 2000). These steps have the potential to represent the initial steps in speciation (Grant and Grant, 1996).

4.4. *Climate and the habitat of upland and highland species*

Whether warming in the past century has had a measurable impact on species distributions, or other ecological variables, in the Wet Tropics is an open question. In fact, the amount of warming in the Wet Tropics is unknown. However, if the regional climate has warmed as much as the 0.5 °C observed for the Southern Hemisphere (Intergovernmental Panel on Climate Change,

2001), the distributions of mobile, cooler climate species may well have contracted. Our estimates for the golden bowerbird in Fig. 3 imply the possibility of considerable range contraction with the amount of warming that already may have occurred. Judging from Fig. 1 and Fig. 4a (1 °C of warming), this may be most noticeable in the highlands between Koombooloomba and the Cardwell Range or in very small isolated habitat patches such as occur near Topaz, west of Bartle Frere, where habitat is the first to disappear with warming. Topography obviously plays a very important role in the rate of change in regional habitat. Relatively flat uplands, at the lower altitudinal range of a species' climatic habitat, suddenly become entirely unsuitable once a temperature threshold is passed. The Koombooloomba region is a good example for the golden bowerbird. Similarly, the relatively conical shape of mountains implies that, with a linear increase in the lower altitudinal limit for a species, the rate of habitat loss is greatest initially (see Fig. 4).

It is known that cool, glacial conditions have restricted the distributions of many species in the Wet Tropics (Schneider et al., 1998). However, expansion of cool-adapted species occurred after the last glacial period and these populations were subsequently fragmented into upland isolates by further warming in the late post-glacial period (Winter, 1997). Our results further emphasise the great importance of interglacial climate warming in restricting habitat for cool-adapted species in mountainous tropical regions. In the Wet Tropics, maximum temperatures during interglacial periods probably had a profound affect throughout the Pleistocene on species diversity and biogeographic patterns. Extrapolating from our results for the golden bowerbird, upland and highland species may have been less affected by cooling and aridity during glacial periods than by high temperatures during interglacials, even if accompanied by increased rainfall. Similarly, it is thought that rainforest remained in the Amazonian lowlands throughout the Pleistocene and the main effect of climate changes may have been on the distribution of heat intolerant plants responding to Holocene warming (Haberle, 1999; Colinvaux et al., 2000; Colinvaux and De Oliveira, 2001). However, general conclusions about the tropics are difficult to infer since continental and regional geography would obviously influence the impact of both warmer and cooler climates. The much greater elevation of mountains in the island of New Guinea and the large latitudinal range of the Western Ghats, for example, would be expected to alter the long-term effect of climate changes on biodiversity in the higher elevation tropics. Nonetheless, cool-adapted species living in tropical highlands may be at risk throughout the tropics.

Two recent meta-analyses indicate very high confidence that effects of global warming on species and

ecosystems have already been observed throughout the globe (Parmesan and Yohe, 2003; Root et al., 2003). While any current effects in the Wet Tropics are unknown, our preliminary analyses clearly indicate that climate change is a major issue for the conservation of Wet Tropics ecosystems and biodiversity. To date there has been very little research on potential impacts in this region and there are many information gaps. It is critical that we begin monitoring for ecological changes in the most sensitive areas. With the resulting knowledge, management and policy can begin to address this challenge creatively and work to preserve as much of the Wet Tropic's biodiversity as possible. Studies such as ours emphasize the need for current conservation efforts to consider climate change in both in situ conservation and reintroduction efforts (McCarty, 2001).

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