






Distinguishing local and global correlates of population change in migratory species

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Abstract

Aim: Understanding the processes driving population declines in migratory species can be challenging. Not only are monitoring data spatially and temporally sparse, but conditions in one location can carry over to indirectly (and disproportionately) affect the population in another location. Here, we explore whether remote factors can sequentially, and potentially cumulatively, influence local population fluctuations in declining populations of shorebirds.

Location: Moreton Bay (Australia) and the East Asian–Australasian Flyway.

Methods: We use N-mixture models to account for variable observer effort and estimate yearly population growth rate. We then use least squares regressions to correlate population growth rates with remotely sensed climate anomalies at different migratory stages. From this, we estimate species-specific climate sensitivity indices and explore whether species which are declining more rapidly, or which rely more heavily on areas undergoing rapid habitat loss, have higher climate sensitivity indices.

Results: We find that species which rely more on the Yellow Sea during migratory stopover (a region which has undergone severe habitat loss) are more sensitive to rainfall anomalies in their Arctic breeding grounds, suggesting that habitat loss reduces the resilience of shorebirds to climate extremes. Furthermore, species with higher sensitivities to climatic conditions during stopover are also those which are declining quickest, suggesting that declining populations may also be less resilient to climate fluctuations at bottleneck sites. We also observed species-specific correlations between climate anomalies at all migratory stages and population growth rates, primarily for eastern curlew and lesser sand plover.

Main conclusion: By applying methods in combination, it is possible to use citizen science data from a single location in a flyway of over 160 sites up to 11,680 km apart, to investigate how different stressors correlate with local population dynamics.

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KEYWORDS

carry-over effects, climate sensitivity, growth rate, migration, N-mixture model, shorebirds

1 | INTRODUCTION

With only 9% of migratory bird species adequately protected throughout their full annual cycle (Runge et al., 2015), migratory species are increasingly qualifying for threatened status on the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species, and often disproportionately so, in comparison with non-migratory species (Kirby et al., 2008). However, understanding the processes driving population declines is challenging in mobile species (Kraan et al., 2009; Norris & Taylor, 2006; Webster, Marra, Haig, Bensch, & Holmes, 2002). Many may travel hundreds if not thousands of kilometres between their breeding and non-breeding grounds, connecting otherwise isolated locations through the transport of nutrients, seeds, pollen and pathogens, thus shaping ecosystem function at a global scale (Bauer & Hoyer, 2014).

Migratory species can be impacted by a wide range of environmental conditions and anthropogenic threats along the pathways they travel (Catry, Dias, Phillips, & Granadeiro, 2013; Harrison, Blount, Inger, Norris, & Bearhop, 2011; Rakhimberdiev, Hout, Brugge, Spaans, & Piersma, 2015). Not only can these threats impact populations at a later date (and therefore at different locations) through carry-over effects (Norris & Taylor, 2006; van Gils et al., 2016), but these impacts can be disproportionately large depending on where and when they occur in the migratory cycle (Aharon-Rotman, Bauer, & Klaassen, 2016; Bauer, Lisovski, & Hahn, 2016; Dhanjal-Adams et al., 2017; Iwamura et al., 2013). Indeed, if a population is restricted to a small number of locations (hereafter, bottlenecks) during breeding or refuelling, or as a result of unfavourable conditions across the rest of their distribution (Runge, Tulloch, Hammill, Possingham, & Fuller, 2014), then a large proportion of the population may be impacted by a threat in a single location (Dhanjal-Adams et al., 2017; Iwamura et al., 2013; Piersma et al., 2016; Rogers, Yang, et al., 2010). Without a good understanding of population-level connectivity, linking remote threats to local population dynamics can be difficult (Marra, Hobson, & Holmes, 1998; Webster et al., 2002), especially given data heterogeneity. Indeed, observer effort can be sparsely distributed over time, and geographically biased towards richer or more accessible areas (Boakes et al., 2010), and sightings can become increasingly rare in declining populations, making estimates of population size, trend and conservation status difficult or computationally demanding to estimate (Bland, Collen, Orme, & Bielby, 2015).

Here, we use a combination of Bayesian hierarchical modelling and frequentist variable selection to correlate migratory shorebird monitoring data at a single heavily studied site in Australia with remotely sensed environmental conditions across their entire migration route, over 160 sites and a 20-year period. By using this

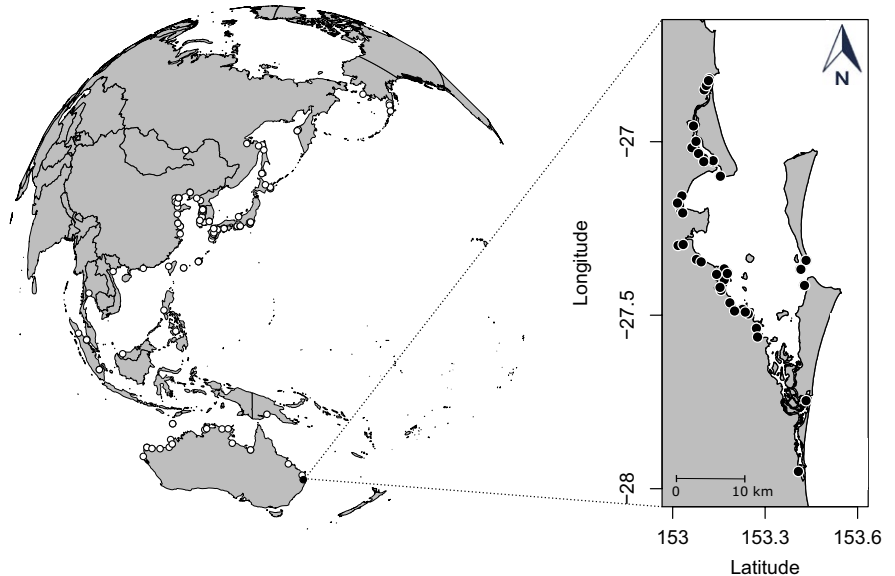
combined approach, we aim to understand how environmental conditions relate to population dynamics in migratory shorebirds of the East Asian–Australasian Flyway (hereafter EAAF). Indeed, this flyway, which extends from the Bering Strait to Tasmania, has one of the highest shorebird species diversities in the world (Amano, Szekely, Koyama, Amano, & Sutherland, 2010). This bird group has one of the most rapidly declining IUCN conservation statuses (Szabo, Butchart, Possingham, & Garnett, 2012), as a combined result of steep population declines (Studds et al., 2017) and poor environmental governance (Amano et al., 2017). Indeed, populations of some shorebird species have declined by 1.4% to 7.5% annually (Studds et al., 2017), and some local non-breeding populations have disappeared altogether at the southern end of their range (Britton & Hunter, 2003; Clemens et al., 2016; Cooper, Clemens, Oliveira, & Chase, 2012). In Australia, the severity of these declines has prompted the recent listing of eight taxa as nationally threatened under the Environment Protection and Biodiversity Conservation Act 1999 (Department of the Environment, 2013).

In part, these trends appear to be influenced by changing temperatures across their Arctic breeding grounds (Murray et al., 2018; van Gils et al., 2016; van Gils & Piersma, 2004; Wauchope et al., 2016), coupled with intertidal habitat loss in an important migratory bottleneck, the Yellow Sea (MacKinnon, Verkuil, & Murray, 2012; Murray, Clemens, Phinn, Possingham, & Fuller, 2014; Piersma et al., 2016; Studds et al., 2017; Yang et al., 2011). However, we have a poor understanding of how these two factors may interact to influence population dynamics. Indeed, it is unclear whether habitat loss is likely to increase a species' sensitivity to climate anomalies, and whether sensitivity to climate extremes is likely to be stronger in declining species. Here, we use citizen science data to explore these potential relationships on population growth rate. The aims of our research are therefore twofold: firstly, to increase our understanding of migratory population dynamics in declining populations of shorebirds; secondly, to illustrate how local citizen science monitoring data can be used to correlate local population dynamics with conditions elsewhere.

2 | METHODS

We analysed 20 years of count data collected between 1992 and 2012 from Moreton Bay (Figure 1), Australia (27.31°S, 153.34°E), with the aim of distinguishing between local and remote correlates of change in seven migratory shorebird species: bar-tailed godwit (*Limosa lapponica baueri*), curlew sandpiper (*Calidris ferruginea*), eastern curlew (*Numenius madagascariensis*), great knot (*Calidris tenuirostris*), grey-tailed tattler (*Tringa brevipes*), lesser sand plover

FIGURE 1 Spatial arrangement of 160 sites used by migratory shorebirds in the East Asian–Australasian Flyway during northward and southward migration (white circles) to and from Moreton Bay, Australia (black circle). Abundance within Moreton Bay is estimated from counts carried out at multiple roost sites (black circles; right)



(*Charadrius mongolus*) and red knot (*Calidris canutus*). In the following sections, we describe (a) the case study system, (b) the shorebird count data, (c) the remotely sensed environmental variables and (d) how we anticipate they will influence population dynamics. We then (e) use an *N*-mixture model to (f) derive estimates of population growth rate. Finally, (g) we use weighted least squares regression to analyse the influence of climate and Yellow Sea reliance on population growth rate.

2.1 | Case study: Moreton Bay

Around 40,000 migratory shorebirds spend the non-breeding season in Moreton Bay, including internationally important numbers of globally endangered eastern curlew (IUCN; BirdLife International, 2017a) and great knot (IUCN; BirdLife International, 2016a), as well as globally near-threatened grey-tailed tattler, bar-tailed godwit, curlew sandpiper and red knot (BirdLife International, 2016b, IUCN; 2017b, 2017c, 2017d). Indeed, between 1993 and 2008 the populations of seven migratory shorebird species declined by 43%–79% within the bay, with non-migratory species (i.e., those that stayed in Australia year-round) showing no directional change in population abundance (Wilson, Kendall, Fuller, Milton, & Possingham, 2011). Factors beyond Moreton Bay therefore appear to be driving local changes in abundance in this population, making it ideal for investigating the relative contributions of local and remote factors on local fluctuations in population growth rates.

2.2 | Data

2.2.1 | Shorebird counts

To estimate population growth rate in Moreton Bay, we analysed count data collected by the Queensland Wader Study Group (QWSG) between 1992 and 2012 at 40 high-tide roost sites

(Milton & Driscoll, 2006). Specifically, count data were used from the non-breeding season between the months of December and February each year, when shorebirds are unlikely to undertake migratory movements due to their annual primary moult (Higgins, Peter, Cowling, Steele, & Davies, 2006; Marchant & Higgins, 1993). Counts were made simultaneously at high-tide roost sites once per month, within 2 hr of the high tide (Zharikov & Milton, 2009). However, variation in observer effort is inherent in most biodiversity monitoring data, and sites were not all surveyed each month. Additional data were recorded from local weather observations during roost site counts, including tide height and wind strength. These were used as covariates for detection probability in an *N*-mixture model. This modelling approach does not allow for missing covariate values (NA). Because all counts within a month were assumed to have been carried out during the highest tide, we replaced any NAs in the tide height covariate data with the highest value for that particular month (Clemens, Kendall, Guillet, & Fuller, 2012; Milton & Driscoll, 2006; Zharikov & Milton, 2009). For the wind strength covariate however, we replaced any NAs with the average value of the counts made that month to reflect average conditions across sites. Count data are available upon request from the QWSG (<http://waders.org.au>).

2.2.2 | Remotely sensed climatic variables

To distinguish between local and remote correlates of population change, we measured climatic conditions throughout the entire migratory cycle: non-breeding (NB), northward migration (NM), breeding (B) and southward migration (SM; see Figure 1 for site locations and Supporting Information Figure S1 for species-specific timing). For each of these migratory stages, we identified all internationally important stopover sites (160 sites in total, with some sites shared between species) and breeding distributions from Bamford, Watkins, Bancroft, Tischler, and Wahl (2008). We then determined the timing of migration

through each of these migratory stages (Supporting Information Figure S1) based on a literature review (Barter & Riegen, 2004; Battley et al., 2012; Beaumont, McAllan, & Hughes, 2006; Branson, Shigeta, Chiang, & Minton, 2010; Driscoll & Ueta, 2002; Higgins et al., 2006; Rogers, Yang, et al., 2010; Tomkovich & Soloviev, 2006) and extracted temperature, rainfall and snow cover variables at all sites corresponding to the estimated timing of presence at each location (Supporting Information Figure S1).

Finally, we calculated weighted mean conditions over all sites for each climatic variable, for each of these migratory stages, for each species. Weights were estimated from maximum population flow networks (full model description in Dhanjal-Adams et al., 2017). Shorebirds migrating from Moreton Bay to the Arctic are unlikely to use all internationally important sites equally. The approach therefore estimates the species-specific proportion of the Moreton Bay population flying through EAAF sites based on (a) the distance between sites, (b) a bird's ability to fly a given distance (based on tracking data) and (c) the number of birds observed at each site. Because tracking data were not available for curlew sandpiper and lesser sand plover, we used tracks from similar-sized birds (sanderling and greater sand plover, respectively (Minton et al., 2013)) to restrict the range of possible flight distances of the species. Using these models, we were also able to calculate the proportion of the Moreton Bay population of each species migrating through the Yellow Sea. These numbers resemble those previously published from expert-derived networks (Iwamura et al., 2013; Studds et al., 2017).

Temperature

We used global monthly gridded air temperature anomaly data freely available from the National Oceanic and Atmospheric Administration (NOAA)—Earth System Research Laboratory (ESRL) (Land Surface Temperature; GHCN CAMS Gridded 2 m Temperature). We used monthly anomalies (calculated as the difference between a given month's temperature and the long-term mean) to allow comparison between different migratory stages.

Rainfall

We used Global Precipitation Climatology Project (GPCP) precipitation data from the NOAA Earth System Research Laboratory (Huffman, Adler, Bolvin, & Gu, 2009). Again, because of marked variation in the magnitude of rainfall, we used anomalies to compare among migratory stages, and capture extreme conditions that had the potential to drive changes in population growth rate (Clemens et al., 2016; Gill et al., 2007; Murray et al., 2018).

Snow cover

We used Climate Data Record (CDR) of Snow Cover Extent for the Northern Hemisphere (NH) from the NOAA Earth System Research Laboratory (Robinson & Estilow, 2012). From these, we extracted date of snowmelt and snowfree duration following van Gils et al. (2016), from which we calculated anomalies to capture phenological mismatches.

2.3 | Predicted impacts of climate anomalies on population growth

2.3.1 | Non-breeding: Moreton Bay

We used Moreton Bay temperature anomaly as an indicator of drought and therefore habitat availability (Figure 2). Shorebirds roost in shallow wetlands. Thus, we anticipate that anomalously high temperatures in Moreton Bay will cause evaporation of water in roost sites and reduce habitat availability, as well as cause thermal stress (Battley, Rogers, Piersma, & Koolhaas, 2003; Geering, Agnew, & Harding, 2007). Birds may need to travel further to roost, consequently impacting their energy intake (Rogers, Battley, Piersma, Gils, & Rogers, 2006; Rogers, Piersma, & Hassell, 2006).

We used Moreton Bay rainfall anomalies as an indicator of roost habitat availability and intertidal habitat quality. Shorebirds are sensitive to water height at roost sites (Rogers, Battley, et al., 2006; Rogers, Piersma, et al., 2006). Abnormally low rainfall can cause roost sites to dry up and become unavailable to birds (Geering et al., 2007). On the other hand, abnormally high rainfall can result in (a) increased sedimentation and therefore a change in intertidal sediment structure and shorebird foraging (Clemens, Skilleter, Bancala, & Fuller, 2012), (b) a change in intertidal chemistry with decreased salinity and bivalve mortality (Matthews, 2006) and finally (c) inundation of roost sites (Rogers, 2003). Abnormal rainfall in inland areas has also been shown to result in the creation of ephemeral wetlands and therefore additional habitat for curlew sandpiper and lesser sand plover—thus benefitting some birds but not all (Geering et al., 2007).

2.3.2 | Stopover: East Asia and Australasia

We used stopover temperature anomaly as an indicator of conditions during migration (Figure 2). Shorebirds rely heavily on intertidal habitats for refuelling during migration (Piersma, 1986). Abnormally low temperatures suggest freezing conditions in the intertidal zone which reduce feeding opportunities (Rogers, Herrod, Menkhurst, & Loyn, 2010). Conversely, abnormally high temperatures can result in algal blooms which influence the abundance of intertidal prey (Estrella, Storey, Pearson, & Piersma, 2011), as well as causing roost sites to dry out (Rogers, Battley, et al., 2006; Rogers, Piersma, et al., 2006), both of which are anticipated to negatively impact the birds.

We used stopover rainfall anomaly as an indicator of conditions during migration. Abnormally high rainfall is likely to increase river runoff onto intertidal mudflats (while also increasing fresh water influx) which is likely to negatively affect species with longer, more slender bills which are intertidal specialists (such as eastern curlew and bar-tailed godwit), but to benefit species which can exploit the ephemeral wetlands created by the additional rainfall (such as curlew sandpiper and lesser sand plover).

We used winter temperature anomaly as an indicator of intertidal habitat productivity. Severe winter temperatures can result in

low spring (NM) numbers of some benthic organisms, and high summer reproductive success in others (Beukema & Essink, 1986).

2.3.3 | Breeding: Arctic

We used date of snowmelt in the breeding grounds as an indicator for nesting habitat availability for shorebirds (Figure 2). Many shorebirds arrive in the high Arctic to breed just as the snow starts to melt so that chicks hatch during peak insect abundance (Rakhimberdiev et al., 2018; Reneerkens et al., 2016). Abnormally early snowmelt can mean a phenological mismatch between shorebird arrival and habitat/food availability, while abnormally late snowmelt can mean birds arrive in the breeding grounds while it is still frozen (Smith, Gilchrist, Forbes, Martin, & Allard, 2010) unable to feed and recuperate from energetically demanding migrations, causing either starvation or reduced egg quality. Indeed, shorebirds are income breeders.

We used breeding rainfall anomaly as an indicator for food availability in the Arctic. Abnormally high rainfall in the breeding grounds can reduce arthropod abundance (Hodkinson, 2003), an important food source for breeding shorebirds and their chicks (Smith et al., 2010).

We used the duration of the snowfree period in the breeding grounds the previous summer as an indicator of productivity during the breeding season. Snowmelt impacts the growing season of plants and therefore both the likelihood of perennials to surviving to the following year and the number of seeds in the seedbank from annuals (Semenchuk et al., 2016).

2.4 | Zero-inflated N-mixture model

We developed a zero-inflated N-mixture model (Royle, 2004) to estimate the abundance of all shorebird species (see Supporting Information Appendix S1 for full model formulation and parameters, Supporting Information Appendix S2 for code and Supporting Information Figure S2 for population trend estimates, Supporting Information Figure S3 for detection probability estimates and Supporting Information Figure S4 for fit statistics). Models were run using JAGS 3.3.0 (Plummer, 2012) in R version 3.1.1 (R Core Team, 2012) with packages R2jags (Su & Yajima, 2012) and R2WinBUGS (Jeon, Kaufman, & Rabe-Hesketh, 2013). We ran three Markov chains in parallel using the packages snow (Tierney, Rossini, Li, & Sevcikova, 2008) and dclone (Sólymos, 2010). Gelman–Rubin diagnostics were used to estimate model convergence when $R \approx 1$ (Gelman & Rubin, 1991; Kéry & Schaub, 2012) in addition to visual inspection of the traceplots. Finally, detection covariates were only considered “significant” when the 95% credible interval (CRI) generated from the posterior distribution did not overlap zero (Gelman & Hill, 2006).

2.5 | Deriving population growth rate from the N-mixture model

N-mixture models assume a population is closed to immigration, emigration, recruitment and mortality (Royle, 2004). However, birds

are known to occasionally move between sites from one count to the next (Coleman & Milton, 2012), violating the closure assumption. Thus, abundance is estimated at each site independently, and birds present at two sites during the same monthly count are classified as false positives. Therefore, we are likely to underestimate detection probability p and overestimate abundance N (Supporting Information Appendix S1 and Figure S3). Yet we can assume that birds move an equal amount between sites from one year to the next (Coleman & Milton, 2012), making these under- and overestimations of detection and abundance (respectively) constant over time and space. The relative change in abundance from one year to the next is therefore also constant over time, providing a reliable estimate of population growth rate. Indeed, we estimated population growth rates for each of the seven species using the following equation (Sibly & Hone, 2002):

$$\lambda_t = \frac{\sum_{i=1}^S N_{i,t}}{\sum_{i=1}^S N_{i,t-1}}$$

where population growth rate λ for the annual cycle t was dependent on abundance N across all sites $i \in \{1, 2, \dots, S\}$ from the current non-breeding season t and the previous non-breeding season $t-1$. Population growth rates were estimated within JAGS, allowing simultaneous estimates of their credible intervals.

2.6 | Effects of climate and Yellow Sea reliance on population growth rate

We used weighted least squares (WLS) regressions to test for the effects of climatic anomalies at each migratory stage on local population growth rate λ (as derived from the N-mixture model above), while also accounting for species-specific responses. WLS allow a greater weight for more precise growth rate estimates to account for uncertainty (with a lower 95% CRI) by setting weight equal to $1/(\text{standard error})^2$. Thus, yearly population growth rate λ_t was used as a response variable, with climate anomalies as predictor variables (according to 2.3), and year as fixed effects, including interactions between species and climate anomalies (i.e., $\lambda \sim \text{Species} + \text{variable} + \text{Species} : \text{variable} + \text{year}$). All species were modelled together with year as a fixed effect, to account for unmeasurable time-varying factors, which might be impacting all species simultaneously, and to deal with the lack of replication within species (one growth rate measure per species per year).

All variables were centred and scaled. North migration temperature was then removed from the analysis due to its correlation with winter stopover temperatures. Similarly, Arctic snowfree period was removed due to its correlation with date of snowmelt, Moreton rainfall due to a correlation with rainfall from the previous year, and Moreton temperature from the previous year due to its correlation with rainfall from the previous year. We then tested for collinearity. We estimated that if the variance inflation factor (VIF) was under the critical value of 10, collinearity was not a problem (Dormann et al., 2013). In fact, variance VIF was below 2 for all variables (when

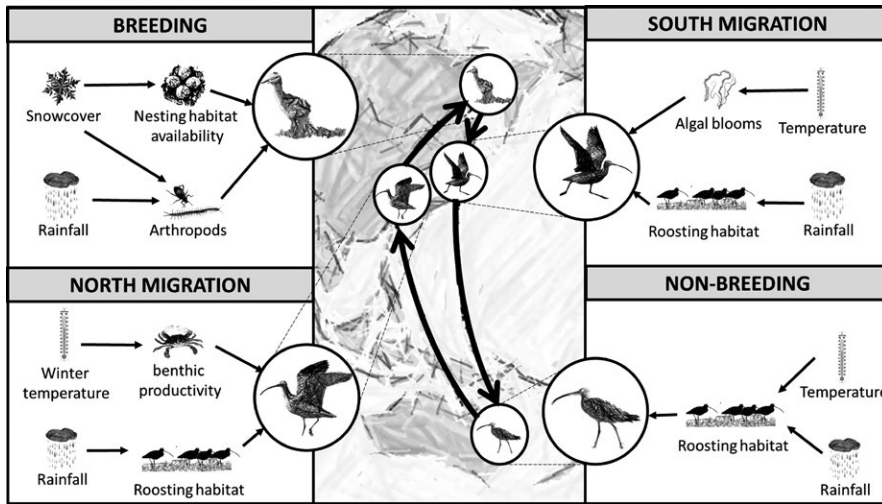


FIGURE 2 Schematic representation of different measured climatic conditions variables that are likely to influence different migratory stages and how. Counts are made during the non-breeding season in the previous and current year to estimate population growth throughout the current annual/migratory cycle

included in one large model). We then used the package MuMin version 1.13.4 (Barton, 2015) to search for the best combination of climatic predictors of population growth rate using Akaike information criterion (AIC). MuMin ranks all possible models for each migratory stage against each other, using ΔAIC to estimate the relative weight w of each model. Finally, we use adjusted R^2 to report effect sizes (Burnham & Anderson, 2002).

Because the best model had a weight of over 0.91 and a $\Delta\text{AIC} > 6$, we used this model to investigate whether a species reliance on the Yellow Sea during migration increased its sensitivity to climatic anomalies at later migratory stages. To do so, we extracted the modelled growth rates over the observed climate anomalies for each species (using the *predict* function and *effects R* package) at the maximum and minimum predicted climatic anomalies (for those species), and then divided the difference of these two values by the difference in minimum and maximum climatic anomalies themselves. This value therefore acted as a species-specific indicator of growth rate sensitivity to climatic variability (climatic variability index). Finally, we compared this climatic sensitivity index (including standard errors in a WLS regression) with Yellow Sea reliance for each species at each migratory stage. We anticipated that an amplification effect of Yellow Sea reliance would result in species with a higher Yellow Sea index to also have a higher climatic sensitivity index.

3 | RESULTS

3.1 | Abundance

The N-mixture models revealed that species varied greatly in population trend (β in Table 1) and that detection probability p was influenced by tide height x_{tide} and wind strength x_{wind} . Our abundance estimates provide strong evidence that curlew sandpiper and eastern curlew declined between 1992 and 2012, with $\beta = -4.8\%$ and -3.8% , respectively (Table 1). Our analyses do not provide evidence of long-term trends in the remaining species. High tide height negatively influenced detection probability across all species but

was steepest for lesser sand plover ($x_{\text{tide}} = -5.31$; Table 1) and red knot ($x_{\text{tide}} = -2.48$; Table 1). Indeed, birds roost during high tide and, consequently, a neap tide will not affect the accessibility of a roost site. However, a spring tide could result in roost site inundation, causing birds to seek an alternative roost site and move out of observer detection range. Wind strength increased detection probability for bar-tailed godwit ($x_{\text{wind}} = 0.9$; Table 1) and eastern curlew ($x_{\text{wind}} = 0.61$; Table 1), suggesting these species (which are larger) are more likely to concentrate inside specific roost sites under high wind conditions.

3.2 | Yellow Sea reliance, climate and population growth rate λ

We found a negative but non-significant correlation between Yellow Sea reliance on population trend ($p = 0.36$, $F = 1.03$, $df = 1$ and 5 ; Supporting Information Appendix S3). This is consistent with Murray et al. (2018) and Studds et al. (2017) who found that shorebird taxa relying more on declining intertidal areas of the Yellow Sea during migration were also declining more rapidly than species that were not.

We then tested for species-specific responses in population growth rate to climatic anomalies at different migratory stages. The model with the lowest AIC score had a weight of 0.91 and $\Delta\text{AIC} > 6$ with the next best model (Table 2; adj $R^2 = 0.69$, $F = 4.91$ on 74 and 58 df , $p = 1.6e^{-09}$), and included snowmelt date, temperature over the winter at stopover sites, temperature during post-breeding migration, temperature at arrival in the non-breeding grounds, as well as rainfall when departing the non-breeding grounds, pre-breeding stopover, breeding and post-breeding stopover (Tables 2 and 3). More specifically, eastern curlew and lesser sand plover showed the largest number of significant relationships (Figure 3 and Supporting Information Appendix S4). Indeed, they displayed a negative response in population growth rate to winter temperatures at stopover sites (Figure 3c,d), a positive response to rainfall anomaly during pre-breeding rainfall (Figure 3a,b), a negative response to post-breeding temperature anomaly (Figure 3j,l), as well as curlew sandpiper (Figure 3k). During post-breeding migration,

TABLE 1 Population trend estimates for seven shorebird species in Moreton Bay, Australia, between 1992 and 2012, together with parameters for detection probability covariates (high tide height and wind strength)

	Trend (β)	SE	Tide (x_{tide})	SE	Wind strength (x_{wind})	SE
Bar-tailed godwit	0.0059	0.0071	-1.22**	0.22	0.9**	0.28
Curlew sandpiper	-0.048**	0.017	-0.88**	0.25	0.21	0.29
Eastern curlew	-0.038**	0.007	-0.86**	0.13	0.61**	0.17
Great knot	0.00013	0.015	-1.28**	0.22	0.32	0.29
Grey-tailed tattler	-0.011	0.014	-0.72**	0.25	0.03	0.35
Lesser sand plover	-0.019*	0.014	-5.31**	17	1.49*	1.05
Red knot	-0.043	0.043	-2.48**	0.41	0.64*	0.55

*Signifies that 25%–75% (50% CRI) of parameter estimates do not overlap 0. **Signifies that 2.5%–97.5% (95% CRI) of parameter estimates do not overlap 0.

TABLE 2 Models selection with lowest AIC and weight >0.01

Model	Adj R^2	F	K	logLik	AIC	delta	weight
Rain B + Rain NB lag + Rain NM + Rain SM + snowmelt + Species + Temp NB + Temp SM + Winter Temp NM + year + Rain B:Species + Rain NB lag:Species + Rain NM:Species + Rain SM:Species + Species:Temp NB + Species:Temp SM + Species:Winter Temp NM	1.41	4.91	76	68.63	14.73	0	0.91
Rain B + Rain NB lag + Rain NM + Rain SM + Species + Temp NB + Temp SM + Winter Temp NM + year + Rain B:Species + Rain NB lag:Species + Rain NM:Species + Rain SM:Species + Species:Temp NB + Species:Temp SM + Species:Winter Temp NM	1.39	4.71	75	64.58	20.84	6.11	0.04
Rain B + Rain NB lag + Rain NM + Rain SM + snowmelt + Species + Temp NB + Temp SM + Winter Temp NM + year + Rain B:Species + Rain NB lag:Species + Rain NM:Species + Rain SM:Species + snowmelt:Species + Species:Temp NB + Species:Temp SM + Species:Winter Temp NM	1.42	4.28	82	71.53	20.93	6.2	0.04

eastern curlew also showed a negative response to rainfall anomalies (Figure 3h) and grey-tailed tattler a positive one (Figure 3i). Finally, in Moreton Bay lesser sand plover displayed a negative response to temperature anomalies on arrival (Figure 3m) and curlew sandpiper a positive response to rainfall on departure (Figure 3n). Thus, more curlew sandpipers were returning to Moreton Bay when the previous summer had been rainier than usual.

We then investigated whether Yellow Sea reliance correlated with an increase in a species' sensitivity to climate anomalies (Supporting Information Appendix S5). We found a positive relationship between climate sensitivity to breeding rainfall anomalies, and Yellow Sea reliance (adj $R^2 = 0.63$ $F = 11.21$ on 1 and 5 df , $p = 0.020$; Rain_B in Supporting Information Appendix S5). Finally, we found a correlation between rate of decline and climate sensitivity index for rain during pre-breeding migration (adj $R^2 = 0.53$, $F = 7.71$ on 1 and 5 df , $p = 0.039$, Supporting Information Appendix S6) and temperature during post-breeding migration (adj $R^2 = 0.57$, $F = 8.83$ on 1 and 5 df , $p = 0.031$, Supporting Information Appendix S6).

4 | DISCUSSION

Here, we use a combination of Bayesian hierarchical modelling and frequentist variable selection to correlate spatially and temporally

variable bird monitoring data with remotely sensed environmental conditions, with the aim of linking distant conditions to local population fluctuations. More specifically, we investigated whether shorebird species that have experienced higher losses of intertidal habitat, and higher declines in abundance, were more likely to be sensitive to climate anomalies throughout their migratory journeys.

Our results suggest that migrating through the Yellow Sea increases a species' sensitivity to rainfall anomalies in the breeding grounds (Supporting Information Appendix S5). Indeed, high rainfall is likely to cause a decrease in arthropod abundance (Smith et al., 2010), a major food source for Arctic breeding shorebirds and their chicks. Thus, as income breeders, shorebirds are likely to be able to recover from bad migratory conditions when conditions in the breeding grounds are also good. However, bad breeding conditions will likely reduce their resilience to habitat loss at stopover sites. These findings add to an increasing body of literature, suggesting that stopover conditions can determine the ability of shorebirds to cope with climate-related changes in the Arctic (Murray et al., 2018; Rakhimberdiev et al., 2018).

We also found that species which were declining more severely showed a stronger response to rainfall anomalies during pre-breeding migration, and temperature anomalies during post-breeding migration (Supporting Information Appendix S6), most likely because algal blooms are more common in the Yellow Sea in late summer when shorebirds

TABLE 3 ANOVA of Interaction terms for model with lowest AIC identified in Table 2

	Sum Sq	df	F value	Pr(>F)
Species	11.37	6	5.10	0.00029***
Rain_B	1.24	1	3.32	0.073
snowmelt	1.36	1	3.65	0.061
Rain_NB_lag	0.17	1	0.45	0.50
Temp_NB	0.64	1	1.72	0.19
Rain_NM	0.011	1	0.029	0.86
Winter_Temp_NM	3.66	1	9.86	0.0027**
Rain_SM	0.57	1	1.54	0.22
Temp_SM	0.064	1	0.17	0.68
year	17.76	18	2.65	0.0026**
Species:Rain_B	4.27	6	1.91	0.094
Species:Rain_NB_lag	5.16	6	2.31	0.045*
Species:Temp_NB	7.31	6	3.28	0.0076**
Species:Rain_NM	7.48	6	3.35	0.0067**
Species:Winter_Temp_NM	5.40	6	2.42	0.037*
Species:Rain_SM	8.61	6	3.86	0.0026**
Species:Temp_SM	11.82	6	5.30	0.00020***
Residuals	21.56	58		

Note. Significant *p*-values are shaded in grey.

*signifies a *p*-value < 0.05 **signifies a *p*-value < 0.01 and ***signifies a *p*-value < 0.001.

are migrating southwards (Keesing, Liu, Fearn, & Garcia, 2011). Also, it is not uncommon for populations which are in low numbers to display higher demographic stochasticity than more stable populations (Ricker, 1954), and to be more sensitive to environmental perturbations (Petchey, Gonzalez, & Wilson, 1997; Ruokolainen & Fowler, 2008). Furthermore, migratory populations are more sensitive to perturbations occurring at bottleneck sites than elsewhere, as is the case of shorebirds migrating through the Yellow Sea (Iwamura et al., 2013). In fact, the species with the steepest declines, eastern curlew, is both a species whose migratory network is very sensitive to habitat loss (Dhanjal-Adams et al., 2017), and who displayed the highest number of significant correlations with environmental anomalies (Supporting Information Appendix S4).

In fact, all species-specific population growth rates (Supporting Information Appendix S4, and Tables 2 and 3) correlated to climatic anomalies as anticipated (Section 2.3) except for eastern curlew, which positively correlated with anomalously high rainfall during pre-breeding migration (Figure 3a), but negatively correlated during post-breeding migration (Figure 3h). It is unclear why this may be the case, but it has been shown that abnormally high rainfall affected eastern curlew more than other species during a flooding event (Clemens, Skilleter, et al., 2012), likely due to increased sedimentation rendering some benthic organisms inaccessible to such a long- and slender-billed species.

Given that many of the rainfall and temperature variables were calculated from weighted anomaly averages over multiple sites

over a period of 2–4 months, the data can only provide insight into whether migratory conditions in one year were on average hotter, colder, drier or wetter than usual throughout the season and across the region. There may be cases where some sites, located thousands of kilometres apart, were hotter than average and others colder and therefore resulted in an overall medium temperature estimate. Our analysis may therefore only be identifying the environmental correlates with the strongest signal, and other variables for other species may also have been important, but impossible to detect given the methodology. Indeed, species with growth rates with larger confidence intervals, such as red knot, are unlikely to yield significant results. The fact that we can still detect a signal from the data given this averaging suggests that there are indeed some years which are hotter and others colder (e.g., El Niño or La Niña), which are related to growth rate in some species. Our analyses are therefore likely to underestimate the impacts of climate on species.

All species studied had previously been reported as declining from 0.8% to 9.1% annually in Moreton Bay (Wilson et al., 2011). In comparison, our estimates of population declines were less severe (Table 1). These differences are probably methodological; previous population trends were estimated using the average number of birds per site to overcome incomplete count data and with linear models. Here, incomplete and variable count data were used to parameterize detection probability, thus accounting for variable observer effort over time and across sites. This high variability increased the credible intervals in this analysis (i.e., 2.5%–97.5% (95% CRI) of parameter estimates did not overlap zero), explaining why fewer population trends were significant. Furthermore, larger 95% credible intervals for abundance flattened the trends, reducing the trend estimate β . Lastly, our analysis used more recent data, and our estimates suggest flattening out of trends in species such as great knot, lesser sand plover and grey-tailed tattler since 2009, when the previous analysis was completed.

One advantage of N-mixture models is that covariates can be fit to detection probability to improve abundance estimates. We found that detection probability was negatively correlated with high tide height, while positively correlated with wind strength in two species (Table 1). Detection probably decreased when tide height was very high because such tides inundate most of the roost sites in Moreton Bay, making them unavailable to birds. This suggests that counts could have higher detectability if not carried out during the seasonally highest tides. Detection also increased under strong wind conditions for the two largest species: eastern curlew and bar-tailed godwit. This suggests these species seek shelter during high wind conditions, concentrating in roost sites and forming tighter easier-to-count flocks. Shorebirds therefore move between roost sites a substantial amount during the non-breeding season in response to local environmental conditions, and further research could help refine detection estimates.

In conclusion, we propose that population growth rates at a single site are influenced by environmental conditions across a migratory flyway, using data comprising (a) count data from one site, (b)

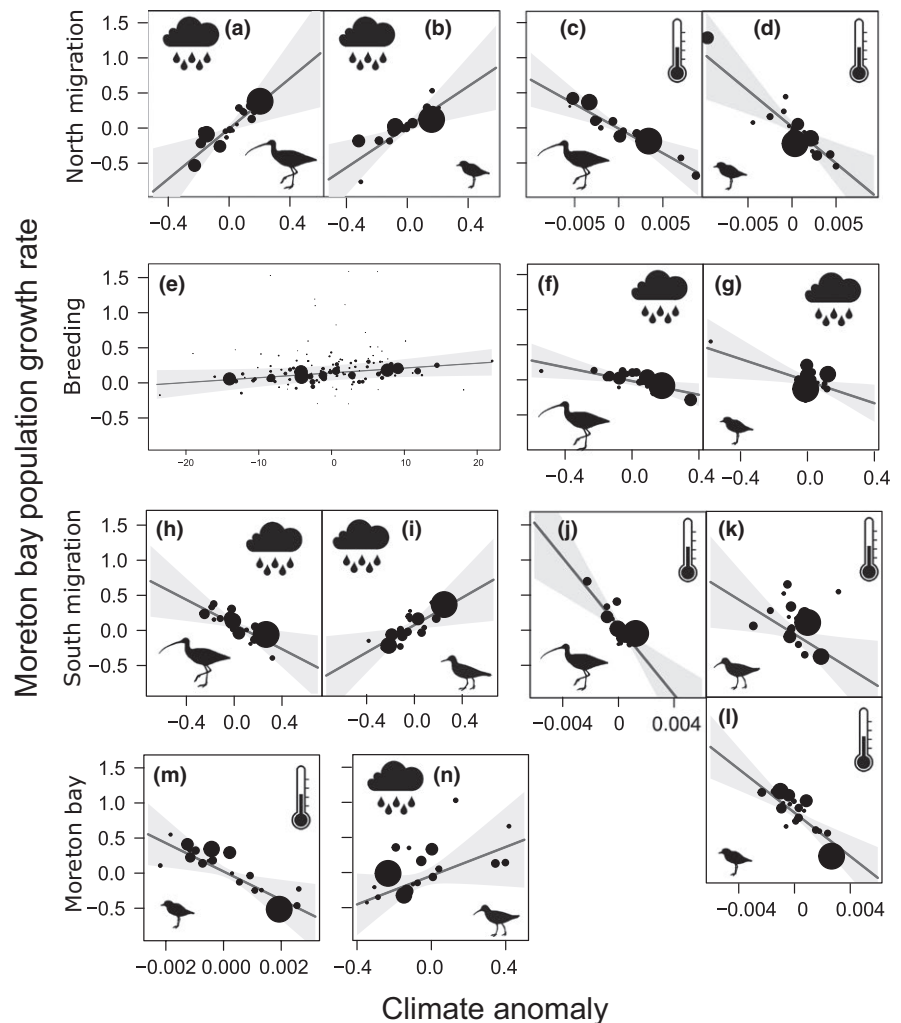


FIGURE 3 Significant species-specific growth rate responses to different environmental variables extracted from the combined model (Tables 2 and 3, and Supporting Information Appendix S5). Panels (a–d) represent north (pre-breeding) migration, (e–g) breeding, (h–l) south (post-breeding) migration and finally (m–n) non-breeding for (a) eastern curlew north migration (NM) rainfall anomaly, (b) lesser sand plover NM rainfall anomaly, (c) eastern curlew winter temperatures before NM, (d) lesser sand plover winter temperatures before NM, (e) date of snowmelt for all species, (f) eastern curlew breeding rainfall anomaly, (g) lesser sand plover breeding rainfall anomaly, (h) eastern curlew south migration (SM) rainfall anomaly, (i) grey-tailed tattler SM rainfall anomaly, (j) eastern curlew SM temperature anomaly, (k) curlew sandpiper SM anomaly, (l) lesser sand plover SM temperature anomaly, (m) lesser sand plover Moreton Bay temperature anomaly on arrival and finally (n) curlew sandpiper Moreton Bay rainfall anomaly at departure

remotely sensed environmental data and (c) a list of potential stop-over sites. Our research provides a much needed first step in understanding how conditions across 160 stopover sites, up to 11,680 km apart, can cumulatively influence population dynamics locally in Moreton Bay. We suggest that the driver of population declines (habitat loss) carries over to increase the likelihood that climatic fluctuations will impact population fluctuations. Thus, climate and habitat loss can be managed differently, with different benefits for population dynamics. Indeed, climate management, though important for many species beyond shorebirds, is a long and slow international process, while the protection, management and creation of intertidal habitats could more rapidly and effectively help alleviate the long-term pressure these shorebirds are under. Indeed, strategic conservation investment can result in win-win situations for both shorebirds and people (Dhanjal-Adams, Mustin, Possingham, & Fuller, 2016; Hansen et al., 2018; Kelly & Condeso, 2017; Stigner, Beyer, Klein, & Fuller, 2016). This research is a small piece in a larger puzzle, and both expand our understanding of correlates of variation in annual growth rates in one of the world's most threatened migratory flyways, while also providing a transferable method of analysing

population dynamics in migratory systems with limited or spatially biased data.

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DATA ACCESSIBILITY

Code is available in appendices. Shorebird count data are available upon request from the QWSG (<http://waders.org.au>). Remotely sensed environmental variables are freely available for download from NOAA Earth System Research Laboratory (<https://www.esrl.noaa.gov/psd/data/gridded/>).

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BIOSKETCH

The authors study the effects of human-driven environmental changes on wildlife populations, and how best to reverse these impacts.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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