

Potential decoupling of trends in distribution area and population size of species with climate change

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Abstract

Global climates are changing rapidly and biological responses are becoming increasingly apparent. Here, we use empirical abundance patterns across an altitudinal gradient and predicted altitudinal range shifts to estimate change in total population size relative to distribution area in response to climate warming. Adopting this approach we predict that, for nine out of 12 species of regionally endemic birds, total population size will decline more rapidly than distribution area with increasing temperature. Two species showed comparable loss and one species exhibited a slower decline in population size with change in distribution area. Population size change relative to distribution area was greatest for those species that occurred at highest density in the middle of the gradient. The disproportional loss in population size reported here suggests that extinction risk associated with climate change can be more severe than that expected from decline in distribution area alone. Therefore, if we are to make accurate predictions of the impacts of climate change on the conservation status of individual species, it is crucial that we consider the spatial patterns of abundance within the distribution and not just the overall range of the species.

Keywords: altitudinal gradient, climate change, population decline, rainforest birds, range shift

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Introduction

It is accepted that contemporary climate change (Folland *et al.*, 2001) is already causing shifts in species' distributions (Hughes, 2000; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003) and that there is the potential for these changes to be devastating in the future (Peterson *et al.*, 2002; Thomas *et al.*, 2004a; Thuiller, 2004). Previous attempts to estimate extinction risk following range shifts have employed modelled projections of 'climate envelopes' to predict the relative extent of potential species' distributions under climate change (Bakkeness *et al.*, 2002; Erasmus *et al.*, 2002; Thuiller, 2003; Pearson & Dawson, 2003). Some models indicate that climate change impacts will largely consist of latitudinal and altitudinal shifts in potential species' distributions (Peterson *et al.*, 2002), while others suggest that the complete disappearance of critical climate

types and dependent species are possible (Williams *et al.*, 2003; Thomas *et al.*, 2004a; Hilbert *et al.*, 2004).

Climate envelope models provide valuable insight into the extent and location of a potential species' distribution under predicted climate scenarios. However, a lack of data on the spatially variable patterns of abundance within a species' range has prevented estimates of change in population size during range contraction or expansion. This is despite assertions that population size and trend are the best correlates of extinction risk (O'Grady *et al.*, 2004) and the wide application of these measures in determining the conservation status of species (e.g. IUCN, 2001 criteria). To date, the implications of abundance patterns remain poorly understood and have not been widely considered in predicting impacts. Predictions of declines in range size are basically assuming that, on average, loss of distribution area results in a loss of population size of similar or equivalent magnitude. But is this realistic? The climate envelope simply represents the full spectrum of climates encountered within the distribution of a species. Most species are expected to exhibit

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complex variability in abundance within this range because of spatial patterns of climate within their range, topography, biological interactions, biogeographic barriers and disturbance (Brown & Lomolino, 1998). Therefore, in order to make more accurate predictions regarding the impacts of climate change, it is critical that we quantify abundance patterns across the most significant environmental gradients within a given species' distribution and use both distribution area and population size in predictive analyses.

Here, we use empirical data describing the altitudinal abundance pattern of 12 endemic rainforest birds of north-eastern Australia to highlight the potential decoupling of trends in population size and distribution area change with increasing global temperature. This is a novel analysis that extends projections of species response to climate change to the population level. Finally, we use the expected change in the altitude-abundance pattern to recommend an appropriate sampling strategy that will enable explicit assessments of change to total population size in the future – a key criterion in estimating extinction risk.

Materials and methods

Predicted shifts in distribution

Rainforest predominantly occurs across windward slopes in the wet tropics of north-eastern Australia where we would expect temperature to decrease at the saturated adiabatic lapse rate of about 1 °C per 200 m altitude under most conditions. Established lapse rates are supported by field measurements collated from 21 weather stations distributed across the Wet Tropics region. A 1 °C decline in temperature corresponds to an upward shift in altitude of between 142 and 250 m, based on minimum and maximum temperatures, respectively (mean monthly maximum temperature = $-0.004 \text{ m altitude} + 28.587$, $r^2 = 0.562$, $P < 0.001$; mean monthly minimum temperature = $-0.007 \text{ m altitude} + 20.152$, $r^2 = 0.807$, $P < 0.001$). The magnitude of change in temperature from field measurements is essentially equivalent to that expected following a saturated adiabatic lapse rate.

Abundance estimates

Abundance data for rainforest bird fauna were collated from standardized field surveys throughout the region (723 surveys at 362 separate locations, years 1996–2003). Surveys were compiled with the expressed purpose of comprehensively sampling rainforest spatially throughout the region while endeavouring to sample the representative range of available environmental condi-

tions. Consequently, sampling effort varied across the gradient with effort generally greatest at midaltitudes where rainforest is most extensive and least towards the highest peaks where rainforest is much more restricted. Each survey consisted of a 30 min, 150 m transect through the forest using both visual observations and calls to identify species. Five major mountain ranges and associated lowlands were sampled covering much of the latitudinal range within the region (16°15'–19°00'S) including the Spec Uplands, Kirrama Uplands, Atherton Uplands, Bellenden-Ker/Bartle-Frere Range, Carbine Uplands and Cairns-Cardwell and Mossman Lowlands (see Williams *et al.* (1996) for subregional boundaries).

Our objective was to document broad patterns of relative abundance of individual species across the altitudinal gradient. Differences in detectability have the potential to confound estimates of relative abundance (Rosenstock *et al.*, 2002) and, as such, specific efforts were made to address this issue. First, we adopted standardized sampling protocols to reduce the influence of confounding environmental factors. Surveys were conducted between 06:00 and 08:30 hours to coincide with peak calling activity and only employed on clear mornings under low wind conditions where detection probability was high, thereby allowing best possible estimates of abundance to be made. Second, we ensured that regional and altitudinal sampling of mountain ranges was interspersed through time. The vast majority of surveys were undertaken in summer with no seasonal bias in altitudinal sampling. Third, all surveys were undertaken within rainforest habitat. More than 90% of detections during surveys were auditory and, as such, detections were expected to be robust to minor variation in vegetation structure and density across the altitudinal gradient.

Population size and distribution area change

The analyses presented here were restricted to 12 regionally endemic species of bird effectively confined to rainforest in the Wet Tropics biogeographic region. The future prognosis of endemic species is of immediate interest as extinction of these species within the region represents an irreplaceable loss of species level diversity. Distribution area was estimated as the available rainforest area within the altitudinal range of a species within the region. Rainforest area was determined for 100 m altitudinal intervals from geographic information system using regional vegetation mapping based on Tracey & Webb (1975) and subsequently updated by the Wet Tropics Management Authority and an 80 m resolution digital elevation model. Altitudinal range was determined from the

abundance dataset with species' presence collated into corresponding 100 m altitudinal intervals. An index of total population size was derived by multiplying the mean abundance of a species across survey transects located within each 100 m altitudinal interval by the total available area of rainforest (km²) within corresponding altitudinal intervals and summing values across the entire gradient. The altitudinal range and estimates of mean abundance at altitudinal intervals within the range were then shifted upward by increments of 200 m to simulate successive increases of 1 °C in temperature (e.g. Grey-headed Robin, Fig. 1). Distribution area and the index of population size were then recalculated for scenarios ranging from 0 m shift (current, assuming no temperature increase) to 1400 m shift (i.e. +7 °C). In doing so, we assume that: (1) species will respond to increasing temperature by shifting along the altitudinal gradient; and (2) the integrity of the altitudinal abundance pattern will be retained as a species shifts along the altitudinal gradient. Change in the index of total population size was presented as a proportion relative to the current scenario estimate (i.e. 0 m shift) for each species.

Results

The 12 endemic species examined showed a range of associations with the altitudinal gradient. Peak mean abundance of one species was recorded in the lowlands, seven species at midaltitudes and four species in the uplands (Fig. 2). Lower range boundaries were scattered across the gradient with five of the 12 species not recorded below 300 m altitude (Fig. 2). As climate warming proceeds, many of the climate types that support species at high density are expected to shift off extensive areas of rainforest at low and middle altitudes onto limited areas of rainforest distributed across mountaintops within the region (e.g. Grey-headed Robin, Fig. 1).

We estimated relative change in population size and distribution area in response to altitudinal shifts in range for 12 species (Fig. 3). The relationship is linear where population size declines in direct proportion to distribution area and curvilinear where population size declines more rapidly or more slowly than distribution area with increasing temperature. The total population size of nine out of 12 endemic bird species is predicted to decline with increasing temperature at a faster rate

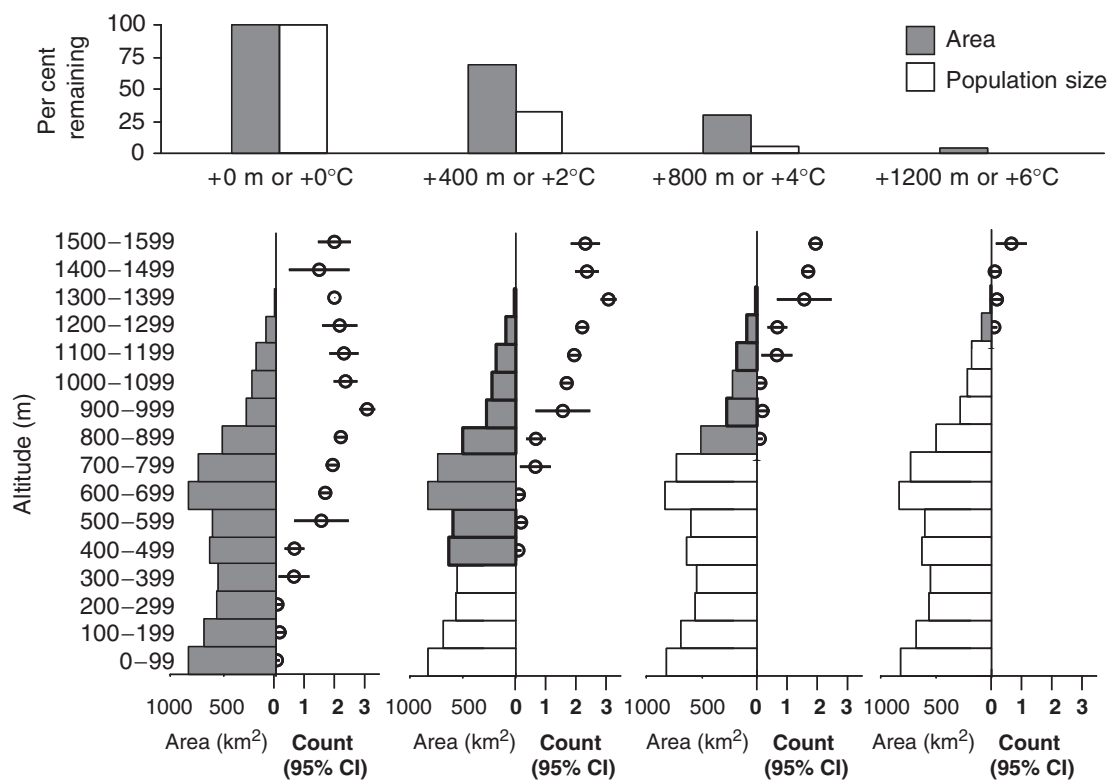


Fig. 1 Diagrammatic representation of altitudinal shifts in the abundance pattern of the Grey-headed Robin (*Heteromyias albispectularis*) with increasing temperature against a breakdown of available rainforest area across the altitudinal gradient; 1 °C equates to approximately 200 m upward shift in altitude. Abundance estimates were multiplied by the corresponding area of rainforest at each altitude and summed across the gradient to provide an index of current population size.

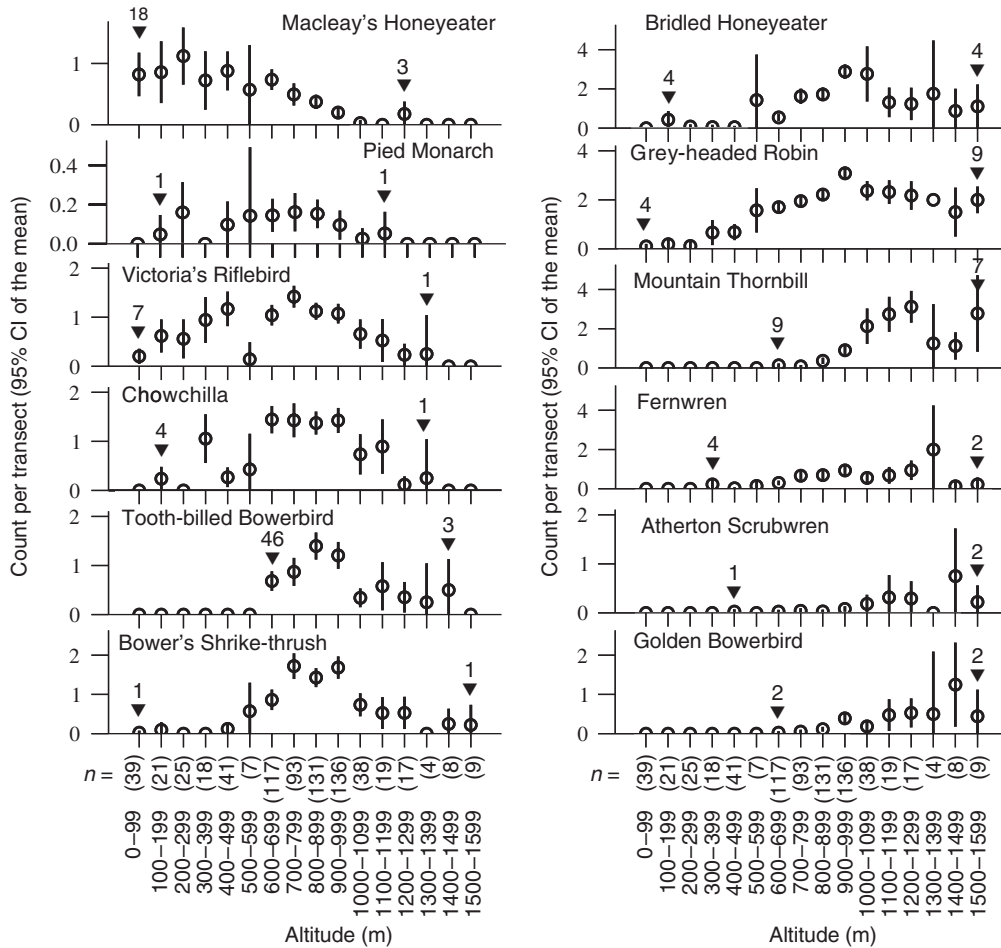


Fig. 2 Altitudinal abundance patterns for 12 endemic rainforest birds of north-eastern Australia. Estimated position of upper and lower range boundaries are represented by inverted triangles with the number of surveys a species was recorded present at the range boundary also indicated.

than their distribution area (Fig. 3). Population size is predicted to decline at an equivalent rate to distribution area for two species and more slowly for one species. Consequently, the extent of change in population size with increasing temperature is expected to be highly variable between species despite a similar reduction in distribution area (Fig. 3). A reduction in distribution to 75% of current area corresponded to between 91% and 38% of population size remaining and distribution area reduced to 50% corresponded to between 62% and 8% of population size remaining. Population size change relative to distribution area was greatest for those species that occurred at highest density in the middle of the gradient. Macleay's Honeyeater *Xanthotis macleayana*, a lowland endemic, was the only species to show a positive bias with distribution area declining more rapidly than population size. Regardless of species, the decoupling of population size and distribution area change became negligible for extreme scenarios where

both population size and distribution area were severely reduced.

Discussion

Climate warming and differential change in distribution area and population size

'An understanding of range reduction and accompanying decline in numbers is vital for the preservation of biodiversity, but this understanding does not yet exist' (Channell & Lomolino, 2000). In the context of climate warming impacts, we show that a documented decline in distribution area will not necessarily be instructive of the extent of change in total population size. Declines in population size can occur at a much faster rate than that suggested by distribution area alone. In fact, nine out of 12 endemic birds examined here are expected to suffer disproportionately large losses in population size

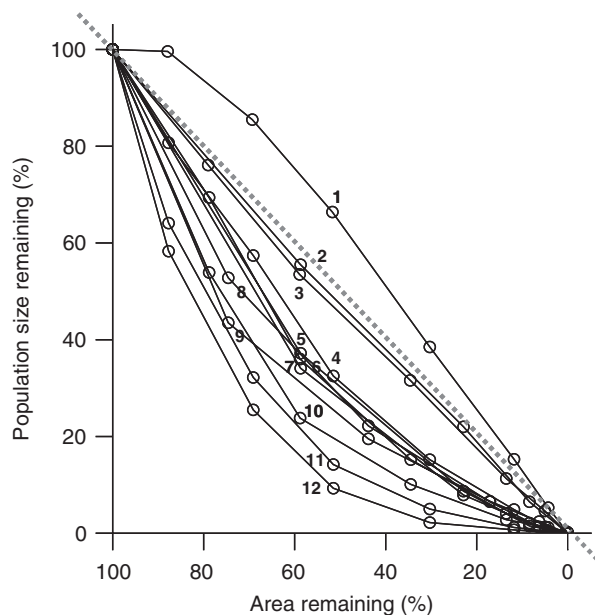


Fig. 3 Projected change in the relative population size and distribution area of rainforest birds following altitudinal range shifts associated with climate warming. The relationship is linear where population size declines in direct proportion to distribution area (i.e. dotted grey line) and curvilinear where population size declines more rapidly or more slowly than distribution area with increasing temperature. Number labels refer to individual species of rainforest birds: (1) Macleay's Honeyeater *Xanthotis macleayana*; (2) Tooth-billed Bowerbird *Scenopoeetes dentirostris*; (3) Pied Monarch *Arses kaupi*; (4) Victoria's Riflebird *Ptiloris victoriae*; (5) Golden Bowerbird *Prionodura newtoniana*; (6) Chowchilla *Orthonyx spaldingii*; (7) Mountain Thornbill *Acanthiza katherina*; (8) Fernwren *Oreoscopus gutturalis*; (9) Atherton Scrubwren *Sericornis kerri*; (10) Bridled Honeyeater *Lichenostomus frenatus*; (11) Grey-headed Robin *Heteromyias albispecularis*; (12) Bower's Shrike-thrush *Colluricincla boweri*.

following an initial reduction in distribution area. These analyses suggest that findings from previous distribution-based studies (Williams *et al.*, 2003; Thomas *et al.*, 2004a; Hilbert *et al.*, 2004) may themselves be conservative, further reinforcing the notion that climate change is a major threatening process for rainforest birds of north-eastern Australia.

That a severely reduced range should correspond to a depleted population size is not of interest in itself. What we want to know about is the trajectory of change in range and numbers toward extinction (Soulé, 1983). Individualistic responses predicted for species here suggests that the detail of the population size–distribution area relationship is likely to be important for estimating extinction risk. A decline in distribution to 75% of current area translates to between 91% and 38% of the population size remaining. A more severe reduction

in distribution area to 50% results in a projected reduction of population between 62% and 8% of current size. Documenting differential change in population size between species will be crucial in identifying species at immediate risk of extinction and understanding processes of change affecting future survival.

In general, we would consider endemic species restricted to mountain peaks within the region to be at greatest risk from impacts arising from climate warming (Williams *et al.*, 2003; Hilbert *et al.*, 2004). Our finding that species occurring at highest density in the middle of the gradient, not upper end, are likely to suffer most from a disproportionate decline in population size is unexpected. In our analysis, the deviation from the expected pattern is attributable to the 'hump shaped' distribution of rainforest area across the gradient. For midaltitudinal species, then, initial warming results in the displacement of climatic conditions that support species at high density off extensive areas of rainforest at middle altitudes and onto limited areas of rainforest scattered across mountaintops within the region. While our results do not consider the timing of extinction risk, for mountaintop species the probable loss of distribution area remains immediate and absolute, we conclude that the generalized notion that species occurring in mountaintop areas will be the focus of negative climate change impacts is overly simplistic. Complex topography and localized patterns of habitat occurrence dictate that, in practice, the 'cone shaped' model (Peterson, 2003) of decreasing habitat area with increasing altitude is not always applicable (e.g. Gottfried *et al.*, 1999), and that the interplay between both the altitude–rainforest area pattern and the altitude–abundance pattern will be important in predicting population impacts for montane species.

Many gaps remain in our understanding of how population size will change as a consequence of global warming. We illustrate the potential for the decoupling of trends in population size and distribution area to result in complex, individualistic responses to climate warming. In turn, this is expected to further contribute to previously identified sources of uncertainty associated with predictions of extinction risk (Thuiller *et al.*, 2004; Thomas *et al.*, 2004b). Some of the most important uncertainties that currently limit our ability to predict change in population size using our model are considered herein.

Factors contributing to uncertainty in predictive models

Predicted range shifts in relation to a changing climate imply that temperature is the primary, over-riding mechanism currently limiting the abundance and distribution of species. The capacity for physical change in

climate to alter species' distributions and result in localized extinctions is evidenced by numerous studies documenting range shifts of species along climatic gradients (Grabherr *et al.*, 1994; Parmesan, 1996; Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Hill *et al.*, 2002; Konvicka *et al.*, 2003; Brommer, 2004; see also Archaux, 2004) and population fluctuations (McLaughlin *et al.*, 2002) in association with contemporary climate change. The literature suggests a pervasive climate-related response with broad congruence in change observed across a diverse taxonomic and ecological range of species. We recognize, however, that other physical factors such as rainfall patterns (Williams, 2003) and basal height of cloud inundation (Pounds *et al.*, 1999), as well as disturbance (Warren *et al.*, 2001; Hilbert *et al.*, 2004) and interactions with other species (Diamond, 1973; Remsen & Graves, 1995; Brown & Lomolino, 1998) may also limit the abundance and distribution of species. Each of these mechanisms along with evolutionary adaptation (Harte *et al.*, 2004) has the potential to alter the predicted impacts of climate warming on the altitude-abundance pattern of species.

Further, it is also conceivable that different processes could be limiting distribution and abundance at respective ends of the climatic gradient (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Brommer, 2004). If for example, as suggested by Thomas & Lennon (1999), 'cool margins of species might be more immediately responsive than warm margins to the direct effects of thermal variation,' we would expect the abundance pattern to become skewed or stretched. Similarly, under stressful conditions, the overall abundance pattern may be depressed or otherwise take on some different, unanticipated form. Unfortunately, at present, a lack of suitable abundance data from long-term monitoring programmes impedes our understanding of change in patterns of spatial abundance within the distribution of species.

In our analyses, the estimated position of altitudinal range boundaries is used to derive an index of distribution area. For our purposes, we defined the position of range boundaries by the lowest and highest documented presence of a species within 100 m altitudinal intervals. The obvious caveat of this approach is that, in practice, one or a few individuals only are needed to extend the altitudinal range of a species and, thereby inflate the estimate of distribution area. The population size index is relatively unaffected as low estimates of abundance effectively down-weight the contribution of additional habitat area at range boundaries. Uncertainty in range boundary estimates are greatest where limits of occurrence are proceeded by a tail of decreasing abundance and most problematic at lower range boundaries where the extent of rain-

forest area within 100 m altitudinal intervals is comparatively large. Although agreement has yet to be reached on the expected shape of species' response curves to an environmental gradient (Austin, 2002), strong altitudinal patterns of abundance do not appear unique to rainforest birds and decreasing abundance at range boundaries has also been documented for other taxa within the region (i.e. arboreal mammals, Trenerry (1993) and Kanowski *et al.* (2001); microhylid frogs, Shoo & Williams (2004)).

Under climate warming, climatic space currently not available in the region will be created at the lowest altitudes. The majority of species included in our analysis have montane distributions and we may infer that the lower range boundary along the climatic gradient represents the extent of 'conditions in which a species (normally) shows a positive demographic balance (rarely the absolute physical limits of a species, but the set of conditions under which it survives in at least some multi-species communities)' (Thomas *et al.*, 2004a). For at least one species (*X. macleayana*), however, the lower boundary is constrained by an imposed barrier (i.e. sea level) and the potential for such a species to take advantage of additional climatic habitat is unclear. While no equivalent climatic space is currently available in the region to measure the response of this species, there is a real potential for such lowland species to expand their range and consequently benefit, at least initially, from increased temperatures, thereby rendering our predictions overly pessimistic.

The spatial extent of upland forest types in the region is predicted to shrink significantly under expected climate change scenarios (Hilbert *et al.*, 2001). Consequently, in the long term, predictions of population change based on the current distribution of rainforest are likely to be conservative. Not only will species shift off the more extensive areas of forest at low altitudes but will struggle to capitalize on habitats that are themselves expected to become increasingly scarce, physiologically stressed and more fragmented under climate warming. In the near future, most rainforest types are expected to experience climates that are more appropriate to some other rainforest type (Hilbert *et al.*, 2001). While the propensity for ecological change is high, the pace at which vegetation change in the region is expected to proceed is currently unknown.

Finally, the analysis based on species' abundance data pooled across mountain ranges does not account for potential spatial heterogeneity in temperature conditions at equivalent altitudes or within-region variability of future warming. The obvious implication of spatial heterogeneity in temperature, if present, is that it would diminish the capacity of altitude as a

surrogate variable to capture small differences in temperature variability throughout the region. Considerable potential exists, therefore, to refine predictive models and increase the capacity of sampling strategies to detect and also predict change by explicitly accommodating spatial variability in climatic conditions.

In the absence of detailed climate information, altitudinal gradients should be selected to encompass secondary gradients such as latitude over which temperature is expected to vary most. The benefits of comprehensive, representative sampling of regional variability in temperature conditions are threefold. Firstly, the sampling design would allow change to be examined along individual altitudinal gradients, thereby removing variability resulting from small-scale differences in temperature across the region. Secondly, the sampling design would provide necessary data in the future to document and account for flow on impacts of heterogeneous warming in the region, should it occur. Thirdly, as high-resolution information becomes available, abundance data could be combined with regional climate models to predict differential change among isolated populations resulting from spatial heterogeneity in climate warming.

Implications

Previous attempts to estimate extinction risk have employed modelled projections of 'climate envelopes' to predict the relative size of potential species' distributions under climate change. Typically, extinction risk has then been evaluated in terms of established threat criteria (i.e. IUCN Red Data Book criteria) or, in the case of Thomas *et al.* (2004a), using species-area relationships. Here, we have used a novel approach to show that upslope movements will translate into previously unanticipated change in the population size of species. Change in the spatial extent of specific climates that support high densities of a species are likely to play a decisive role in ameliorating or exacerbating biological impacts of projected climate change. We suggest that critical climate change impacts may be underestimated or proceed unnoticed if, in the pursuit of monitoring range boundaries, we neglect to take notice of the populations that reside within them. There is an urgent need to not only track changes in location and extent of distribution area but also spatial patterns in the relative density of species within current and future distributions.

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