# Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change

Jeremy VanDerWal[1]*, Helen T. Murphy[2], Alex S. Kutt[3], Genevieve C. Perkins[3], Brooke L. Bateman[1†], Justin J. Perry[3] and April E. Reside[1,3]

Species are largely predicted to shift poleward as global temperatures increase, with this fingerprint of climate change being already observed across a range of taxonomic groups and, mostly temperate, geographic locations[1-5]. However, the assumption of uni-directional distribution shifts does not account for complex interactions among temperature, precipitation and species-specific tolerances[6], all of which shape the direction and magnitude of changes in a species' climatic niche. We analysed 60 years of past climate change on the Australian continent, assessing the velocity of changes in temperature and precipitation, as well as changes in climatic niche space for 464 Australian birds. We show large magnitude and rapid rates of change in Australian climate over the past 60 years resulting in high-velocity and multi-directional, including equatorial, shifts in suitable climatic space for birds (ranging from 0.1 to 7.6 km yr^{-1}, mean 1.27 km yr^{-1}). Overall, if measured only in terms of poleward distribution shifts, the fingerprint of climate change is underestimated by an average of 26% in temperate regions of the continent and by an average of 95% in tropical regions. We suggest that the velocity of movement required by Australian species to track their climatic niche may be much faster than previously thought and that the interaction between temperature and precipitation changes will result in multi-directional distribution shifts globally.

The future velocity of climate change is expected to be high[7], largely outpacing the potential of species to adapt[8,9], and as such, distributional shifts are considered the most likely species response. There is increasing evidence that changing climates of the past century have already resulted in a globally consistent fingerprint of poleward or rising elevation shifts in species distributions[2–4,6,10]. For example, a recent meta-analysis reported that the distributions of species across a wide range of taxonomic groups and geographic locations have shifted to higher latitudes at a median rate of 1.69 km yr^{-1}, and to higher elevations at a median rate of 1.1 m yr^{-1} (ref. 4). The authors conclude that the velocity of distribution shifts generally matches that expected on the basis of average temperature change in the regions of study, but note the high levels of variation in response within taxonomic groups.

The expectation that species will shift poleward or upward is based on analyses using a relatively certain and easily understood metric of climate change—global temperature—which is broadly correlated with latitude and elevation. Changes in precipitation with global warming are much more difficult to predict and are more likely to be regionally specific[11,12]. In addition, species biological responses to temperature are often better understood than they are for precipitation and therefore precipitation has often been omitted
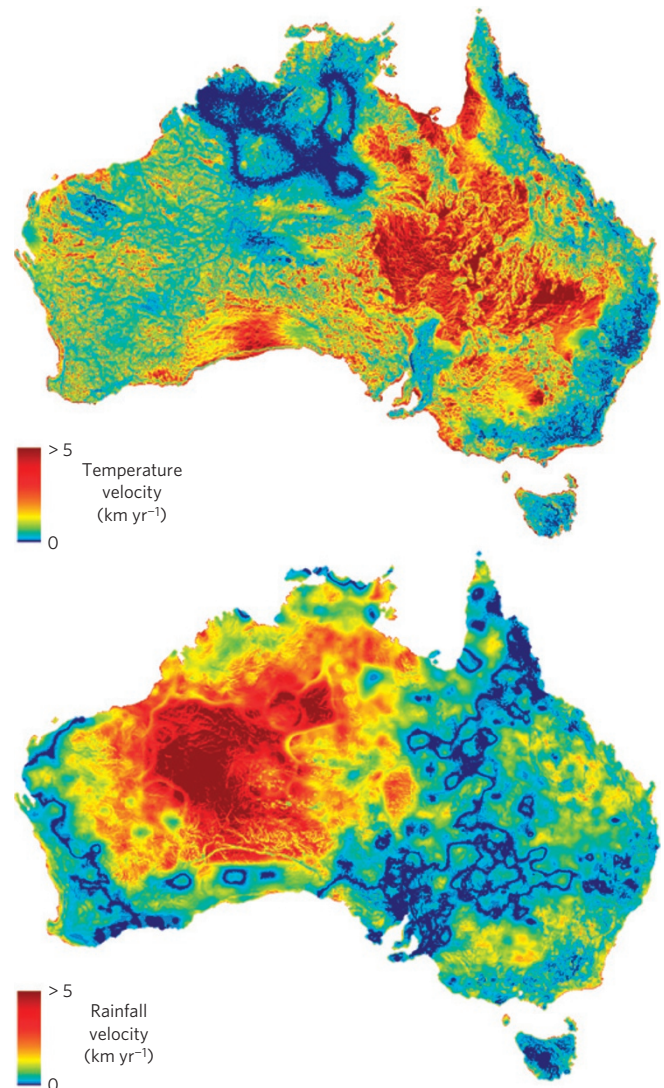
Figure 1 | Velocity of change in temperature and precipitation from 1950 to 2010. Velocity is defined as the instantaneous local speed needed to maintain constant temperature or precipitation (km yr^{-1}).

from analyses that consider the fingerprint of climate change on species distributions[3]. However, complex interactions among

[1]Centre for Tropical Biodiversity and Climate Change, School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia, [2]CSIRO Ecosystem Sciences, PO Box 780, Atherton, Queensland 4883, Australia, [3]CSIRO Ecosystem Sciences, PMB PO, Aitkenvale, Queensland 4814, Australia. [†]Present address: SILVIS Laboratory, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin 53706, USA. *e-mail: jjvanderwal@gmail.com.
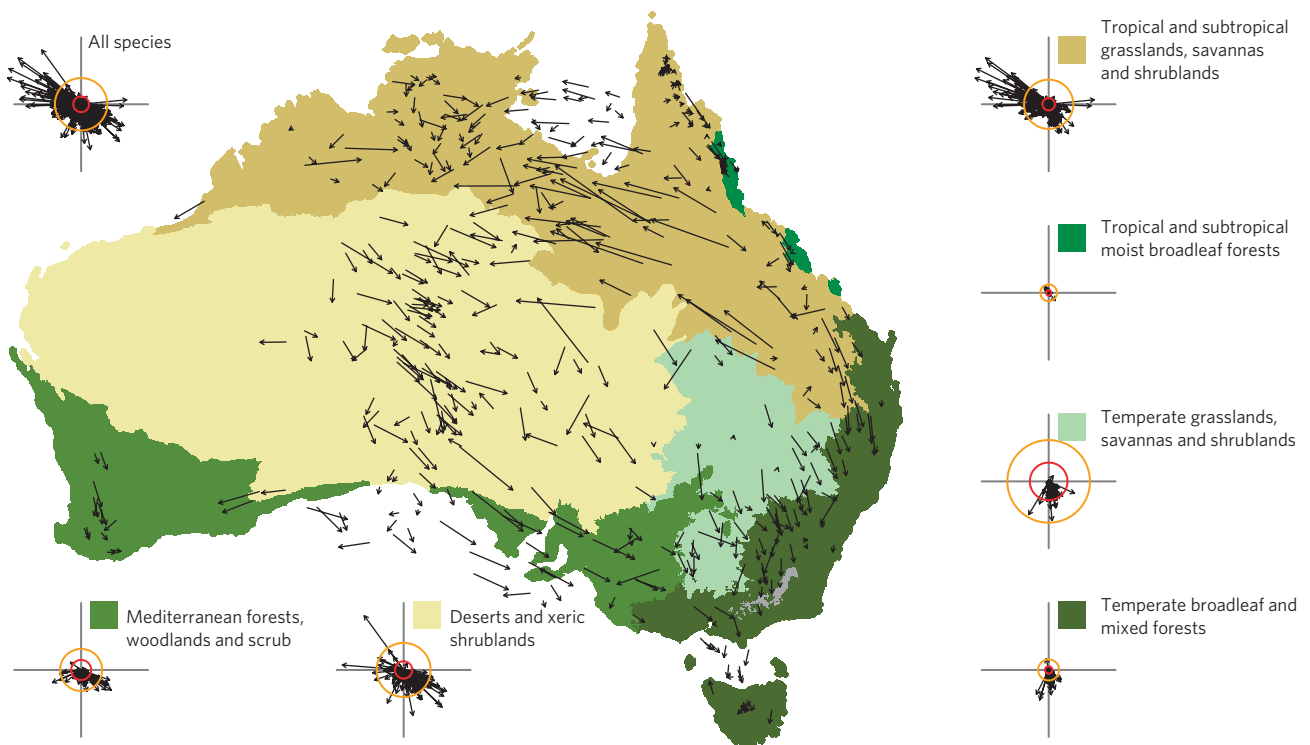
Figure 2 | Change in the distribution of the climatic niche of 464 Australian bird species from 1950 to 2010. The arrows represent the distance (magnitude) and direction of change at the centroid of the climatic niche over the 60-year period. The wind roses summarize the distance and direction of shift for each biome. The coloured rings on each wind rose represent the geometric mean (red) and the mean plus 1 s.d. (orange) for velocity of shift in distribution of climatic niche. The grey axis bars on the wind roses are scaled to represent 400 km in length (from 0, 0 to tip). Note that the apparent gap in the central west region of Australia is not an artefact of poor sampling; rather species that occur in the desert areas of Australia tend to have very broad distributions resulting in their range centre points being located in central Australia.

temperature, precipitation and species-specific tolerances influence both the velocity and direction of distribution shift required to track climate change; exploring the influence of recent climate change may help elucidate these complex interactions. To understand the velocity and direction of changing climate and resulting changes in species-specific suitable climatic space we computed the centroid (two-dimensional midpoint of the distribution) of back-projected monthly climatic niche space from 1950 to 2010 as a function of temperature and precipitation change[13] (Fig. 1) for 464 species of Australian birds. The linear trends in species-specific area and the latitude and longitude of the centroid describe the velocity and direction of distribution change required to keep pace with changing climate over the past 60 years (Fig. 2).

The mean velocities of change for temperature (Fig. 1a) and precipitation (Fig. 1b) over the past 60 years on the Australian continent were 0.77 and 0.67 km yr^{-1}, respectively (Table 1), compared with global mean estimates of 0.42 (0.11–1.46) and 0.22 (0.08–1.90) km yr^{-1} for the period 2000–2100 (ref. 7). These relatively high velocities result, in part, from the shallow climatic gradients and low relief on the Australia continent (Supplementary Fig. S1); in flatter areas even modest changes in temperature result in large geographic displacement[7]. In particular, temperate grasslands and savannas and Mediterranean forests in Australia have both experienced more than three times the velocity of warming predicted for those biomes globally in the future[7] (Table 1). The velocity of future temperature change for the remaining biomes[7] is predicted to be similar to that experienced over the past 60 years (Table 1).

The velocities in geographic shift of species-specific climatic niche space ranged from 0.01 to 7.9 km yr^{-1} with a mean of 1.26 km yr^{-1}. In most biomes species-specific velocities were greater than either temperature or precipitation velocities alone

(Table 1). This is due largely to the ecologically irrelevant scaling of temperature and precipitation as single measures of climate-change velocity for any individual species. Our species-specific velocities take into account the interaction between several temperature and precipitation variables, species-specific sensitivities to those variables and the spatial variability in velocity of those weather variables across a species geographic range (see Methods), and thus provide a more complete picture of the likely fingerprint of climate change. Often, the combined effect of the spatial variability in velocity of several climatic variables exceeds the velocity of temperature or precipitation alone, resulting in species-specific velocities in climatic niche space that are higher than expected on the basis of a single climatic variable.

Species with geographic ranges adjacent to the east coast of Australia have experienced the anticipated net poleward shift in climatically suitable space towards the southeast (Fig. 2), apparently shifting away from increasing temperatures (Fig. 1a). However, shifts in climatically suitable space show no consistent poleward trend across much of the remainder of the continent. Indeed, the spatial pattern of climate change is such that it forces many species with ranges centred in northern Australia towards the Equator (Fig. 2), away from rapidly warming temperatures (Fig. 1a) and towards areas of increasing precipitation (Fig. 1b and Supplementary Fig. S1). Furthermore, for species in the desert and xeric shrublands, many climatic niches shifted towards, rather than away from, warming conditions, as a result of the pattern of increasing precipitation. Across the continent, there has been no consistent latitudinal gradient in temperature increases that would suggest poleward movements should be the expectation (Fig. 1a and Supplementary Fig. S1).

The assumption that poleward distribution shifts should be expected in response to climate change forms the basis for several

Table 1 | Geometric mean velocities (±1 s.d.) for climate and species climatic niches.

|	Future predicted velocity	Past observed velocity				Underestimate	No. of spp.
	Temp.	Temp.	Precip.	Niche space	Poleward niche space	%	(# N, # S)
Australia-wide		0.77 (0.23–2.57)	0.67 (0.18–2.55)	1.27 (0.60–2.72)	0.59 (0.042–1.04)	53.5%	464 (94 N, 370 S)
Tropical and subtropical grasslands, savannas and shrublands	0.67	0.61 (0.15–2.41)	0.63 (0.19–2.01)	1.22 (0.52–2.87)	0.23 (−0.24–0.68)	81.1%	188 (68 N, 120 S)
Temperate grasslands, savannas and shrublands	0.59	1.84 (0.84–4.05)	0.32 (0.11–0.95)	1.44 (0.79–2.63)	1.18 (0.44–1.75)	18.1%	37 (3 N, 34 S)
Mediterranean forests, woodlands and scrub	0.26	0.98 (0.47–2.06)	0.32 (0.10–1.05)	1.29 (0.68–2.43)	0.76 (0.29–1.48)	41.1%	51 (3 N, 48 S)
Tropical and subtropical moist broadleaf forests	0.33	0.26 (0.08–0.82)	0.13 (0.03–0.57)	0.52 (0.22–1.23)	−0.045 (−0.32–0.53)	108.6%	15 (8 N, 7 S)
Temperate broadleaf and mixed forests	0.35	0.36 (0.13–1.03)	0.38 (0.15–0.97)	0.87 (0.44–1.72)	0.71 (0.33–1.51)	19.4%	60 (2 N, 58 S)
Deserts and xeric shrublands	0.71	0.85 (0.27–2.65)	1.08 (0.28–4.24)	1.80 (1.13–2.87)	1.03 (0.56–1.21)	42.8%	113 (10 N, 103 S)

Future predicted and past observed climate data are shown with past modelled changes in distribution of species-specific climatic niche for the entire niche space and when only poleward movement is calculated. The underestimate (%) reflects the difference between calculating velocity over the entire range compared with calculating the poleward velocity alone. The number of species with the centroid of their range in each biome is shown along with the number of species moving in a net poleward (S) direction compared with a net equatorial (N) direction. Future predictions represent global averages given the Special Report on Emissions Scenarios A1B scenario reported in ref. 7; past values represent trends covering 1950–2010 for Australia alone.

high-profile meta-analyses and reviews of the response of species to recent climate change, inferred from temperature alone, and primarily focused on the Northern Hemisphere[2–4,14]. The evidence of the past 60 years in Australia challenges this assumption as a global generality and has several implications for estimates of the velocity of distribution shift required by species to track their climatic niche space. For example, in a meta-analysis of distribution shifts in response to climate change based on a range of taxonomic groups, it was reported[4] that 22% of species shifted in the opposite direction to that expected on the basis of the movement of thermal isotherms. However, species that seem not to be responding in a manner sufficient to track increasing temperature (that is, not shifting their distribution fast enough in a poleward direction) may actually be tracking precipitation, or interacting effects of temperature and precipitation, resulting in non-poleward shifts. As we have found for the Australian continent, there may not be clear latitudinal gradients in temperature or precipitation or the velocity of climate change across a species range and suitable climatic space may be pushed towards cooler climates in any direction, towards warmer climates, or towards drier or wetter climates depending on individual sensitivities. The velocity of these shifts may be significant and overlooked in analyses that focus on uni-directional change, resulting in an underestimate of the mean velocity of distribution change in response to climate.

If we were to consider only the poleward velocity of geographic changes in Australian birds' climatic niche, the actual velocity is underestimated by an average of 53% (Table 1). The greatest underestimates occur in the tropical and subtropical grasslands and savannas, where the range centroids of the largest number of Australia's birds occur (n = 188) and where 36% of species have experienced high-velocity shifts in their climatic niche distributions in an equatorial rather than poleward direction. Large underestimates also occur in the tropical forest biome;

however, the sample size here is relatively small (n = 15), and in this mountainous region distribution shifts are more likely to be upslope[15]. The velocity of species distribution shifts for temperate regions was underestimated by an average of 26%, compared with an average of 95% for the two tropical biomes. In the more temperate biomes of Australia (temperate grasslands, savannas and shrublands, temperature and Mediterranean forests), the suitable climatic space for most species does move in a general poleward direction (Fig. 2), consistent with the fingerprint of climate change detected in previous work in temperate regions[2,4,5]. However, even where consistent poleward shifts are detected, the velocity of these shifts may be underestimated when considered over the entirety of the species range. Poleward shifts can actually take an overall bearing anywhere between 90° and 180° (Fig. 2): the farther the shift is to the east or west the more overall species poleward velocity is underestimated.

The velocity of geographic shifts in climatic niche can also be underestimated depending on whether species distributions are expanding, contracting or simply shifting (Fig. 3). More than 50% of the species whose ranges were centred in tropical and temperate forest and in temperate grasslands and savanna experienced a contraction in suitable climatic space over the past 60 years (Fig. 3c). As species' ranges in these areas abut the Australian continental edge, their scope for expansion at the leading range edge is truncated. The velocity of movement required to track climate change for these species may be underestimated because the static leading edge (due to the continental limit) will result in a trailing edge moving at twice the velocity calculated in the centroid of the range. Similarly, for species whose ranges are expanding (Fig. 3a), the leading edge will be moving at approximately twice the velocity calculated at the centroid of the range if the trailing edge remains static as with many species in the tropical and subtropical grasslands, savannas and shrublands.
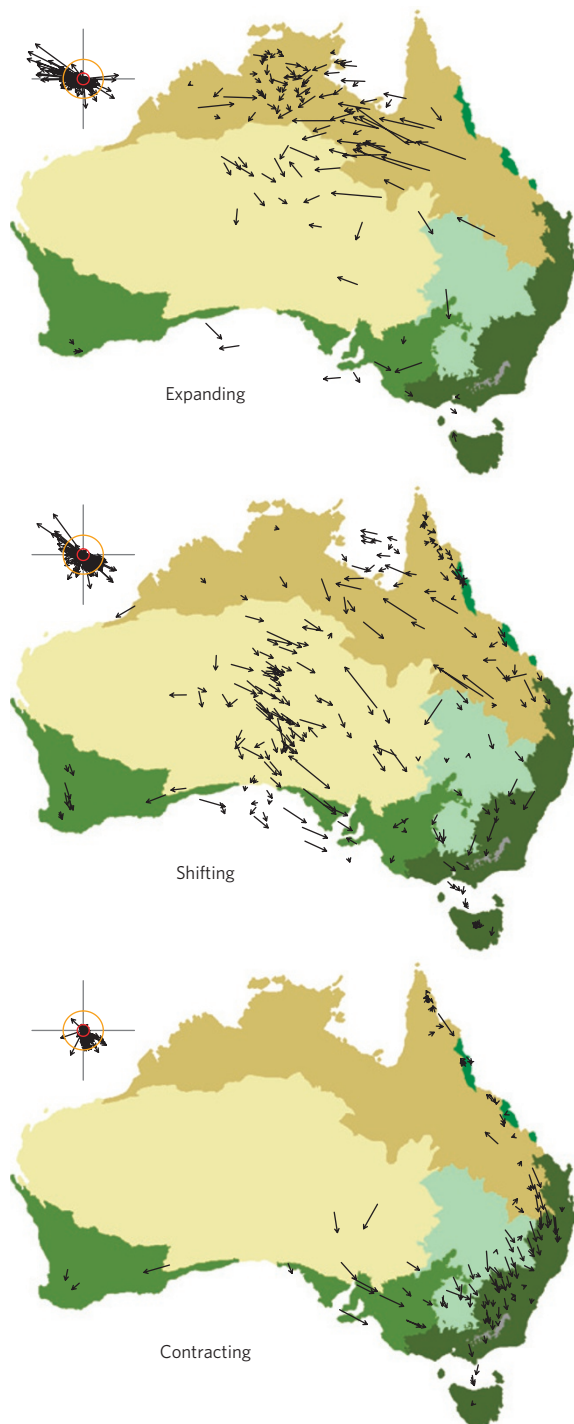
Figure 3 | Distribution of species with expanding, shifting and contracting climatic niche geographic space. The symbols and scales are the same as in the legend for Fig. 2.

We have not analysed actual changes in species past range distributions here; however, other work has shown that highly vagile species such as birds adjust their geographic range to track climate change[16,17], although they may show a lag in response time[18]. The importance of precipitation and its interaction with temperature in determining shifts in the climatic niche for birds is empirically demonstrated in an analysis of site occupancy over the past century for 53 bird species in the Sierra Nevada Mountains of California[16]. Overall 90% of species were considered to have tracked their climatic niche; 40% seemed to track precipitation more closely

than temperature, whereas another 26% tracked both temperature and precipitation[16]. However, although range changes in Australian birds are increasingly reported, few can be unequivocally linked to climate change[19,20].

Climate change of the recent past is often considered to have been relatively mild[6,21] when compared with that predicted for the future. However, we have shown that the velocity of climate change has been rapid over the past 60 years in Australia, more rapid than that predicted in global analyses for the future, and that geographic distribution of the climatic niche for 464 species of Australian birds has undergone high-velocity and multi-directional change. Furthermore, we have actually presented a conservative estimate of the velocity of past climate change by analysing the past 60 years together; in fact, temperature and precipitation velocities have increased in Australia between 1950 and 2010 (Supplementary Table S1) resulting in even faster velocities of shift in climatic niche space during the last part of the analysis period (mean of 3.43 km yr^{-1}, range 1.5–8.1 for the period 1971–1990).

Globally, we expect the fingerprint of climate change to manifest as multi-directional shifts in species distributions, albeit perhaps in a net poleward direction, as climate changes interact with individual species' sensitivities to determine the direction, magnitude and velocity of change in climatic niche space. Our results, when considered in conjunction with the results of research that shows a coherent fingerprint of climate change on species responses in temperate areas of the globe[2,4,5], suggest that these multi-directional shifts may be more pronounced in tropical regions. Unfortunately, there has been far less research on range-boundary shifts for tropical species[14] than for temperate species, despite their being considered particularly vulnerable to climate change owing to narrower climatic tolerances[22].

In our analysis we have not been hampered by the uncertainty associated with future climate changes, in particular for precipitation; by using actual climate data from the past 60 years we are able to demonstrate that if species track climate change in the future, they are likely to shift their distributions in a range of directions. Although establishing generalities about future shifts in distributions for species as a function of both temperature and precipitation is fraught with uncertainty, understanding the influence of this interaction on change in species-specific climatic niche space using actual data from the recent past allows us to more accurately estimate the requirement for future response. We suggest that shifts in distribution of climatic niche for Australian species are likely to occur at faster velocities than predicted at present for the future and that the fingerprint of climate change on species distributions globally may be much stronger than previously thought.

Methods

Weather data. Monthly maxima and minima temperature, and total rainfall for the period 1949 to 2010 were sourced from the Australia Water Availability project[23] (http://www.bom.gov.au/jsp/awap/). These data were sourced at a spatial resolution of 0.05° × 0.05° (approximately 5 km × 5 km) over 732 monthly time slices (1950–2010).

Past climate change. The velocity of climate change was estimated as the ratio of the temporal trend to the spatial gradient as in ref. 7. The temporal trend of change in temperature and precipitation was calculated as the slope of the linear regression of monthly temperature or precipitation as a function of time (Supplementary Fig. S1). The spatial trend was calculated as the mean slope estimated on the basis of a 3 × 3 cell neighbourhood using the average maximum technique. This was modified to accommodate different geographic projection where cell widths change with latitude; cell sizes were estimated using Vincenty's formula[24] as applied in ref. 25.

Species distribution modelling. Over 9.4 million bird occurrences were collated from personal, institutional and published databases (for example, Birds Australia Atlas[26,27] and Centre for Tropical Biodiversity and Climate Change[28]). These data records represented observations between 1950 and 2010 with spatial accuracy <10 km for 464 Australian terrestrial bird species. This spatial accuracy threshold is approximately two times the resolution of the climatic data (∼5 km × 5 km); thus, over-prediction errors caused by the use of coarse-resolution occurrence data are

likely to be minimal[29]. However, we note that models based on observations post 1990 (which consistently show finer-resolution records due to the use of widespread global positioning system technology) are likely to have slightly higher AUC (area under the curve of the receiver operating characteristic curve) values[29]. The effect of this on the results and conclusions presented here is minimized as we excluded from analysis species where the model accuracy scores were insufficient to be reliable (AUC < 0.7). Species that were excluded from the analysis included seabirds and water birds, vagrant species and species with <20 occurrences. The mean AUC for the remaining 464 bird species models was 0.90 (see Supplementary Table S2 for all model results, sample sizes used in the models and predicted mean distribution areas and see the discussion on model accuracy in the Supplementary Information).

For modelling bird species distributions, the weather data were aggregated for a 12-month period preceding the individual monthly time slices into spatial estimates of mean, minimum, maximum and standard deviation of monthly temperature, sum and coefficient of variation of precipitation, and sum of wettest and driest quarter for precipitation. Using weather data for the 12 months preceding each observation (rather than long-term climate averages) to train species distribution models permits seasonal relationships between climate and species distributions to be incorporated in the model (see Supplementary Movies S1 and S2). It has been demonstrated[13] that weather models consistently achieve higher model scores than climate models for vagile species.

All distribution modelling was done using Maxent[30]. Maxent is a presence-only distribution modelling algorithm based on the principle of maximum entropy that builds statistical relationships between where a species occurs and the available environment (also known as the background). Occurrence records were unique combinations of latitude, longitude and date for a species. To counter both the spatial and temporal biases in the occurrence records, we used a target group background (sampling of the available environment)[31]. By using all occurrence records across all species for our background, the temporal and spatial bias that may occur in single species occurrences is mimicked in the background records and thus effectively cancels out the influence of the biases. All models were projected onto spatial surfaces representing monthly weather across Australia for each month from January 1950 to December 2010.

Species-specific velocities. Binary species distributions were generated using a threshold based on balancing the training omission rate, predicted area and logistic threshold value; this threshold provided realistic predictions of Australian bird distributions[13]. For any single species, 732 predictions were created representing each month between 1950 and 2010. The distributional area and centre of gravity (midpoint of the distribution weighted by area of individual spatial pixels/cells) for each of the 732 monthly predictions for each species was calculated using the R package SDMTools[25]. Linear regression of distributional area and latitude and longitude of the centre of gravity with time permitted characterization of changes in distributional area and associated velocities in distributional shifts. For purposes of classifying species distributional area changes, the 25% of species with the greatest positive slopes (linear model of area with time) were considered to be increasing in area and the 25% of species with greatest negative slopes were considered to be decreasing. The fitted values of the regressions of latitude and longitude for January 1950 and December 2010 were used as endpoints from which the velocity and direction of distributional shifts were calculated; this was calculated using Vincenty's formula[24] as applied in ref. 25. To calculate distribution shifts in a north–south direction, longitudinal changes were ignored and the velocity and direction were recalculated.

We also calculated temperature, precipitation and species-specific velocities for 20-year time slices between 1950–2010 (Supplementary Table S1). Species velocity exceeded both temperature and precipitation velocity alone independently of start and end years. Temperature velocities increased over time, whereas precipitation velocities increased through 1950–1990 and dropped slightly in the period 1991–2010. The highest species velocities were achieved in the period 1971–1990, when both temperature and precipitation velocities were relatively high.

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Author contributions

J.V., A.S.K. and A.E.R. conceived the study. J.V., A.S.K., B.L.B. and A.E.R. designed the study. G.C.P. and J.J.P. collated and vetted data. J.V., H.T.M., G.C.P., B.L.B. and J.J.P. performed the analysis. H.T.M. and J.V. wrote the paper. All authors discussed and commented on the manuscript.

Additional information

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Competing financial interests

The authors declare no competing financial interests.