Electric crows: powerlines, climate change and the emergence of a native invader

S. J. Cunningham, C. F. Madden, P. Barnard and A. Amar

ABSTRACT

Aim Climate change and other anthropogenic global change drivers act in complex, mutually exacerbating ways to alter the abundance and distribution of species. In South Africa, pied crows Corvus albus have increased in numbers and range in recent decades. Popular opinion links these changes to urbanisation and infrastructure development, but there has been no empirical test of this idea. We aimed to clarify the drivers of pied crow population changes in South Africa.

Location South Africa.

Methods We used publicly available long-term datasets, the Southern African Bird Atlas Project and University of Delaware Gridded Climate Database, and spatial data from government bodies, to assess relationships between pied crow population and range changes, land use, infrastructure, urbanisation and climate change.

Results Pied crow numbers have increased significantly in the past three decades, but rate of increase varied geographically, with crows declining in the northeast and increasing in the south-west of South Africa. Pied crow population changes were strongly correlated with climate change. Crows have benefited most from climate warming in the shrubland biomes of south-western South Africa. Pied crows are tree nesters, and within these shrublands, there is a strong positive relationship between the rate of population increase and the density of powerline infrastructure, which may facilitate pied crows’ increase by providing nesting sites.

Main conclusions Pied crow numbers have increased in response to climate warming, with their spread facilitated by electrical infrastructure in south-western South Africa, providing a clear example of compound influence of multiple global change drivers promoting a significant change in species range and reporting rate. Pied crows are generalist predators and there is popular concern about their ecological impact in areas where increases have occurred. We highlight the importance of understanding the ecosystem-level implications of increased numbers of pied crows in South Africa’s shrubland biomes.

Keywords climate change, Corvus albus, Karoo, native invader, powerlines, range change.
The effects of climate change on biological communities are also compounded by other anthropogenic impacts (e.g. habitat modification, overexploitation of species and species introductions; Brook, 2008). In particular, anthropogenic habitat modification has large effects on the ability of species to respond to climate change by range shifting (Hof et al., 2011) and may alter the direction or speed with which species can to shift. The combined effects of climate and other anthropogenic changes are expected to be much more severe than in isolation (Root et al., 2003; Mantyka-Pringle et al., 2012), and compound effects are expected to be common (Mora et al., 2007; Brook, 2008; Kampichler et al., 2012). Significant reshuffling of biological communities as a result of diverse drivers of global change is already occurring (Le Roux & McGeoch, 2007, 2008; Hawkins et al., 2008), with largely unknown consequences for ecosystem functioning and conservation issues. Under such circumstances, convincingly disentangling climate change from other anthropogenic drivers of changes in species’ ranges and abundance is difficult, and to date has received limited investigation (Grenouillet & Comte, 2014). A better understanding of how other environmental factors interact with climate change will be vital if we are to explicitly account for such issues within predictive statistical models (Grenouillet & Comte, 2014).

Currently, much conservation research is preoccupied with declines of specialized, endemic or rare species (Peery & Henry, 2010; Herzog et al., 2012; Salmona et al., 2012). Conversely, when population expansions are explored, they are typically of invasive alien species (Hulme, 2009; Fennell et al., 2012). Significant reshuffling of biological communities as a result of diverse drivers of global change is already occurring (Le Roux & McGeoch, 2007, 2008; Hawkins et al., 2008), with largely unknown consequences for ecosystem functioning and conservation issues. Under such circumstances, convincingly disentangling climate change from other anthropogenic drivers of changes in species’ ranges and abundance is difficult, and to date has received limited investigation (Grenouillet & Comte, 2014). A better understanding of how other environmental factors interact with climate change will be vital if we are to explicitly account for such issues within predictive statistical models (Grenouillet & Comte, 2014).

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information). Hofmeyr et al. (2014) suggest that because reporting rates are monotonically related to abundance, albeit nonlinearly, they can be used to infer changes in abundance. We explicitly test the directionality of pied crow population change in South Africa, and explore the correlation with spatially explicit measures of change in temperature and precipitation as well as two measures of anthropogenic development: urbanisation and powerlines. Thus, we explore key drivers of change and test the evidence for a poleward shift in reporting rates, which has rarely been attempted for a southern hemisphere species. Finally, in an area where increases in reporting rates were apparent, we explore whether powerlines may have helped facilitate the observed increase.

**METHODS**

**Pied crow survey data**

We used data on pied crow occurrence from the first and second Southern African Bird Atlas Projects (SABAP1, 1987–1993, Harrison 1997; and SABAP2, 2007-ongoing; we used data up to August 2012; http://sabap2.adu.org.za/). SABAP is a citizen science survey, based on checklist surveys (also known as ‘cards’), which record all the bird species seen in a given area, over a given period of time (minimum 2 h, max 1 month). SABAP 1 was carried out at the scale of quarter-degree grid cells, QDGC, ca. 26 km × 27 km; SABAP 2 at the scale of pentads, nine pentads in one QDGC; ca. 9 km × 9 km. Checklists are submitted to SABAP by ‘citizen scientists’, > 5000 of whom are registered with the project. The mean number of checklist cards (‘repeat surveys’) submitted per QDGC in SABAP1 was 54 ± 115 SD (total cards submitted for SABAP1 > 140,000). The mean number of checklist cards submitted per QDGC (collated from the nine pentads contained within each QDGC, to enable comparison between surveys) in SABAP2 was 49 ± 137 SD (cards submitted for SABAP2 to date, > 120,000). Further details of data collection protocol are supplied in the Supporting information.

Spatial and temporal differences in protocol introduce several difficulties, not insurmountable, in comparing SABAP1 with SABAP2 (Bonnevie, 2011; Bled et al., 2013; Loftie-Eaton, 2014). Despite this, similar estimates of population change have been found when comparing SABAP surveys with other independent surveys (Amar et al., in press). This suggests that, despite discrepancies between SABAP1 and SABAP2 protocols, SABAP data do enable accurate documentation of population changes (Hofmeyr, 2012).

For each QDGC, we used data on the total number of checklist cards and the number of checklist cards recording pied crows (‘positive cards’) to calculate a reporting rate for each cell in each period (number of positive cards/total cards). We assumed no false positives, i.e. that the species was always correctly identified. This was a reasonable assumption, as the species is common, large, conspicuous and highly distinctive.

**Environmental data**

Environmental data for each QDGC were extracted using ARCGIS, version 9.3 (ESRI 2011). Data sources for land use, infrastructure and climate are listed below under the appropriate subheadings. The QDGC grid was reprojected to Albers Equal Area to minimise distortion. The area for each QDGC was tabulated using zonal statistics, setting the processing cell size at 100 m.

**Land-use data**

Appropriate data on changes in land cover and electrical infrastructure between SABAP1 and SABAP2 periods were not available. Instead, we sourced information on current levels of each of these. We also obtained information on the current protected areas status of each QDGC. Data extraction methods for these variables are described below.

**Land cover data**

We used the South African National Land Cover (version 1.1) (Van den Berg et al., 2000), which is derived from satellite remote sensing, to estimate the dominant land cover (%) within each QDGC. QDGCs were then assigned to one of seven groups, based on dominant land-cover type (classified as > 50% of total QDGC area), including: cultivated, degraded, natural grassland, plantation, shrubland, urban and bushland.

**Electrical infrastructure**

Data on electricity transmission and distribution lines (hereafter ‘powerlines’) were provided by the South African electricity public utility (Eskom 2011). Current existing powerlines were included, defined as existing, commissioned and decommissioned lines and all three categories were used (≤ 33 kV, 44–110 kV, ≥ 132 kV). The summed length (metres) of powerlines for each QDGC was calculated and was related to the cell area (km²) to derive powerline density, which was used in subsequent analyses.

**Protected areas**

Information on the amount of protected land within each QDGC was derived from the following datasets: National Protected Area Expansion Strategy 2002 (updated in June 2006, BGIS, 2011); World Database of Protected Areas (www.protectedplanet.org); and the National Biodiversity Assessment (BGIS, 2011). These databases included both formal protected areas (i.e. statutory protected areas) and informal protected areas (i.e. statutorily unproclaimed private nature reserves, game reserves and game farms). QFGCs were classified as protected if ≥ 50% area of their area was covered by formal or informal protected areas.
Climate data

We derived data on mean annual rainfall and temperature for each year between 1987–2010 from the Gridded Monthly Data Set from the University of Delaware’s Centre for Climate Research 1900–2010 (version 3.01; Matsuura & Wilmott, 2012). This dataset uses globally distributed land-based weather stations interpolated to the half-degree grid cell to provide monthly climate data. The half-degree grid cell resolution of this data meant every four adjacent QDGCs shared the same measure. The rate of change for each climate measure was calculated for each QDGC as the slope of a linear regression line fitted through each time series (Amar et al., 2006). To assess whether pied crows preferred (i.e. had higher reporting rates within) areas of certain temperature or rainfall, we also calculated a single value of the mean temperature (°C) or rainfall (mm) for each SABAP period, for each QDGC with positive cards for pied crows.

Statistical analyses

Only QDGCs which had at least five checklist cards in each SABAP survey were included in our analyses, to increase the reliability of the population change measure for each cell. This excluded 751 (37%) of QDGCs from the analysis. Cells where pied crows were never found in either period were also excluded. In total, we therefore examined change across 1155 QDGCs across SA (Fig. 1).

We used generalised linear models (GLMs) to assess changes in reporting rates of pied crows between SABAP1 and SABAP 2. These models were fitted with a binomial error structure and logit link function. Our response variable was the number of positive checklist cards in each QDGC, in each survey period, as the numerator; and the number of negative checklist cards in each QDGC, in each survey, as the denominator. In this way, we explicitly accounted for differences in survey effort (i.e. number of cards) between QDGCs and also within QDGCs between survey periods.

Pied crow population changes

We assessed in which areas of South Africa pied crows had highest reporting rates in SABAP1 and SABAP2, by examining absolute reporting rates in each time period (see Supporting information).

Drivers of change in pied crow reporting rates

We examined the influence of climate change and anthropogenic development on pied crow reporting rate changes at the scale of the entire country, using each QDGC as an individual observation. We explicitly accounted for potential spatial autocorrelation using a Generalised Linear Mixed Model with Penalised Quasi-Likelihood (GLMPPQL), with the latitude and longitude coordinates of each QDGC specified as an exponential correlation structure within the random component of the model (Dormann et al., 2007). We weighted our analysis by the log of the minimum number of checklist cards (in either survey period), to account for our increased confidence in the reporting rate change measure for QDGCs with a higher frequency of surveys. The log of this value was used, since we would expect confidence to increase as survey frequency increased, not in a linear manner, but rather to approach an asymptote at sites with more surveys.

Our response variable was a change metric calculated for each QDGC as follows: SABAP2 reporting rate/SABAP1 reporting rate + SABAP2 reporting rate (Amar et al., 2006, 2010). This metric returns a value between 0 and 1, with...
values > 0.5 indicating increases, and values < 0.5 indicating declines. These data were approximately normally distributed. In this analysis, we excluded all plots with zero counts in the SABAP1 surveys because these ‘colonization events’ would have a disproportionately higher value in the response variable than plots showing large increases of pre-existing populations (Amar et al., 2010, 2011). Exclusion of these colonization events resulted in the loss of 81 of 1155 QDGCs.

We predicted that drivers of pied crow population change could include: temperature change (represented by the slope of the temperature time series for each QDGC); precipitation change (represented by the slope of the rainfall time series for each QDGC); ‘urban’ land use (%); density of powerlines; or interactions between these four (e.g. a response to one factor could be facilitated by a change in another). We included all four explanatory variables and all two-way interactions in our initial full model.

Models were fitted assuming a normal distribution. Since GLMMPQL models do not provide an Akaike’s information criterion value (AIC), we used the predict function in R to derive a specialized r² value to assess the model fit. We assessed the significance of explanatory terms using their partial (Type III) significance values (χ² tests) from the full model including all terms (Whittingham et al. 2006).

A P-value < 0.05 was taken to indicate significance. All models were carried out using R version 3.0 (R Core Development Team, 2009).

RESULTS

Patterns of pied crow population change

Across South Africa, we found a significant increase in the reporting rates of pied crows between the two SABAP survey periods (mean reporting rates: SABAP1, 35%; SABAP2, 39.5%; χ² = 12.8, d.f. = 1, P < 0.001). Overall, reporting rate increased by around 13%. This increase masked differential changes across the range; 47% of the QDGCs showed increases (n = 584), and 25% more than doubled in reporting rates, i.e. > 100% increase. However, within 31% (n = 389) of QDGCs there were declines.

Declines occurred mostly in the east and increases in the mid-west (Fig. 1). Explicit examination of geographical patterns of change showed significantly stronger increases in pied crow reporting rates in the south and west of the country, compared with the north and east (reporting rate change along the y-coordinate; χ² = 93.5, d.f. = 1, P < 0.001; along the x-coordinate; χ² = 539.5, d.f. = 1, P < 0.001). This result was mirrored by examination of absolute reporting rates, which showed that pied crows were more common in the south and west of the country than the north and east during SABAP2; while in SABAP1 the birds were more evenly distributed geographically (see Supporting information). The south-west of South Africa is largely dominated by treeless Karoo and Fynbos shrublands (Mucina & Rutherford, 2006).

In keeping with the geographical patterns in reporting rate change of pied crows, we found significant increases not only in reporting rates in the shrubland, but also in urban areas (Fig. 2). None of the other five major land-cover types we assessed (cultivated, degraded, natural grassland, plantation and bushland) showed significant changes in pied crow reporting rates between SABAP1 and SABAP2 (Fig. 2, inset).

Exploring the potential drivers of pied crow population changes across South Africa

Habitat alteration outside of protected areas

Pied crow reporting rates were significantly higher in non-protected areas than protected areas in both survey periods (mean reporting rate across both periods: non-protected areas 38%; protected areas 15.5%; χ² = 4.4, d.f. = 1, P = 0.03). However, there was no significant interaction between protected area status and survey period (χ² = 0.2; d.f. = 1, P = 0.63). This suggests that reporting rate changes between SABAP1 and SABAP2 were similar inside and outside of protected areas, reducing the likelihood that habitat alteration outside of protected areas is the main factor driving pied crow increases, although ‘spill-over’ effects cannot be ruled out.

Climate change and anthropogenic infrastructure

The climate of South Africa has warmed most dramatically in the arid mid-west of the country, Fig. 3(a). Contrary to the assumption implicit in many climate change studies, temperatures have actually become, on average, cooler in northern latitudes of South Africa < 25° south of the equator (Fig. 3a). In the northeast where crow declines have been greatest, the climate has become cooler and has also tended to become drier (Fig. 3a,b). Drying of the climate is also occurring in the east and far south-west of South Africa, and, more slowly, in the interior (Fig. 3b).

Eskom maps of the current electricity grid show a much higher density of electrical infrastructure in the north and east than the south-west of the country (Fig. 3c).

After controlling for spatial autocorrelation, we found that changes in pied crow reporting rates between SABAP1 and SABAP2 correlated with changes in both temperature and precipitation, with increases in reporting rates being greatest in areas which had become warmer and where rainfall had declined the least (Fig. 4). There was no significant interaction between these variables on pied crow population changes, suggesting that crows respond to temperature and rainfall independently. We found no correlation between changes in reporting rates and current levels of urbanisation or powerline density (Table 1). We also found no evidence of an interaction between urbanisation or powerline density and either of the two climate variables on reporting rate change. This suggests that climate change had similar levels of influence on the pied crow population irrespective of the amount of anthropogenic influence.
In both SABAP1 and SABAP2 survey periods, reporting rate was closely associated with temperature. There was no change in the temperature ‘preference’ of the crows between the two survey periods; highest reporting rates in both periods occurred in QDGCs with mean annual temperature (averaged across 1987–1992 for SABAP1 and 2007–2010 for SABAP2) of 19 °C, with a steep drop-off in reporting rates in QDGCs warmer than this (Fig. 5).

Exploring potential drivers of pied crow population changes in shrubland areas only

Shrublands covered the largest area of QDGCs (1155 or 26.9% of QDGCs included in our analyses; Fig. 2), and were one of two habitat types in which pied crow reporting rates increased (Fig. 2 inset). However, this vegetation type is historically treeless (Mucina & Rutherford, 2006). Since pied crows are tree nesters (Maclean, 1993; Dean, 2005), it seems plausible that electrical infrastructure could have facilitated their response by providing nesting sites, allowing them to shift into a favourable climate space. Density of powerlines is on average 62% lower in shrubland than elsewhere in South Africa ($\chi^2 = 22.8$, d.f. = 1, $P < 0.001$, controlling for spatial autocorrelation), which could explain the lack of power of the model in Table 1 to find such an effect. We therefore decided to examine whether density of powerlines was correlated with changes in pied crow reporting rates in shrubland specifically, when controlling for spatial autocorrelation, climate change and urbanisation.

Considering only shrubland data, we found a significant relationship between increases in pied crow reporting rates, and the density of powerlines (Table 2; Fig. 6). Within shrublands, temperature and precipitation changes, and degree of urbanisation did not correlate with changes in pied crow reporting rates (Table 2).

DISCUSSION

We found that climate change and anthropogenic infrastructure have acted in concert to promote increases in pied crows...
crows in South Africa, particularly in the south-west of the country. This has resulted in a shift in the ‘centre of gravity’ of pied crows’ distribution, (sensu Fraixedas et al., 2015), but not exclusively in the poleward direction commonly expected (Erasmus et al., 2002; Hockey et al., 2011). This response may be explained by the highly non-uniform pattern of warming across South Africa over the past several decades. In keeping with other recent studies using weather-station data sourced from the South African Weather Service (Kruger & Sekele, 2012; Cunningham et al., 2013), our analyses of the University of Delaware’s Gridded Monthly Dataset (Matsuura & Wilmott, 2012) show that the south-western region of the country has warmed most rapidly since the late 1980s. The recent increases in pied crow reporting rates have correlated with this warming trend. In contrast, north-eastern regions of South Africa – closer to the equator – have in fact cooled, and pied crow reporting rates have declined in these areas. Thus, unlike the purely poleward (i.e. southerly) range shift usually predicted under an assumption of uniform warming, pied crows have responded by tracking their preferred temperature envelope both into the south, and strongly, the west. Although poleward range shifts are well represented in the literature (reviewed by Parmesan & Yohe, 2003; Parmesan, 2006), idiosyncratic shifts in species ranges or centres of abundance also appear relatively common (Chen et al., 2011; Tingley et al., 2012). In light of this, we caution that other studies exploring climate-related distribution changes should take into account observed patterns of climate change within the study region, as well as explicitly investigating potential non-climatic drivers (Grenouillet & Comte, 2014).

Increases in reporting rates of pied crows in south-western South Africa between SABAP1 (1987–1993) and SABAP2 (2007–2012) were principally driven by significant increases within the Karoo and Fynbos shrubland biomes, largely treeless habitats which dominate the landscapes of south-western South Africa (Fig. 2, Mucina & Rutherford, 2006). In these areas, pied crows have attained average reporting rates (as opposed to reporting rate changes) close to 50% in SABAP2, compared to approximately 22% in SABAP1. Within these habitats, changes in pied crow reporting rates also correlated with powerline infrastructure, with reporting rates sometimes exceeding 90% in shrubland areas with high powerline density in SABAP2. Correlations between powerline infrastructure and abundance have also been seen in other tree-nesting corvid species invading treeless environments (e.g. Howe et al., 2014). We suggest that in South Africa, powerline infrastructure plays a facilitative role, allowing pied crows to respond to increasingly favourable climate conditions via the provision of essential resources (e.g. nest sites).

Compound impacts of different anthropogenic drivers are increasingly being documented under global change (Kampichler et al., 2012; Grenouillet & Comte, 2014; Fraixedas et al., 2015). These synergies are expected to promote ecosystem reshuffling, resulting in novel communities and altered ecosystem function (Hobbs et al., 2009). Ecosystems may be especially strongly affected if some species become superabundant – even when these species are naturally occurring in the area (Gaston & Fuller, 2008). Such species

Figure 3 (a) Temperature (°C) and (b) rainfall (mm) trends in South Africa from 1987 to 2010; (c) current powerline infrastructure in South Africa. Values for (a) and (b) were derived from the slope of rainfall or temperature change over the 23-year period, the same time span over which changes in reporting rates of pied crows were examined. In figure (a) reds, oranges and yellows indicate warming trends, while blues indicate cooling trends. In figure (b) increasing precipitation is indicated by blue areas, while drying is indicated by red and orange areas. In figure (c), it can be clearly seen that South Africa’s electricity grid is densely developed in the east of the country but sparse across the mid-west. (Alber’s equal area projections.)
can become ‘native invaders’ if their increased abundance negative affects other native species within the ecosystem (Carey et al., 2012). The noisy miner in the box-ironbark

Figure 4 Rate of change of temperature (°C) and rainfall (mm), along a west-easterly (a, b) and south-northern (c, d) direction. Solid lines represents the changes in pied crow *Corvus albus* (Müller 1776) reporting rate, while dashed lines represent the environmental covariates. Data presented are rounded to the nearest degree latitude or longitude, means ± 1 SE presented for ease of visual interpretation. Analyses were carried out on the raw data set. Note the exceptionally close correlation between temperature change and reporting rate change in figure (a).

Table 1 Factors affecting change in reporting rates of pied crows *Corvus albus* (Müller 1776) across South Africa. Model output (significance, $\chi^2$, and parameter estimates) is from a generalised linear mixed model (penalised quasi-likelihood) controlling for spatial autocorrelation. Degrees of freedom (d.f.) for each model term was 1. All possible two-way interactions between main terms were fitted one by one, and discarded from the model as none were significant.

<table>
<thead>
<tr>
<th>Main term</th>
<th>Parameter estimate</th>
<th>$\chi^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.523 ± 0.022</td>
<td>580.3</td>
<td>&lt; 0.001***</td>
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<td>Rainfall</td>
<td>0.052 ± 0.022</td>
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<td>0.017*</td>
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<tr>
<td>Temperature</td>
<td>1.095 ± 0.506</td>
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<td>0.030*</td>
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<tr>
<td>Urban areas</td>
<td>0.0009 ± 0.001</td>
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<td>0.398 NS</td>
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<tr>
<td>Powerlines</td>
<td>0.000017 ± 0.00003</td>
<td>0.4</td>
<td>0.506 NS</td>
</tr>
</tbody>
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NS, non-significant.

*Significant at the 5% level.

***Significant at the 0.1% level.

can become ‘native invaders’ if their increased abundance negative affects other native species within the ecosystem (Carey et al., 2012). The noisy miner in the box-ironbark

Figure 5 The relationship between pied crow *Corvus albus* (Müller 1776) reporting rate and annual mean temperature values in both SABAP periods (mean ± 95% confidence limits). SABAP1: open circles with dashed line. SABAP2: filled circles with solid line.
Table 2 Factors affecting change in reporting rates of pied crows Corvus albus (Müller 1776) in shrubland only. Model output (significance, $\chi^2$, intercept, and parameter estimates) is from a generalised linear mixed model (penalised quasi-likelihood) controlling for spatial autocorrelation. Degrees of freedom (d.f.) for each model term was 1. All possible two-way interactions between main terms were fitted one by one, and discarded from the model as none were significant.

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<thead>
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<th>Main term</th>
<th>Parameter estimate</th>
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<th>$P$</th>
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<td>Intercept</td>
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<td>393.1</td>
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<tr>
<td>Rainfall</td>
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<tr>
<td>Temperature</td>
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<td>Urban areas</td>
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<tr>
<td>Powerlines</td>
<td>0.0002 ± 0.00007</td>
<td>9.6</td>
<td>0.002**</td>
</tr>
</tbody>
</table>

NS, non-significant.
**Significant at the 1% level
***Significant at the 0.1% level

woodlands of Australia is an excellent example. This aggressive passerine has increased in abundance apparently in response to a combination of habitat fragmentation and climate drying (Bennett et al., 2015). The presence of noisy miners in bush patches reduces the reproductive success of other native birds, especially those of smaller body mass than miners (Bennett et al., 2015).

Impacts of native invaders can be complex, and ecosystem perturbation following the emergence of a native invader may trigger trophic cascades (Carey et al., 2012; Butt et al., 2015). In South Africa’s shrublands, there is anecdotal evidence of heavy predation pressure by pied crows on threatened or restricted-range species (Fincham & Lambrechts, 2014) and of negative interactions with raptors (Simmons & Barnard, 2011). These reports suggest pied crows may profoundly impact relative abundances of other shrubland species, and may therefore fit the definition of a native invader. Corvids are highly visible birds and often provoke strong emotive responses in people, which may result in overestimation of their perceived impacts (Madden et al., 2015). Nonetheless, it seems likely pied crows may have complex impacts in the Karoo, because a major cause of nest failure in Karoo passerines is predation by snakes and small mammals (Nalwanga et al., 2004). A ‘native invasion’ by pied crows, as strong dietary and behavioural generalists, might suppress numbers of such mesopredators through direct predation (Dean, 2005). In theory, this could have the potential to alter entire trophic cascades. However, despite these concerns, the ecological consequences of increased numbers of pied crows in the Karoo and Fynbos remain unknown (Anderson, 2013).

Successful avian biological invaders, native or otherwise, are highly likely to be behavioural generalists (Sol et al., 2002). However, behavioural and dietary generalism need not correlate with generalist climatic tolerances. A particularly striking example of this is the Ethiopian bush crow, Zatvattariornis stresemanni. This species inhabits highly modified landscapes and is a dietary generalist with a complex range of behaviours, but is confined to an extremely narrow ‘climate pocket’ in the highlands of Ethiopia (Donald et al., 2012). Although less extreme than the Ethiopian bush crow, our data suggest pied crows might also be limited by climate, perhaps explaining their very strong response to recent warming. One of the most striking features of pied crows’ centre of abundance shift is the consistent manner in which the birds have tracked a ‘favoured’ temperature envelope across South Africa. In both SABAP1 and SABAP2, highest reporting rates of pied crows were in QDGCs with an average annual temperature of 19 °C, with lower reporting rates in hotter or cooler QDGCs (Fig. 5).

Climate change is ongoing, therefore, climate-driven increases in abundance of native species may be short lived, especially if behavioural generalism does not correlate with broad climatic tolerance and species are unable to adapt physiologically. That is, under a scenario of limited adaptive evolutionary response, we might expect to see ‘flux’ in populations of many species as the climate becomes first more, and then less, suitable for them. Although few vertebrate studies yet exist that are long-term enough to document such a process, transient responses to rising CO2 have been modelled for northern temperate forest trees (Solomon, 1986). The lack of evidence for an upward shift in pied crows’ realised temperature niche between SABAP1 and 2 (i.e. over the last 20 years) is in contrast to realised niche shifts observed in a number of studies of range expansion (e.g. Broennimann et al., 2007; Da Mata et al., 2009; Medley,
2010 and others). It is therefore possible that pied crows' 19 °C mean annual temperature preference might reflect a fundamental aspect of their thermal physiology. If so, current high reporting rates of pied crows in south-western South Africa may be a transient phase in their response to climate change: if average annual temperatures continue to warm past 19 °C, it is possible they will begin to decline again. However, even transitory changes in species abundance may leave a legacy of permanent effects. These may manifest as impacts on other resident species, leaving them vulnerable to extinction, or via priority effects, altering the ability of other species to respond to climate change (Gilman et al., 2010).

The current unprecedented level of disruption to ecosystems caused by compound effects of habitat alteration and climate change is likely to promote the emergence of ever more native invaders (Carey et al., 2012). The increase of pied crows in the shrublands of South Africa provides an important opportunity to better understand compound climate change impacts on terrestrial ecosystems. Elevated numbers of pied crows have the potential to alter the balance of interactions between this and other species, resulting in impacts that could resonate throughout shrubland communities (Winder & Schindler, 2004). Anecdotal evidence of potential threats to already uncommon species (Simmons & Barnard, 2011; Fincham & Lambrechts, 2014) suggests that detailed ecological research into the conservation impacts of pied crows is urgently needed. Such research will provide information desperately required by the conservation managers of South Africa (Anderson, 2013), while also improving our understanding of the impacts of native invaders, especially in the case that these invaders are dietary and behavioural generalists with the potential to directly affect multiple trophic levels within ecosystems.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** We provide details of the SABAP data collection protocol and assess whether the changes in abundance in Pied Crow populations in South Africa observed between SABAP1 and SABAP2 constitute a centre of abundance (‘centre of gravity’) shift in the population.

**Figure S1** Comparison of SABAP1 and SABAP2 reporting rates of Pied Crows along (a) latitudinal and (b) longitudinal gradients within South Africa.

**Table S1** Difference between SABAP1 and SABAP2 reporting rates of Pied Crows in eastern, western, northern and southern regions of South Africa.

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