Austral Ecology (2006) **31**, 22–29 doi:10.1111/j.1442-9993.2006.01539.x

Detecting climate change induced range shifts: Where and how should we be looking?

LUKE P. SHOO,[1,3]* STEPHEN E. WILLIAMS[2,3] AND JEAN-MARC HERO[1]
[1]*School of Environmental and Applied Sciences, Griffith University Gold Coast, PMB 50 Gold Coast Mail Centre, Bundall, QLD 9726, Australia (Email: L.Shoo@griffith.edu.au),* [2]*School of Tropical Biology, James Cook University of North Queensland, Townsville, Queensland, Australia and* [3]*Cooperative Research Centre for Tropical Rainforest Ecology and Management Cairns, Queensland, Australia*

Abstract: Global climate warming is expected to cause systematic shifts in the distribution of species and consequently increase extinction risk. Conservation managers must be able to detect, measure and accurately predict range shifts in order to mitigate impacts on biodiversity. However, important responses to climate change may go unnoticed or be dismissed if we fail to collect sufficient baseline data and apply the most sensitive analytical tests. Here we use randomizations of a contemporary data set on rainforest birds of north-eastern Australia to quantify the sensitivity of three measures for assessing range shifts along altitudinal gradients. We find that smaller range shifts are detectable by analysing change in the mean altitude of presence records rather than upper or lower range boundaries. For a moderate survey effort of 96 surveys, measurements of change in the mean altitude of 34 species have the capacity to provide strong inference for a mean altitudinal range shift as small as 40 m across the species assemblage. We also show that range shifts measured at range boundaries can be potentially misleading when differences in sampling effort between contemporary and historical data sets are not taken into account.

Key words: altitudinal gradient, climate change, minimum detectable range shift, rainforest bird, range boundary, statistical power.

INTRODUCTION

Immediate detection of biological responses to contemporary climate change is vital if we are to improve our capacity to predict change and attempt to initiate management strategies in time to counter species loss and mitigate impacts on biodiversity. Upslope and poleward shifts in species' distributions have regularly been cited as evidence of climate-related change (e.g. Parmesan & Yohe 2003; Root *et al.* 2003). To date, however, documentation of upslope shifts has lagged behind that of poleward shifts. This is despite the potential for upslope shifts to mask important poleward shifts (Hill *et al.* 2002) and the immediate threat of climate warming on mountaintop-restricted species (Williams *et al.* 2003; Hilbert *et al.* 2004) that by virtue of their distribution are incapable of migrating latitudinally.

In many instances, evidence for altitudinal range shifts has been derived from a single or small number of permanent sampling plots established at a select position along the climatic gradient. Change within the narrow observation window has then been interpreted, in relation to range shift predictions, by using additional knowledge of the distribution of species along the altitudinal gradient outside the census area. Examples include increased abundance and species richness of premontane birds in a long-term montane census plot (Pounds *et al.* 1999) and increased species richness in summit floras (Grabherr *et al.* 1994). However, these studies assume that change at one point can be 'unambiguously interpreted as range shifts, rather than as merely local density changes, range expansions or contractions' (Parmesan 1996).

For poleward shifts, more comprehensive evidence has come from analyses that have utilized atlas data to broaden coverage of sampling effort across the latitudinal gradient (Thomas & Lennon 1999; Hill *et al.* 2002; Brommer 2004; Hickling *et al.* 2005). Similar attempts to expand the investigation of range shifts across the altitudinal gradient have struck difficulties (Hill *et al.* 2002; Konvicka *et al.* 2003). The course spatial scale of atlas data imposes limits on the detection of trends in vertically diverse grid cells, rendering the method unsuitable for detecting shifts in vertically restricted montane species (Konvicka *et al.* 2003) – the very species that are of greatest concern (Williams *et al.* 2003; Hilbert *et al.* 2004). Further, there is a lack of altitudinal replication of grid squares, which precludes the application of important subsampling techniques to equalize sampling effort between time periods (Hill *et al.* 2002). For these reasons, transects or point counts are likely to be more appropriate for

---

*Corresponding author.

Accepted for publication June 2005.

investigating altitudinal range shifts in response to contemporary climate warming (Archaux 2004).

Research to date has provided valuable first evidence of altitudinal range shifts (Grabherr *et al.* 1994; Pounds *et al.* 1999; Hill *et al.* 2002; Konvicka *et al.* 2003; but see Archaux 2004). However, most analyses have been reliant on the comparison of contemporary data with historical data sets not originally collected with the explicit purpose of investigating range shifts. Therefore, an evaluation of baseline data characteristics most likely to promote the detection of range shifts would be both timely and valuable for informing the design of future monitoring programmes. Here we use randomizations of a high-resolution data set on rainforest birds of north-eastern Australia, compiled from recent transect surveys, to evaluate the potential for efficient and reliable detection of altitudinal range shifts. Specifically, we determine and compare the effect of sampling effort on the magnitude of minimum detectable range shifts across a species assemblage for three measures of altitudinal position (lower and upper range boundaries: Thomas & Lennon 1999; Hill *et al.* 2002; Brommer 2004; Hickling *et al.* 2005; mean position of presence records: Konvicka *et al.* 2003; Archaux 2004). Further, we examine the effect of differential sampling effort on estimates of range shift. Knowing what to measure and how much survey effort is required will greatly improve our capacity to achieve sufficiently strong inference so that important responses to climate change will not go unnoticed in the future.

METHODS

The data set

Presence data for rainforest bird fauna were collated from standardized abundance surveys along altitudinal gradients throughout the Wet Tropics biogeographical region of north-eastern Queensland, Australia (680 surveys at 397 separate locations, during 2000–2004). Each survey consisted of a 30-min, 150-m transect through rainforest using both visual observations and calls to identify species. Surveys were conducted between 06.00 hours and 08.30 hours to coincide with peak calling activity and only carried out on clear mornings under low wind conditions where detection probability was high. Ten major mountain ranges and associated lowlands were sampled covering much of the latitudinal range within the region (15°40′–19°00′S), including the Spec Uplands, Kirrama Uplands, Hinchinbrook Island, Atherton Uplands, Bellenden-Ker/Bartle-Frere Range, Black Mountain Corridor, Carbine Uplands, Windsor Uplands, Thornton Uplands, Mount Finnegan Uplands and Townsville Lowlands, Cairns-Cardwell Lowlands, Mossman Lowlands, Thornton Lowlands and Bloomfield-Helenvale Lowlands (see Williams *et al.* 1996 for subregional boundaries).

Measuring change in altitudinal position of the assemblage

Three measures for determining range shifts along the altitudinal gradient were considered: (i) the lower position of presence records; (ii) the upper position of presence records (i.e. range boundaries: Thomas & Lennon 1999; Hill *et al.* 2002; Brommer 2004; Hickling *et al.* 2005); and (iii) the mean position of presence records (Konvicka *et al.* 2003; Archaux 2004). Infrequently recorded species are unlikely to be good candidates for investigating systematic range shifts as the addition of a small number of records has the potential to alter estimated position along the gradient drastically. Similarly, range shift measures are unlikely to provide meaningful information where change in the measure is already constrained by the upper or lower limits of the gradient. For example, species currently occupying the highest mountaintops in the region are incapable of colonizing higher altitudes and, as a consequence, the upper range boundary does not allow for a test of upslope range shifts. We address both limitations by adopting a two-tier selection process to determine which species to include in the analysis for each of the three measures of altitudinal position. First, for low recording frequency we excluded those species that were not recorded on each of the random subsamples of the complete data set (see below). Second, species with upper or lower range boundaries that fell within 300 m of either end of the gradient were excluded from analysis for the respective measures. As a result, 3, 12 and 34 species were available for analyses of lower, upper and mean position of presence records, respectively.

Effect of sampling effort and measure choice on minimum detectable range shifts

Range shift data are amenable to analysis following a paired-sample *t*-test design with matched pairs arising from the desire to quantify temporal change in the estimated position of individual species between two time periods. The analysis is therefore concerned with temporal differences in the estimated position of species along the gradient (d) and can be calculated directly by subtracting the estimated position of a species at one time period from that of another. If the null hypothesis of no difference is correct, we would expect multiple values of d derived from the pool of available species to be distributed about a mean of zero (i.e. H_0:

$\bar{d} = 0$). The likelihood of rejecting the null hypothesis is then dependent on both the magnitude of the observed mean difference ($\bar{d}$) and the standard error of $\bar{d}$ according to the equation (Zar 1996):

$$t = \frac{\bar{d}}{s_{\bar{d}}} \quad (1)$$

For the purpose of the study, we ask how small a difference in $\bar{d}$ (hereafter referred to as δ) can be detected using a paired-sample *t*-test with $1 - \beta$ power, at an α level of significance, using a specified number of species, *n*. The minimum detectable range shift across a species assemblage (δ) using a two-tailed paired-sample *t*-test can be derived from the following equation (Zar 1996):

$$\delta = \sqrt{\frac{s_d^2}{n}}\left(t_{\alpha(2),v} + t_{\beta(1),v}\right) \quad (2)$$

where s_d^2 is the variance of sample values of *d*, *n* is the number of species and $v = n-1$. For all tests, an α level of 0.05 and β of 0.1 (i.e. difference between $\bar{d}$ and zero that is detectable 90% of the time) was adopted.

We simulated time series comparisons of range shifts using randomized subsamples of the complete data set. This allowed us to quantify variability in our field data and estimate change in minimum detectable range shift with increasing sampling effort. In order to retain a broad coverage of sampling across the gradient spanning 0–1600-m altitude, one to six surveys were randomly selected from each of consecutive 100-m altitudinal intervals along the gradient, resulting in total sampling effort ranging from 16 to 96 surveys. Ten paired random subsamples of the complete data set (simulated Time 1 and 2) were extracted in this manner and the position of lower, upper and mean presence records determined for each species with successive increases in sampling effort. Differences in the estimated position of individual species (*d*) between simulated time periods were determined (e.g. see Table 1) and the minimum detectable range shift across a species assemblage (δ) calculated for each measure of altitudinal position and for intervals of sampling effort.

We expect variance of *d* and subsequently the minimum detectable range shift across a species assemblage (δ) to decline as more species are included in the analysis. As the number of species available for analysis at lower and upper range boundaries was low, 3 and 12 species, respectively, we performed analyses of the mean position of presence records on subsets of species common to range boundary analyses. This allowed us to control for the effect of number of species when making comparisons between estimates of minimum detectable range shift (δ) resulting from analyses of the mean position of presence records and range boundaries. Estimates of minimum detectable range shift (δ) were also derived for analyses of the mean position of presence records utilizing the full 34 available species.

Effect of uneven sampling effort on range shift estimates

We also used paired random subsamples of the complete data set to simulate time series comparisons with uneven sampling effort between time periods. Specifically, we examined the potential for disproportionate sampling effort to result in a biased estimate of mean range shift across a species assemblage ($\bar{d}$). Instead of increasing sampling effort in both simulated time periods concurrently, then, sampling effort in simulated Time 2 was fixed at 96 surveys (i.e. six surveys per 100-m altitude) and the sampling effort in simulated Time 1 varied between 16 and 96 surveys (i.e. one to six surveys per 100-m altitude). This allowed us to determine the sensitivity of range shift estimates to the uneven distribution of sampling effort in time series comparisons.

RESULTS

Effect of sampling effort and measure choice on minimum detectable range shifts

For all three measures, minimum detectable range shift across a species assemblage declined with increasing sampling effort (Fig. 1a,b). Controlling for differences in the number of species between analyses, mean position of presence records enabled lower minimum detectable range shifts than either lower or upper range boundaries at equivalent sample sizes (Fig. 1a,b). A larger pool of species was available for analysis using the mean position of presence records than either lower or upper range boundaries. An analysis of the mean position of presence records using the full 34 species further reduced the minimum detectable range shift, ranging from 76 to 124 m at a sampling effort of 16 surveys to 20–39 m at a sampling effort of 96 surveys (Fig. 2).

Effect of uneven sampling effort on range shift estimates

Uneven sampling effort between time periods resulted in a systematic bias in range shift estimates at lower and upper range boundaries (Fig. 3a,b). A disproportionately large sampling effort in the second time period resulted in the false impression that range boundaries had extended outwards. The sampling artefact diminished as the difference in sampling effort

Table 1. Mean altitude of presence records (Alt) and number of recorded presences (p) for 34 species derived from a paired random subsample (simulated Time 1 and Time 2, 96 surveys or six surveys per 100-m altitude) of the complete data set

	Simulated time 1		Simulated time 2		
Species	p_1	Alt_1	p_2	Alt_2	d
Brown Cuckoo-Dove (*Macropygia amboinensis*)	42	799	37	765	−34
Wompoo Fruit-Dove (*Ptilinopus magnificus*)[†]	29	542	33	557	16
Superb Fruit-Dove (*Ptilinopus superbus*)	36	661	41	674	13
Sulphur-crested Cockatoo (*Cacatua galerita*)	44	611	48	599	−12
White-throated Treecreeper (*Cormobates leucophaeus*)	38	972	48	957	−15
Fernwren (*Orescopus gutturalis*)[‡]	30	987	33	964	−23
Yellow-throated Scrubwren (*Sericornis citreogularis*)	28	984	26	967	−17
Large-billed Scrubwren (*Sericornis magnirostris*)	53	752	61	790	38
Brown Gerygone (*Gerygone mouki*)[†]	37	613	31	615	2
Mountain Thornbill (*Acanthiza katherina*)[‡,§]	38	1180	42	1176	−4
Macleay's Honeyeater (*Xanthotis macleayana*)[†‡]	29	432	28	411	−20
Lewin's Honeyeater (*Meliphaga lewinii*)[†,§]	36	854	32	866	12
Yellow-spotted Honeyeater (*Meliphaga notata*)[†]	35	295	36	295	0
Graceful Honeyeater (*Meliphaga gracilis*)[†]	31	273	34	307	33
Bridled Honeyeater (*Lichenostomus frenatus*)[‡]	34	1065	34	1107	42
Pale-yellow Robin (*Tregellasia capito*)[†]	25	527	23	498	−29
Grey-headed Robin (*Heteromyias albispecularis*)[‡]	66	959	69	946	−13
Chowchilla (*Orthonyx spaldingii*)[‡]	42	763	41	765	2
Eastern Whipbird (*Psophodes olivaceus*)	51	934	49	936	2
Golden Whistler (*Pachcephala pectoralis*)	46	914	38	963	49
Little Shrike-Thrush (*Colluricincla megarhyncha*)[†]	36	312	37	363	51
Bower's Shrike-Thrush (*Colluricincla boweri*)[‡]	30	919	34	880	−39
Yellow-breasted Boatbill (*Machaerirhynchus flaviventer*)[†]	18	437	20	443	6
Black-faced Monarch (*Monarcha melanopsis*)	21	725	24	786	60
Spectacled Monarch (*Monarcha trivirgatus*)[†]	42	502	49	518	16
Rufous Fantail (*Rhipidura rufifrons*)	19	674	21	752	78
Grey Fantail (*Rhipidura fuliginosa*)	37	872	38	851	−22
Varied Triller (*Lalage leucomela*)[†]	13	367	16	311	−56
Black Butcherbird (*Cracticus quoyi*)[†]	11	321	18	347	25
Pied Currawong (*Strepera graculina*)	26	1112	25	1121	9
Victoria's Riflebird (*Ptiloris victoriae*)[‡]	38	577	42	593	16
Spotted Catbird (*Alluroedus melanotis*)	45	743	51	749	6
Tooth-billed Bowerbird (*Scenopoeetes dentirostris*)[‡,§]	20	990	24	928	−62
Mistletoebird (*Dicaeum hirundinaceum*)	19	630	25	560	−70

A sample estimate of minimum detectable range shift (δ) calculated from differences in the measured altitudinal position of species (d) is provided. Taxonomy and common names follow Christidis and Boles (1994). Number of species (n) = 34, $\nu = n - 1 = 33$, $\alpha(2)$ level of 0.05 and $\beta(1)$ of 0.1.Minimum detectable range shift across species assemblage (δ) = 19.6 m. [†]Species included in upper range boundary analysis; [‡]Regionally endemic species; [§]Species included in lower range boundary analysis.

between the two simulated time periods approached zero. The same systematic bias was not apparent for range shift estimates derived from the mean position of presence records (Fig. 3a,b) where increased sampling effort simply reduced the variability between range shift estimates.

DISCUSSION

Detecting climate change induced range shifts along the altitudinal gradient

While it seems intuitive that edges of ranges will be the most sensitive areas to monitor range shifts, to date, there has been no evaluation as to whether range boundaries provide the most effective 'signal' with which to identify systematic change. Here we have used randomizations of a high-resolution data set to show that the mean position of presence records consistently allows for a smaller detectable range shift than do range boundary estimates (Fig. 1a,b). Extensions or contractions of range boundaries are dependent on fewer individuals than change measured at the mean where the entire pool of available records is utilized. Archaux (2004) reasoned previously that change in species at the mean altitude was more indicative of a population response than change measured at range boundaries. It is the capacity of the mean to draw upon information from throughout the distribution of

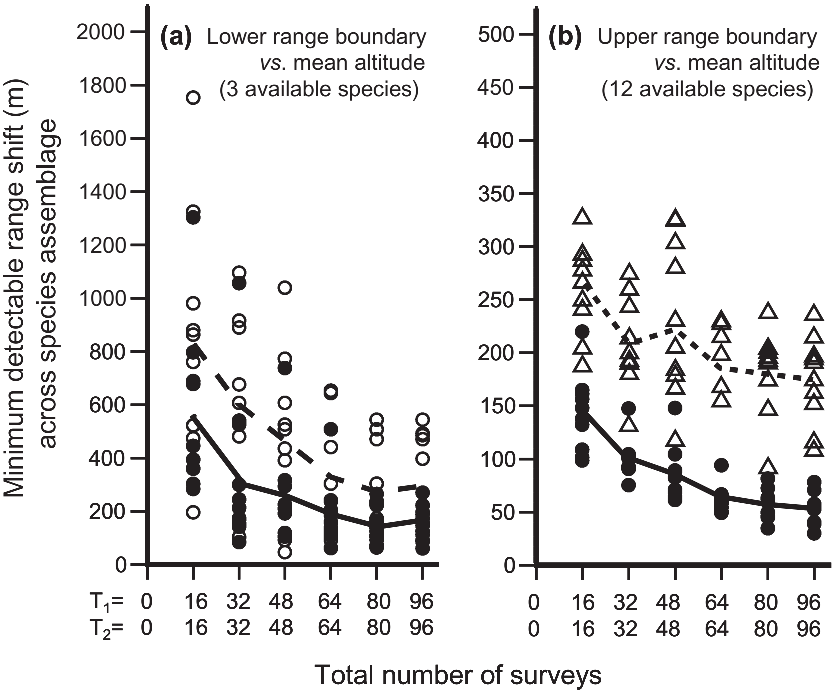

Fig. 1. Effect of measure choice on the minimum detectable range shift across a species assemblage. Range shifts measured at the mean altitude of presence records (closed circles, solid line) were compared with range shifts measured at (a) upper range boundaries (open circles, broken line) and (b) lower range boundaries (open triangles, dotted line) using subsets of species common to both measures. Estimates of minimum detectable range shift were derived from 10 paired random subsamples of the complete data set. Sampling effort was adjusted simultaneously for both simulated Time 1 (T_1) and simulated Time 2 (T_2) and varied between 16 and 96 surveys along the altitudinal gradient. Lines connect mean estimates of minimum detectable range shift at intervals of sampling effort. Note that the scale of minimum detectable range shift on the *y*-axis varies between figures.

a species that is likely responsible for the lower random variability between simulated time period estimates and consequently the more sensitive detection limit of the measure.

Annual mean temperature for Queensland is projected to increase by 0.3–2.0°C by the year 2030 relative to 1990, with 0.8–6.0°C of warming possible by 2070 (Walsh *et al.* 2002). Rainforest predominantly occurs across windward slopes in the Wet Tropics where we would expect temperature to decrease at a saturated adiabatic lapse rate of about 1°C per 200-m altitude under most conditions. The combined information suggests that isotherms under warmer predicted climates for 2030 are likely to be 60–400 m higher than in 1990, calibrating to a 15–100-m altitudinal shift per decade. Using randomizations of our data set, measuring change in mean altitude of the full 34 species and a sampling effort of 96 surveys, we demonstrate potential to confidently detect altitudinal range shifts as small as 40 m (Fig. 2). A repeat of 96 surveys in the future, then, is expected to allow detection of predicted range shifts in response to mid-range or greater warming projected within 10 years and minimum range or greater warming projected within 20–25 years. In addition, an extrapolation of the trend in declining minimum range shift with increasing sampling effort suggests that there is further potential to reduce the detection limit by sampling in excess of the 96 surveys.

We also show that, unlike estimates of mean altitude, the position of range boundaries is strongly dependent on sampling effort. Low sampling effort generally corresponds to an underestimate of the actual position of the range boundary and, as a consequence, additional sampling results in an extension of the range boundary. While such difficulties can be overcome by subsampling data to equalize sampling effort between time periods (Hill *et al.* 2002), it is important to note that, to date, such techniques have rarely been applied.

For the purpose of hypothesis testing, the implication of a systematic bias in the estimated shift at range boundaries, as an artefact of unequal sampling effort, is twofold. Upper range boundaries will be seen to be expanding more rapidly than is actually the case (i.e. Type I error) and lower range boundaries will be seen to be stable or even extending despite a true retraction in the position of boundaries (Type II error). These biases could explain, at least in part, the phenomenon reported for European butterflies (Parmesan *et al.*

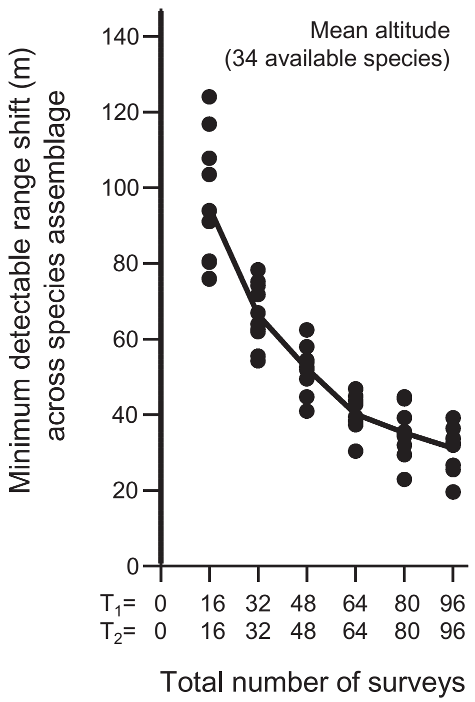

Fig. 2. Relationship between sampling effort and minimum detectable range shift measured at the mean altitude of presence records across an assemblage of 34 species of rainforest birds.

1999), British birds (Thomas & Lennon 1999) and odonates (Hickling *et al.* 2005), and Finnish birds (Brommer 2004) where northern range boundaries have expanded more than southern range boundaries have retracted. Such observations have previously led to the conclusion that 'cool margins of temperate species might be more immediately responsive than warm margins to the direct effects of thermal variation' (Thomas & Lennon 1999). Our results indicate that similar trends can potentially arise from disproportional sampling effort between time periods. Interestingly, in a recent analysis of British butterflies, Hill *et al.* (2002) applied subsampling techniques to equalize sampling effort between time periods and found no evidence for a systematic shift northwards across all British butterflies.

Potential limitations

Data pooled across multiple mountain ranges do not allow for potential spatial heterogeneity in current and future climatic conditions throughout the region. Although the Wet Tropics region is narrow in latitudinal extent (approximately 400 km north–south), a minor latitudinal cline in temperature at equivalent altitudes is possible. Further, differential patterns of

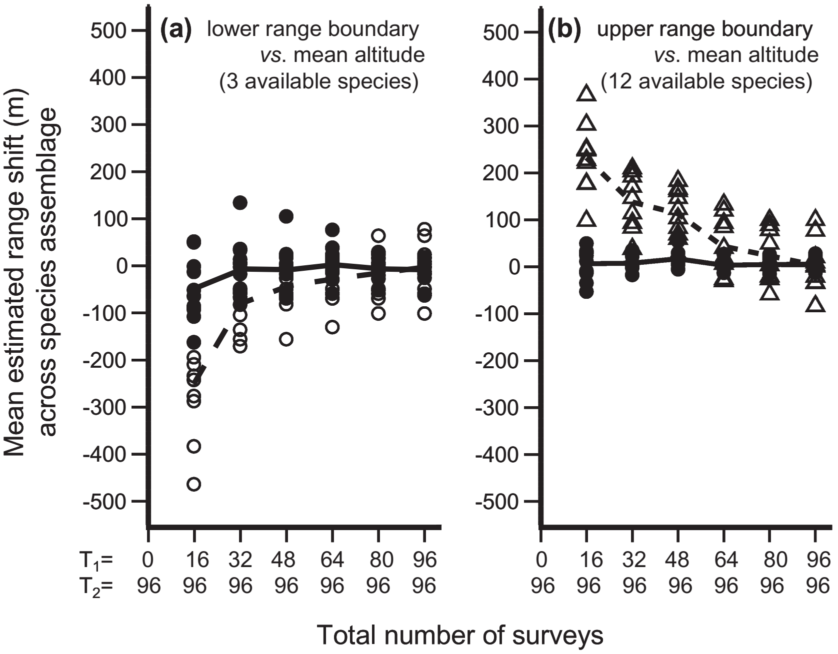

Fig. 3. Effect of measure choice on the mean estimated range shift across a species assemblage when sampling effort is uneven between time periods. Range shifts measured at the mean altitude of presence records (closed circles, solid line) were compared with range shifts measured at (a) upper range boundaries (open circles, broken line) and (b) lower range boundaries (open triangles, dotted line) using subsets of species common to both measures. Estimates of minimum detectable range shift were derived from 10 paired random subsamples of the complete data set. Sampling effort in simulated Time 2 (T_2) was held constant at 96 surveys and sampling effort in simulated Time 1 (T_1) varied between 16 and 96 surveys along the altitudinal gradient. Lines connect mean estimates of range shift at intervals of sampling effort.

cloud inundation between small isolated mountains and main ridges of major mountain ranges (Grubb 1971) or mountain ranges with differing adjacent land use (Lawton *et al.* 2001) may also influence small scale variability in the altitudinal distribution of species throughout the region. Pounds *et al.* (1999) provided correlative evidence for a link between height of cloud inundation and the abundance and altitudinal distribution of premontane birds in highland rainforest of Monteverde, Costa Rica. Considerable opportunity therefore exists to improve the sensitivity of monitoring programmes by stratifying sampling across the region to explicitly account for regional climatic variability.

Our analysis was based on a compilation of 680 surveys from 397 separate locations. The approach was necessary to provide comprehensive coverage of the altitudinal gradient and sufficient sample sizes to allow for randomized subsampling of a large data set. If temporal variability in survey data is substantially lower within locations than among locations at equivalent altitude, our estimates of minimal detectable range shift may be unduly large. A comparison of repeat surveys both within and among locations would therefore be valuable in quantifying variability in survey data as a function of location and would allow us to ascertain properly the relative merit of resurveying the same location between consecutive time periods.

The capacity of a monitoring programme to detect change in species' distributions in response to contemporary warming is dependent not only on the sensitivity of the analysis but also on the rate and magnitude of the range shift response. Although we may predict that, as a consequence of probable warming between 1990 and 2030 (Walsh *et al.* 2002), species will eventually be displaced 60–400 m along the altitudinal gradient, it is not yet known how quickly species will be able to track change in their preferred climatic environment. Konvicka *et al.* (2003) reported a maximum altitudinal range shift of 148 m for Czech butterflies between the periods 1951 to 1980 and 1995 to 2001, but the magnitude of change varied widely between species and altitudinal position even decreased in some cases. While Konvicka *et al.* (2003) found no consistent habitat affiliations that differentiated displaced from stable species, elsewhere rapid responses have predominately been observed in highly mobile generalist species (Warren *et al.* 2001; Hill *et al.* 2002). For the purpose of our analysis, estimates of minimum detectable range shift are dependent on change averaged across multiple species from a range of ecological guilds. Conceivably, therefore, a time lag between shifting climate and distribution in some species will reduce the capacity of the analysis to detect immediately coherent fauna-wide range shifts in response to future warming. Similarly, predicted extinctions related to climate change (Williams *et al.* 2003; Hilbert *et al.* 2004) or declines in the population size (Shoo *et al.* 2005) of species are likely to reduce the number of species available for analysis and consequently the statistical power of future tests.

Implications

Despite accumulating evidence, field biologists have encountered difficulty in convincing other disciplines, policy makers and the general public that important biological impacts of climate change are already apparent (Parmesan & Yohe 2003). Part of the difficulty is that biologists seek evidence of small systematic trends that may become important in the longer term (Parmesan & Yohe 2003). 'Noise' in biological data is inherently problematic for confidently establishing differences where the effect size is small. More recently, in an attempt to establish strong evidence for a coherent 'fingerprint' of climate change impacts, some researches have moved away from single-case examples and pursued meta-analyses, synthesizing correlational evidence from numerous studies (Parmesan & Yohe 2003; Root *et al.* 2003).

We believe that direct evidence from single-study examples of climate-related range shifts across altitudinal gradients could be greatly improved if two key analytical tools were adopted. First, subsampling should be used to equalize sampling effort between contemporary and historical data sets when assessing change at range boundaries. It is crucial that 'real' change is not clouded by artificial trends arising from comparisons between data sets with different underlying properties. Second, the statistical power of range shift analyses to detect change needs to be ascertained and appropriate steps taken to ensure that researchers are collecting the appropriate data and expending enough sampling effort to detect range shifts of the desired magnitude.

Here we provide a methodological framework, using randomizations, for quantifying the detection limit of range shift analyses, and we demonstrate high potential for detecting even small amounts of change in the future. We encourage others to report detection limits in published analyses so that we may work towards establishing more general guidelines for baseline monitoring programmes that may be applicable for different taxa or in other regions.

ACKNOWLEDGEMENTS

The authors thank Emily Bolitho, Samantha Fox and Sara Townsend for valuable assistance in the field. Naomi Doak, Kerry Kriger, Simon Hodgkison and two anonymous referees provided useful comments on earlier drafts of the paper. This research was supported by the Cooperative Research Centre for Tropical Rainforest Ecology and Management, Australian Research Council, Earthwatch Institute, Griffith University and James Cook University.

REFERENCES

Archaux F. (2004) Breeding upwards when climate is becoming warmer: no bird response in the French Alps. *Ibis* **146,** 138–44.

Brommer J. E. (2004) The range margins of northern birds shift polewards. *Ann. Zool. Fennica* **41,** 391–7.

Christidis L. & Boles W. E. (1994) *The Taxonomy and Species of Birds of Australia and its Territories*. Royal Australian Ornithologists Union, Melbourne.

Grabherr G., Gottfried M. & Pauli H. (1994) Climate effects on mountain plants. *Nature* **369,** 448.

Grubb P. J. (1971) Interpretation of the 'Massenerhebung' effect on tropical mountains. *Nature* **229,** 44–5.

Hickling R., Roy D. B., Hill J. K. & Thomas C. D. (2005) A northward shift of range margins in British Odonata. *Global Change Biol.* **11,** 502–6.

Hilbert D., Bradford M., Parker T. & Westcott D. A. (2004) Golden bowerbird (*Prionodura newtonia*) habitat in past, present and future climates: predicted extinction of a vertebrate in tropical highlands due to global warming. *Biol. Conserv.* **116,** 367–77.

Hill J. K., Thomas C. D., Fox R. *et al.* (2002) Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proc. R. Soc. Lond. B.* **269,** 2163–71.

Konvicka M., Maradova M., Benes J., Fric Z. & Kepka P. (2003) Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecol. Biogeogr.* **12,** 403–10.

Lawton R. O., Nair U. S., Pielke R. A. & Welch R. M. (2001) Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science* **294,** 584–7.

Parmesan C. (1996) Climate and species' range. *Nature* **382,** 765–6.

Parmesan C. & Yohe G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421,** 37–42.

Parmesan C., Ryrholm N., Stefanescu C. *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399,** 579–83.

Pounds J. A., Fogden M. P. & Campbell J. H. (1999) Biological response to climate change on a tropical mountain. *Nature* **398,** 611–15.

Root T. L., Price J. T., Hall K. R., Schneider S. H., Rosenzweig C. & Pounds J. A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421,** 57–60.

Shoo L. P., Williams S. E. & Hero J.-M. (2005) Climate warming and the rainforest birds of the Australian Wet Tropics: Using abundance data as a sensitive predictor of change in total population size. *Biol. Conserv.* **125,** 335–43.

Thomas C. D. & Lennon J. J. (1999) Birds extend their ranges northward. *Nature* **399,** 213.

Walsh K., Cai W., Hennessy K. *et al.* (2002) *Climate Change in Queensland under Enhanced Greenhouse Conditions: Final Report, 2002*. CSIRO Atmospheric Research, Victoria.

Warren M. S., Hill J. K., Thomas J. A. *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414,** 65–8.

Williams S. E., Pearson R. G. & Walsh P. J. (1996) Distribution and biodiversity of the terrestrial vertebrates of Australia's Wet Tropics: a review of current knowledge. *Pacific Conserv. Biol.* **2,** 327–62.

Williams S. E., Bolitho E. E. & Fox S. (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Pro. R. Soc. Lond. B.* **270,** 1887–92.

Zar J. H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice-Hall International Limited, London.