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Potentially negative ecological consequences of animal redistribution on beaches during COVID-19 lockdown

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ABSTRACT

Significant changes in the intensity or distribution of human activities, like during the 2020 COVID-19 lockdowns, can cause rapid changes to the diversity, distribution and abundance of animals. These changes are usually viewed as positive for ecosystems. Here, we mapped the abundance and habitat associations of coastal vertebrates along approximately 50 km of ocean beaches on the Sunshine Coast in eastern Australia using baited trail cameras before (April–June 2018 and 2019) and during the April–May 2020 COVID-19 lockdown. Many Torresian crows (*Corvus orru*) occur in urban areas where they scavenge for human-derived food. When this food source collapsed during the COVID-19 lockdown, Torresian crows moved to beaches where we recorded a 6-fold increase in abundance. Torresian crows principally moved to beaches with greater extent of remnant vegetation and larger average tree height. Because anthropogenic food sources would be less abundant on these more natural beaches, rapid changes in the abundance of these aggressive feeders on beaches could result in Torresian crows 1) outcompeting scavengers like large raptors for naturally occurring carrion, 2) consuming insects, crustaceans and other small animals (like small mammals and reptiles) along more natural coastlines, causing potentially significant changes to animal assemblage structure along beaches, and 3) depredating eggs and hatchlings from nests of other birds. Our results highlight that the ecological effects of changes to human pressures are nuanced, depending strongly on the functional role and behaviour of species and the landscape attributes in which they interact with the broader assemblages and ecosystem.

1. Introduction

Human activities have pervasive effects on the diversity, abundance and distribution of animals across landscapes (García Molinos et al., 2015; Morrison et al., 2007). In many instances these pressures have caused fundamental changes to the species composition of ecosystems (Grimm et al., 2008; Halpern et al., 2008). There have, however, been several key examples globally of animal assemblages changing significantly and rapidly in response the removal of anthropogenic stressors (Duarte et al., 2020; Hostert et al., 2011; Letcher and Chazdon, 2009). Ecological shifts following reduced human activity are usually viewed as positive and result in biodiversity recovery, fewer conflicts between humans and wildlife, higher reproductive output of threatened species, and improved ecosystem condition and services (Manenti et al., 2020). Whether shifts in the diversity, abundance and distribution of species have positive or negative outcomes for ecosystems depends on the functional role and behaviour of species affected. For example, a plausible outcome of increases in aggressive, synanthropic (i.e. species associated with human activity) predators, may be the suppression and displacement of other species. Identifying how impacts like urbanisation and fragmentation affect ecosystems is crucial in understanding ecosystem recovery dynamics.

Urbanisation causes habitat loss and fragmentation (Fischer and Lindenmayer, 2007), changes animal diet and behaviours (Cronk and Pillay, 2020; Henderson et al., 2019; Hisano et al., 2016; Walker and Marzluff, 2015) and concentrates toxicants (Gilby et al., 2020). Synanthropic animals thrive in cities, where others have become locally extirpated (Faeth et al., 2012; Grimm et al., 2008; Henderson et al., 2020; Withey and Marzluff, 2009). For example, urbanisation often favours generalist species who can take advantage of a diversity of

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opportunities within urban landscapes including the provision of human-sourced food (Concepción et al., 2015; Olds et al., 2018). The immediate effects of reductions in human impacts may therefore be changes in the distribution of generalist and often competitively dominant species as their usual human-associated food resources reduce in availability (Concepción et al., 2015). This may have consequences for the diversity, abundance and distribution of other species across landscapes (Henderson et al., 2020).

Changes in animal diversity, abundance and distribution during the initial stages of reduced human activity are due to either population responses of rapidly reproducing species, or the movement of animals to seek new opportunities elsewhere. Therefore, the spatial positioning of sites within the broader landscape is often an important predictor of assemblage structure when impact levels change (Angeler and Alvarez-Cobelas, 2005; Crk et al., 2009; Goodridge Gaines et al., 2020). For example, sites that are well connected to previously impacted sites by their proximity to stretches of remnant vegetation may attract animals as they redistribute across landscapes. Such shifts in animal distribution are likely to be most pronounced for mobile species that can adapt to wide range of diets in a range of settings (Concepción et al., 2015; Piano et al., 2017). Understanding how assemblage-level changes affect the distribution of both species and the functions they perform is a key indicator of how ecosystem condition might change (Mouillot et al., 2013).

Lockdowns in 2020 due to coronavirus disease 2019 (COVID-19) resulted in governments restricting the movements and activities of people to encourage social distancing, causing substantial and unprecedented reductions in human activity worldwide (Saraswat and Saraswat, 2020). As a consequence, there have been both quantitative and anecdotal observations of animals changing in abundance or distribution during lockdowns (Bates et al., 2020; Rutz et al., 2020). These changes are typically viewed as positive for ecosystems, and often are, as they usually represent a perceived sensitive or iconic species returning to a former location or abundance. By contrast, we do not understand how synanthropic species may respond to massive changes in human-supplied food, and what consequences this may have for ecological assemblages and functions. It is possible that not all changes are positive at all sites within the broader landscape.

Human impacts and urbanisation are often centralised in the coastal zone, resulting in significant and sustained consequences for animal populations (Halpern et al., 2019). For example, beaches are important sites for recreation and support a suite of important coastal ecosystem services like fisheries and protection from storm surges and large seas (Barbier, 2015; Olds et al., 2017; Schlacher et al., 2014). Beaches are, however, under increasing ecological stress due to human activities and this has led to declines in beach condition globally (Schlacher et al., 2016). Coastal vertebrates (i.e. land based vertebrates in the coastal zone, principally mammals, reptiles and birds), including many species who regularly inhabit beaches (Schlacher et al., 2014), provide a suite of key ecological functions that support the resilience of beach ecosystems. For example, scavenging animals reduce the abundance of carrion that washes onto beaches from oceans, thereby reducing disease risk (Blandford et al., 2019). Predators regulate the abundance of prey species on beaches, thereby maintaining food web structure (Schlacher et al., 2014). Some coastal vertebrates move over many kilometres, including from human developments, to maximise feeding opportunities on beaches (Kimber et al., 2020; Schlacher et al., 2013), and so can be either positively or negatively affected by human activities. For example, a diversity of birds are negatively affected by increasing urbanisation in the dunes surrounding beaches (e.g. raptors like white bellied sea eagles and brahminy kites). Other groups, especially generalist species (e.g. silver gulls and Torresian crows) have increased in abundance substantially on beaches near urban developments (Huijbers et al., 2015; Huijbers et al., 2013). This means that many coastal vertebrates have the capacity to rapidly change their distribution in response to changes in human activity and so might redistribute readily during COVID-19 lockdowns.

In this study, we quantify whether the species richness, abundance and distribution of coastal vertebrates changed in response to the 2020 COVID-19 lockdown on beaches on the Sunshine Coast in central eastern Australia. COVID-19 lockdowns in the region were implemented rapidly and caused a reduction in human activity both on beaches and in nearby urban areas. We hypothesised that the assemblage structure of animals would change on beaches in response to changes in human activities during the 2020 COVID-19 lockdown and that the species driving this change would be highly mobile and abundant opportunists that can quickly take advantage of new conditions. Further, we hypothesised that the position of sites relative to urban developments and remnant vegetation would affect the distribution of animals during the 2020 COVID-19 lockdown.

2. Methods

2.1. Study area

Beaches on the Sunshine Coast are commonly used for recreation by both local people and tourists and occur along a gradient from highly urbanised with extensive nearby urban residential and industrial lands, to relatively natural dunes with extensive vegetation protected by national parks (Kimber et al., 2020). Previous studies in the region have shown relationships between both natural and anthropogenic features of the dunes and surrounding urban developments with coastal vertebrate assemblages (Huijbers et al., 2013; Kimber et al., 2020). We surveyed animals at 20 beaches, with 92 sites in 2018, and 100 sites in each of 2019 and 2020. Survey beaches were spread evenly across the Sunshine Coast and therefore represent the regional gradient of urbanised to relatively natural beaches (Fig. 1). Sites were surveyed in random order each year.

The 2020 COVID-19 lockdown changed the abundance and activity patterns of people both on and around beaches on the Sunshine Coast. The Queensland State Government declared a public health emergency on January 29th, 2020, following a suite of positive COVID-19 cases. COVID-19 lockdowns in the region were implemented in a staged process from April 2nd, 2020. From this date, residents were not permitted to leave their principal place of residence except for the essential needs of work, shopping for essential goods (i.e. food) and exercise. All outdoor gatherings were limited to either immediate family groups, or a maximum of two people from separate households. Restrictions were tightened again on April 9th, 2020, with all non-essential businesses being fully closed, and restaurants and cafes allowed to provide take away services only. The allowance for leaving a principal place of residence for exercise meant that local people were still able to walk and exercise on beaches, but that tourists were entirely limited from beaches during the survey period. The highest-level border restrictions for access to the state of Queensland were implemented from April 11th, 2020, and ordered that all international and interstate arrivals required a permit, and people from COVID-19 hotspots (all international arrivals, and specific locations within Australia) must undertake compulsory quarantine in hotels for 14 days. These restrictions prevented tourists from the Queensland state capital of Brisbane (located approximately 100 km to the south) and other regions from visiting Sunshine Coast beaches, thereby reducing the number of people potentially on beaches. Restrictions began to lift in a staged approach from 15th May 2020, with stage one relaxations allowing retail shopping to recommence, restaurants and cafes allowed to open with 10 person maximum seating, and recreational travel restricted to locations within 150 km of a person's principal place of residence. Stage two of lifted restrictions began on June 1st, 2020. Our surveys in 2020 commenced on April 6th, 2020, and were completed by the end of May. This means that approximately the last two weeks of our surveys, encompassing three of our twenty beaches, were undertaken during stage one relaxations only. However, the fact that we surveyed our beaches in random order reduces the potential

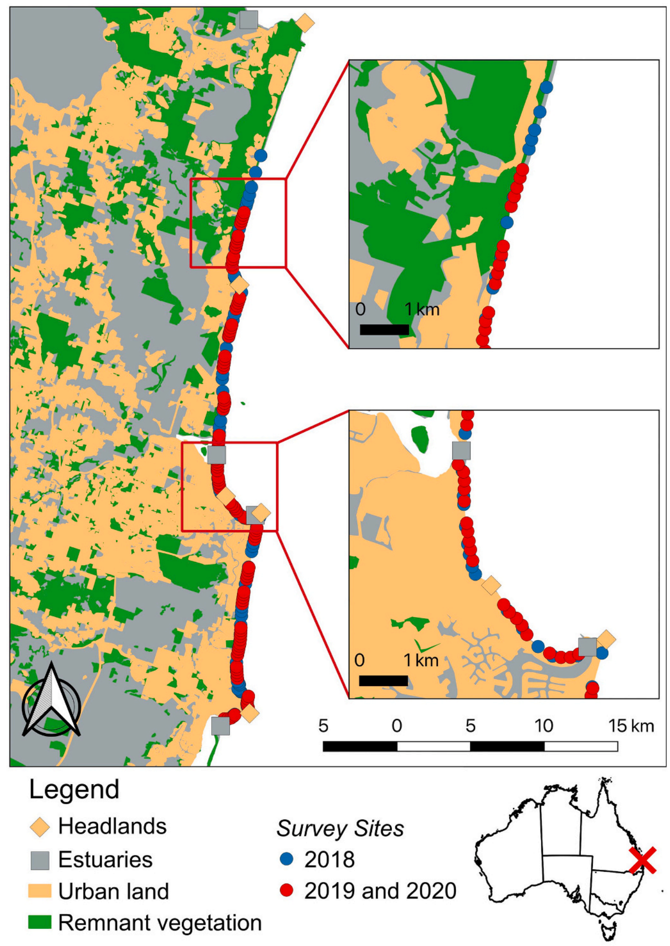

Fig. 1. Map of survey sites and key environmental features of coastlines and surrounding land.

for this to affect our results. Surveys in 2018 were undertaken in April and May, and surveys in 2019 were undertaken in June.

2.2. Coastal vertebrate surveys

We surveyed coastal vertebrates at all sites using baited motion detected trail cameras (either ScoutGuard Zero Glow or Browning DarkOps Pro, deployed randomly). Two cameras were positioned in the foredunes approximately 5–6 m from the baits, with one camera set to record 10 s high definition (i.e. 1080p) videos, and the other set to take bursts of three 16 megapixel images upon detecting movement around the bait. Cameras were set to the highest sensitivity levels possible to ensure that all animals were recorded. All deployments were baited with a single sea mullet *Mugil cephalus*. Cameras were deployed at each site at sunset on the first night of surveys with baits checked and replaced every 12 h for a 48 h total deployment period at each site. Coastal vertebrate assemblage structure was quantified as the maximum number of individuals for each species identified at any time during the 48 h survey period at each site. A maximum of twenty sites could be surveyed at any one time due to equipment limitations.

2.3. Data analysis

We included 12 environmental variables in analyses. All variables have been previously shown to be important in the distribution of coastal vertebrates in the region (Huijbers et al., 2013; Kimber et al., 2020; Meager et al., 2012). Firstly, we included the survey year to identify effects between years and of the 2020 lockdown. We included measures of the distance (in meters) of each site to the nearest headland, estuary mouth, urban land and remnant vegetation. We included the area (in square meters) of urban land and remnant vegetation within a 1, 2 and 5 km radius of each site. These radii were chosen as they best represent the usual home ranges of the animals surveyed (Huijbers et al., 2015). Finally, we included the average tree height at each site. This was measured by running a 100 m transect directly west into the forested dunes and measuring the height of each tree that intersected this line using a clinometer. Urban land and remnant vegetation maps were sourced from the Queensland Government (Queensland Government, 2015a, 2015b), and all spatial variables were calculated from these layers in QGIS (QGIS Development Team, 2020). All included variables had pairwise R values of <0.7.

We quantified correlations between environmental variables and the assemblage structure of coastal vertebrates (i.e. a matrix of species abundance by site) and identified indicator species using a ManyGLM in the *mvabund* package (Wang et al., 2012) of the R statistical framework (R Core Team, 2020). The ManyGLM was calculated using a negative binomial family and the best fit ManyGLM was identified using reverse stepwise simplification on Akaike's Information Criterion (AIC). Results of the ManyGLM were visualised using non-metric multidimensional scaling (nMDS) ordinations with Pearson vector overlays used to show effects of best-fit environmental variables and indicator species. We further interrogated the relationships between variables and indicator species from the best fit ManyGLM and coastal vertebrate species richness using generalised additive models (GAMs) in the *mgcv* package (Wood, 2019) of R. Best fit GAMs were also identified using reverse stepwise simplification on AIC. GAM overfitting was minimised by restricting models to four knots or fewer (k = 4).

3. Results

3.1. Assemblage composition

The composition of coastal vertebrate assemblages on beaches was best explained by the year of survey ($\chi^2 = 7.21$, p = 0.005), the proximity of sites to headlands ($\chi^2 = 13.27$, p = 0.001) and estuaries ($\chi^2 = 10.63$, p = 0.001), the area of natural vegetation within 1 ($\chi^2 = 7.7$, p = 0.001) and 5 km ($\chi^2 = 8.6$, p = 0.001) of each site, the area of urban development within 1 km of each site ($\chi^2 = 8.09$, p = 0.002) and the height of surrounding trees ($\chi^2 = 7.12$, p = 0.001) (Fig. 2A,B). These patterns were best explained by variation in the abundance of Torresian crows *Corvus orru*, domestic dogs *Canis lupus familiaris*, red foxes *Vulpes vulpes*, brahminy kites *Haliastur indus*, silver gulls *Chroicocephalus novaehollandiae* and black rats *Rattus rattus* (Fig. 2A,C).

3.2. Effects on species

We identified a significant decline in species richness at our sites between 2018 and 2019, and 2020 (Fig. 3A, Table 1). Here, species richness declined by 28.6% in 2020 (2.72 species) from its peak in 2019 (4.36 species). Similarly, domestic dog abundance was highest in 2018 (0.88 dogs/site) and 2019 (0.94 dogs/site) and declined by 63.8% during COVID-19 lockdown in 2020 (0.34 dogs/site) (Fig. 3B, Table 1). Neither species richness nor domestic dog abundance varied spatially according to the environmental variables tested in this study. Red foxes were also lowest in abundance in 2020 (0.13 foxes/site), having declined in abundance by up to 79.8% during COVID-19 lockdown (from 0.25 and 0.32 foxes per site in 2018 and 2019 respectively). However, red fox abundance also varied according to the proximity of sites to estuaries (Fig. 3C, Table 1). Here, there was a tendency for fox abundance to be greatest at sites approximately 5000 m from estuaries; however, the scale of this effect varied between years.

We identified significant changes in the abundance and spatial distribution of Torresian crows at our sites between years (Fig. 4, Table 1). Here, Torresian crow abundance was 597% higher in 2020 (2.79

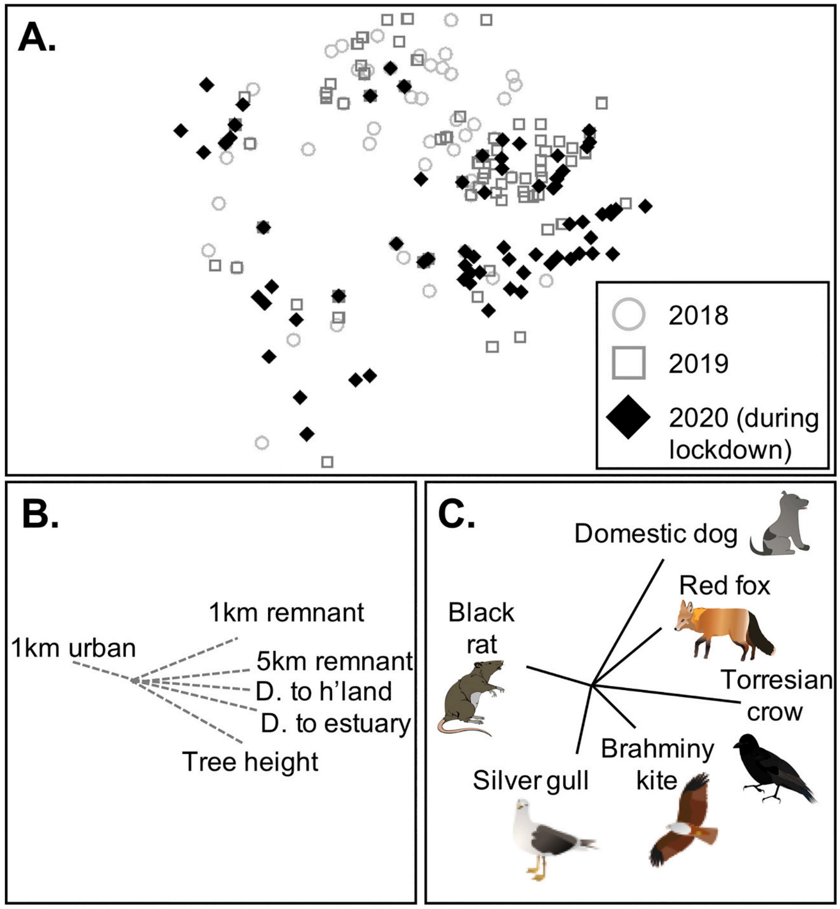

Fig. 2. (A) Non-metric multidimensional scaling ordination of assemblage level effects of (B) environmental variables, and (C) the key indicator species (identified by ManyGLM) driving this pattern. Vector overlays (B and C) are Pearson correlations. nMDS stress = 0.12.

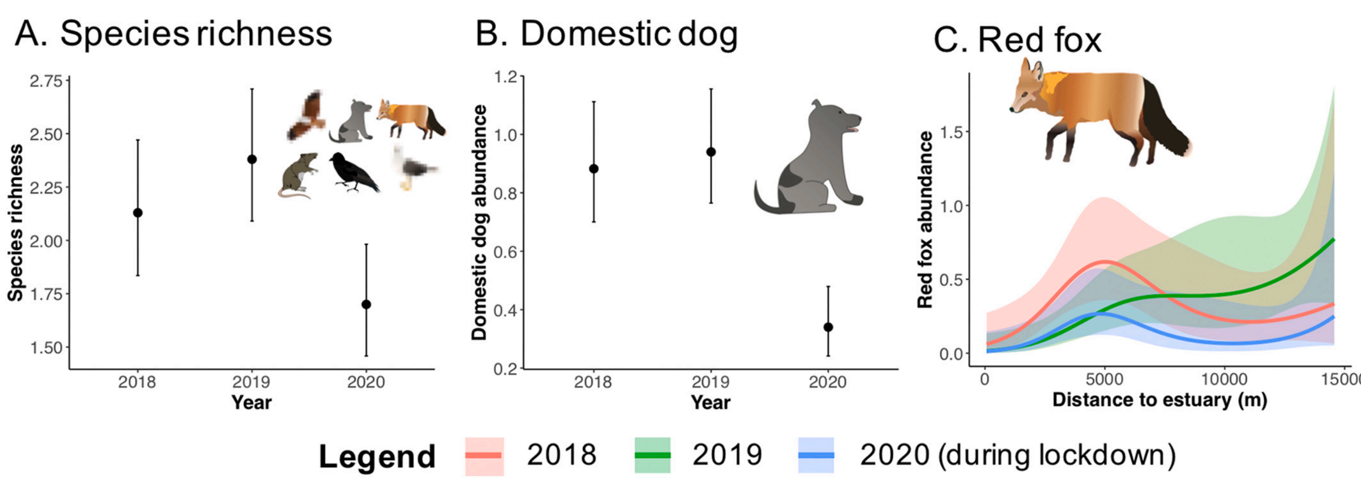

Fig. 3. Generalised additive model (GAM) outputs showing relationships between A) species richness, B) domestic dogs, and C) red foxes and significant variables from analyses.

Torresian crows/site) than in 2018 (0.4 Torresian crows/site), and 34.7% higher in 2020 than in 2019 (2.07 Torresian crows/site). Torresian crow abundance also varied significantly across the landscape according to the area of remnant vegetation within 5 km of the site, the area of urban development within 1 km of each site, the average tree height of each site, and the proximity of sites to headlands (Fig. 4). Here, Torresian crow abundance was 334% greater in 2020 than in 2018 and 2019 at sites with >10,000,000 m^2 of remnant vegetation within 5 km. Similarly, Torresian crow abundance was 146% greater in 2020 than in 2018 and 2019 at sites with <1,000,000 m^2 of urban development within 1 km. Finally, Torresian crow abundance was 49% greater in 2020 than in 2018 and 2019 at sites with average tree height >6 m.

We identified three indicator species from the best fit ManyGLM whose abundance varied spatially across our sites, but not between years, and so whose distribution was not affected by COVID-19 lockdown. Brahminy kites were in highest abundance at sites furthest from

Table 1
Significance of relationships between environmental variables and indicator species from the best fit MANY GLM model. Blank cells indicate no significant effect of the variable on that particular species.

Species	Year	Distance to headland	Distance to estuary	1 km urban area	1 km remnant vegetation area	5 km remnant vegetation area	Average tree height
Species richness	$\chi^2 = 10.46$, $p < 0.005$						
Torresian crow	$\chi^2 = 120$, $p < 0.001$	2018- $\chi^2 = 1.44$, $p = 0.6$ 2019- $\chi^2 = 28.38$, $p < 0.001$ 2020- $\chi^2 = 36.39$, $p < 0.001$		2018- $\chi^2 = 5.86$, $p = 0.12$ 2019- $\chi^2 = 2.9$, p-0.23 2020- $\chi^2 = 68.19$, $p < 0.001$		2018- $\chi^2 = 2.96$, $p = 0.32$ 2019- $\chi^2 = 40.29$, $p < 0.001$ 2020- $\chi^2 = 83.42$, $p < 0.001$	2018- $\chi^2 = 5.63$, $p = 0.08$ 2019- $\chi^2 = 53.44$, $p < 0.001$ 2020- $\chi^2 = 37.04$, $p < 0.001$
Red fox	$\chi^2 = 7.68$, $p = 0.02$		2018- $\chi^2 = 7.13$, $p = 0.06$ 2019- $\chi^2 = 12.69$, $p < 0.005$ 2020- $\chi^2 = 5.17$, $p = 0.15$				
Domestic dog	$\chi^2 = 27.84$, $p < 0.001$						
Brahminy kite		$\chi^2 = 28.49$, $p < 0.001$	$\chi^2 = 35.54$, $p < 0.001$			$\chi^2 = 36.01$, $p < 0.001$	
Silver gull			$\chi^2 = 24.57$, $p < 0.001$			$\chi^2 = 35.82$, $p < 0.001$	$\chi^2 = 51.95$, $p < 0.001$
Black rat		$\chi^2 = 42.73$, $p < 0.001$	$\chi^2 = 32.72$, $p < 0.001$				

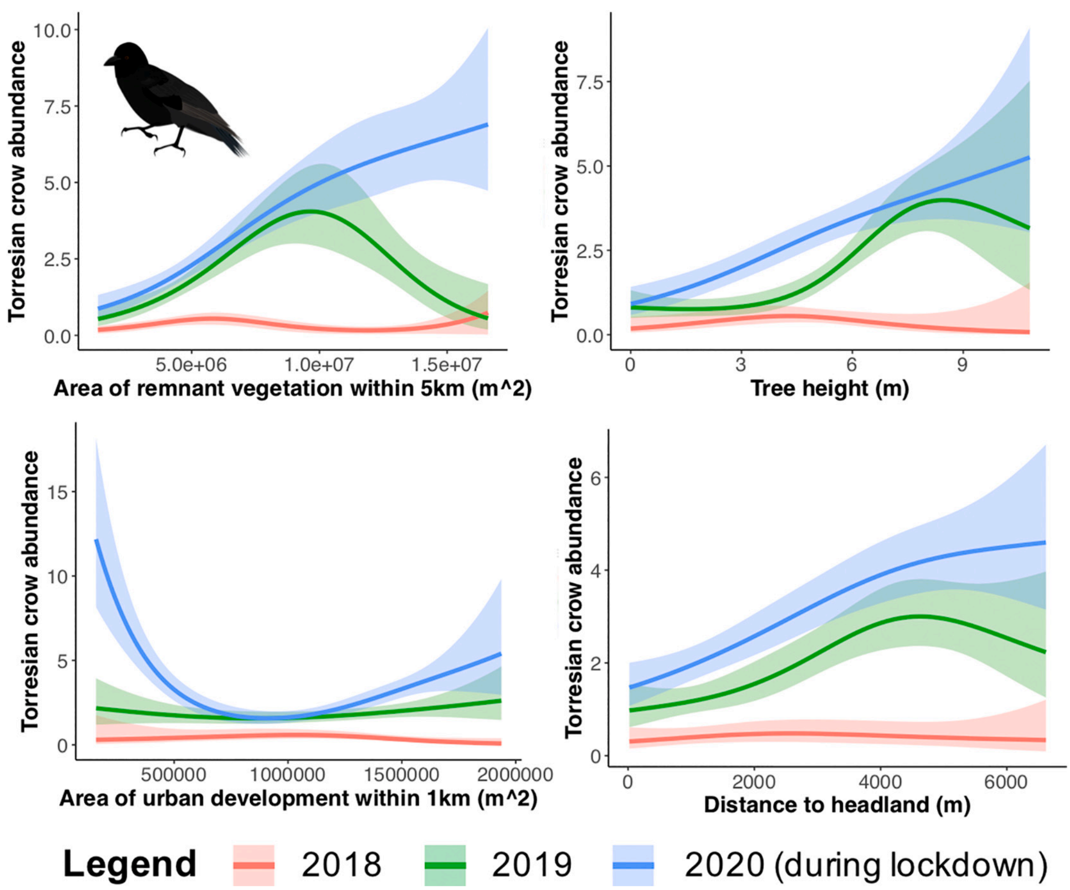

Fig. 4. Generalised additive model (GAM) outputs showing relationships between Torresian crow abundance and significant variables from analyses.

headlands, at intermediate distances to estuaries, and at sites with intermediate extent of remnant vegetation within 5 km (Fig. 5A, Table 1). Silver gull abundance reduced exponentially with increasing tree height, distance to estuaries and area of remnant vegetation within 5 km of each site (Fig. 5B, Table 1). Finally, black rat abundance decreased exponentially with increasing distance from headlands and estuaries (Fig. 5C, Table 1).

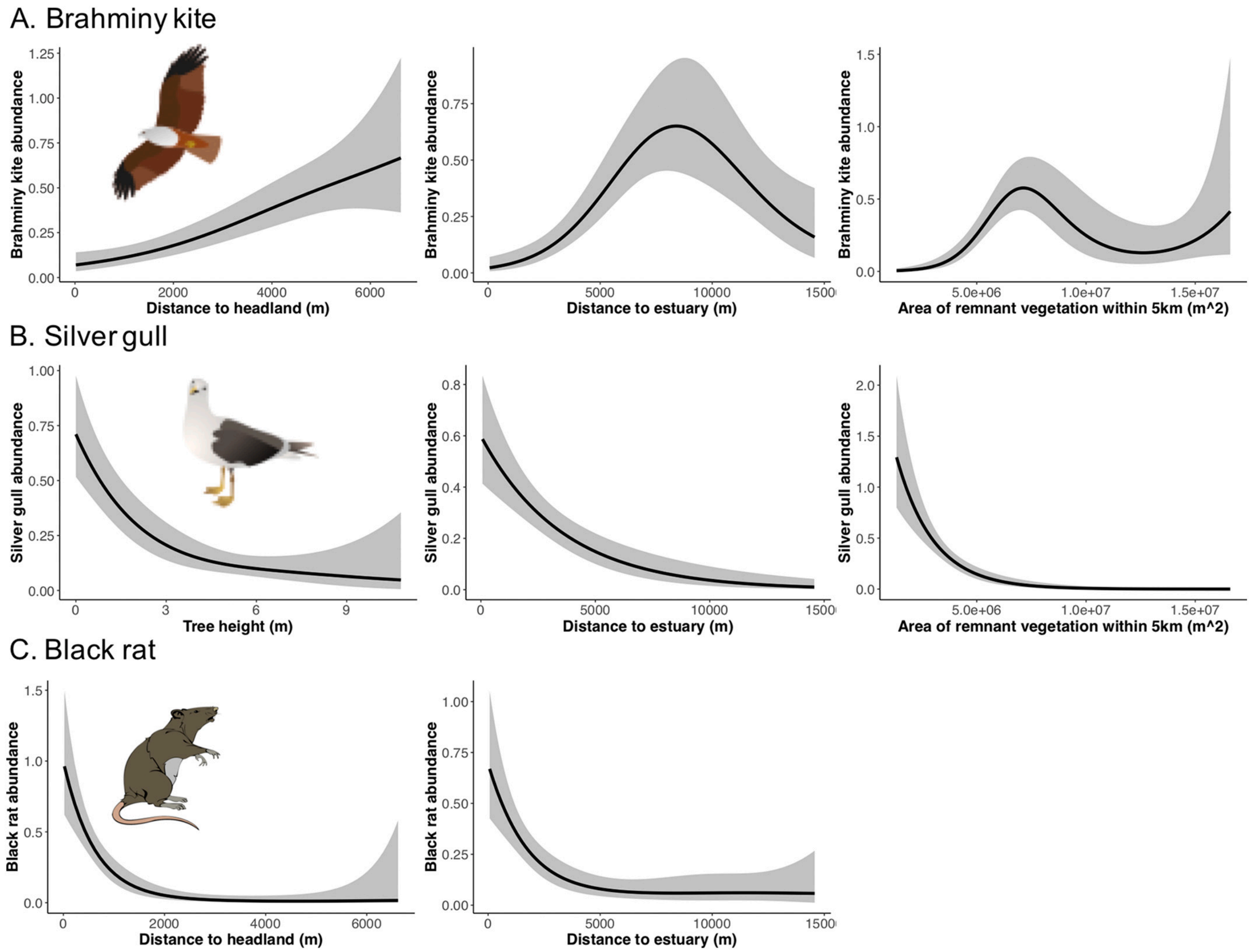

Fig. 5. Generalised additive model (GAM) outputs showing relationships between A) brahminy kite, B) silver gull, and C) black rat abundance and significant variables from analyses.

4. Discussion

Changes in the intensity and distribution of human activities can have implications for animal assemblages. There have been many examples globally of animals re-occurring at sites and species richness increasing during COVID-19 lockdowns (Manenti et al., 2020). For example, the ecological condition of many highly impacted beaches has improved due to the lack of tourists during COVID-19 lockdowns (Zambrano-Monserrate et al., 2020). Whilst these ‘lockdown effects’ are typically viewed as positive for the ecological condition of ecosystems, we cannot assume that lockdowns lead to ecosystems changing towards a more natural, ‘unimpacted’ state (Bates et al., 2020). In this study, we identified a significant change in the assemblage composition of coastal vertebrates on beaches during the 2020 COVID-19 lockdown on the Sunshine Coast, Australia. These assemblage-level differences were caused by changes in the abundance of a variety of coastal vertebrate species; from domestic dogs whose abundance is intimately tied to the presence of people on beaches, to Torresian crows whose abundance increased on beaches during lockdown, and red foxes whose abundance decreased on beaches during lockdowns. The stark increase in Torresian crow abundance on beaches during COVID-19 lockdown is concerning given their aggressive and generalist feeding behaviours (Clifton and Jones, 2017; Maslo et al., 2016b). Persistence of this pattern could have consequences for ecosystem condition.

The 2020 COVID-19 lockdown caused a significant change in the activity level and distribution of people across the Sunshine Coast. Travel restrictions limited people to their principal place of residence and reduced the number of tourists. There was some anecdotal evidence of a slight increase in the number of local people exercising on beaches in the region during the lockdown, but it is unlikely that this would have offset the loss of tourists. Data to support this assumption is lacking. Our assumption is, however, further supported by the significant decline in domestic dogs detected on beaches during COVID-19 lockdown. Domestic dogs cannot roam freely in this region, and so were not simply roaming from their homes to the beach during any of our surveys. Therefore, domestic dog detections on our trail cameras were due to them exercising off leads with their owners on beaches. We know that dogs were correctly identified as domestic dogs because all had collars and were breeds typically kept by people in the region. We identified two dogs during the study that were clearly ‘wild’ dogs because 1) they are known wild dogs by people in the area and the local council, and 2) they were detected on trail cameras only at night when domestic dogs are no longer on the beach.

Arguably the key change in human activity that affected the results of this study was the reduction in human activity around industrial, entertainment, dining and retail precincts during COVID-19 lockdown; all non-essential businesses were shut entirely during the lockdown, and restaurants and cafes could provide take away services only. This means that animals that had relied on these locations for food, especially the Torresian crow, would likely have been forced to find new sources of food. Arguably, therefore, this clear pattern in reduced human activity around urban areas is more crucial to our result than whether the number of people changed on beaches during lockdown. Animals that originally occurred in these urban areas and that redistributed to beaches during lockdown would not have been negatively affected by even marginal increases in people on beaches as they are often well accustomed to human activity.

Torresian crows are highly abundant in urban and agricultural areas in Queensland, and take advantage of human activities to scavenge and prey on small animals in open environments (Everding and Montgomerie, 2000; Everding and Jones, 2006). Torresian crows have increased substantially in abundance in urban areas within the region in recent decades (Sinden, 2002; Woodall, 2004). We identified an unexpected spatial pattern in Torresian crow redistribution on beaches during COVID-19 lockdown. It might have been hypothesised that the abundance of Torresian crows on beaches would have been greater during lockdown at sites nearer to expansive urban areas given their usual association with these habitats. In this study, however, the opposite was true. We found that when Torresian crows moved to beaches, they preferred to inhabit sites with greater average tree height, greater extent of remnant vegetation and lower extent of urban land nearby. In this sense, we suspect that Torresian crows transitioned to a more natural diet of small animals (principally insects, crustaceans, small mammals and reptiles) whilst at these more natural locations (Clifton and Jones, 2017) as extensive anthropogenic food sources would be absent. Beach cast carrion is a randomly delivered resource from the sea, so there is no evidence to suggest that carrion is in higher abundance at natural beaches than at urban beaches in this region.

Persistence of this redistribution of Torresian crows to beaches with more natural features over a longer period of time would likely have three key ecological effects. Firstly, the aggressive feeding behaviour and abundance of crows could result in scavenging species (e.g. some raptors) being outcompeted for available carrion (Huijbers et al., 2015; Huijbers et al., 2013). This effect would, of course, be mediated by any potential redistribution of scavenger feeding behaviour. Secondly, a broadened and modified diet by Torresian crows could eventually have implications for prey populations like insects and small vertebrates in dunes (Clifton and Jones, 2017). Many of these prey species are either food for other animals, or provide vital ecological functions like plant pollination (Schlacher et al., 2014), and so this could have implications for ecological condition of these ecosystems if the pattern of Torresian crow redistribution persists. Confirmation of this hypothesis would have required dietary analysis of Torresian crows during lockdown, and this was not possible. Finally, Torresian crows have been shown in previous studies in this region to be significant predator of bird nests on beaches, including consuming both eggs and fledglings of small plover species (Maslo et al., 2016b). Therefore, ongoing presence of Torresian crows at these more natural beaches may have effects on smaller dune and beach bird communities. Whilst the patterns we found in this study are likely a temporary redistribution due to short-term change in human activity patterns during lockdowns, the results of this study give important insights into the potential effects of ongoing changes to the distribution and abundance of synanthropic species like the Torresian crow.

We found a significant decline in red fox abundance on beaches during the 2020 COVID-19 lockdown. This was somewhat surprising given the result for Torresian crows, as generally both Torresian crows and foxes share a similar opportunistic, generalist diet (Clifton and Jones, 2017; O'Connor et al., 2019). Local governments undertake extensive control programs within the region to reduce the abundance of the invasive red fox (Kimber et al., 2020), so increased control effort during the lockdown would have led to reductions in red fox abundance. However, there was no indication from local authorities of increased red fox control effort or success during the 2020 COVID-19 lockdown, and previous studies in the region have indicated a lack of significant effect of red fox control programs on the abundance of red foxes on beaches in the region (Kimber et al., 2020). Red foxes are cautious and tend to avoid active interactions with people. Red foxes are, however, highly effective opportunist species who can quickly take advantage of changes in human activities (Díaz-Ruiz et al., 2016; O'Connor et al., 2019). On the Sunshine Coast, red foxes typically associate with higher dunes and extensive nearby remnant vegetation; more natural beaches that are isolated from human populations and developments (Kimber et al., 2020). Reductions in human activity within residential landscapes might therefore have led to red foxes moving to feed in nearby urban lands where food may be in greater supply, but where there is typically too much human activity for them to preferentially occupy. The reasons for the pattern found in this study, therefore, require further investigation.

We identified three species whose abundance did not change between years, but which correlated significantly with spatial attributes of the beach and dune ecosystem. Brahminy kites preferred locations with lower topographic relief (far from headlands) and with intermediate landscape heterogeneity (estuaries and remnant vegetation); likely to maximise chances of identifying their key food resources of beach cast carrion (Bingham et al., 2018). Conversely, silver gulls and black rats preferred specific locations with greater food availability. Headlands and estuaries in the region are important sites for picnic and recreation grounds, likely leading to significant human food resource availability. These sites are likely favoured by silver gulls (who are simply not affected by human presence) and black rats (who feed at night when humans are absent), as opposed to Torresian crows who are less likely to occur in these areas of extreme human activity (Brown and Jones, 2016). Alternatively, it may have been that both silver gulls and rats have a lower capacity to redistribute during lockdowns as they have higher site fidelity. Our findings align with the results of previous studies both within this region (Kimber et al., 2020; Meager et al., 2012) and beyond (Lafferty, 2001; Maslo et al., 2016a; Maslo et al., 2019), and further highlight the importance of considering spatial and environmental variables when disentangling the effects of urbanisation on animal assemblages.

One caveat of our study is that surveys encompass only a single timepoint within each year and did not span several seasonal cycles. These effects are, however, controlled for somewhat by the fact that 1) surveys were undertaken in the same season each year and 2) COVID-19 lockdowns occurred only during the austral autumn, meaning that surveys for pre-lockdown effects were consistent between years. Our lack of human distribution data both on beaches and in nearby urban areas somewhat limited our capacity to make solid conclusions regarding the direct effects of human activity change on beaches for animals. Whilst no data was available for either pre- or during-lockdown periods, the result for domestic dogs (as discussed above) goes some way to supporting out assumptions here.

The long-term and pervasive effects of urbanisation on animal assemblages means that the immediate effects of reductions in human activities are likely to be the redistribution of animals that were formerly tightly associated with people (Concepción et al., 2015). We found significant changes in animal assemblages, mostly associated with changes in synanthropic species with respect to urban areas; findings that support our hypotheses. The potential negative effects of COVID-19 lockdowns and associated economic downturns (e.g. reductions in biodiversity conservation budgets, less ecotourism) are relatively well understood for conservation more broadly (Bates et al., 2020), however, potentially negative ecological consequences caused by the redistribution of animals are less understood (i.e. Torresian crows in this study). The effects of this experimental but temporary removal of human activities from landscapes provide important ecological information for ecologists and managers regarding the early recovery of ecosystems following human impact removal. These results highlight the importance of considering the ecological roles and behavioural ecology of species when anticipating the effects of human activity removal. They also provide important insights into the long-lasting and pervasive effects of urbanisation on ecosystems, and their capacity for recovery. We highlight the importance of considering the ecological implications of redistributing species, and the spatial footprint of these effects when anticipating the effects of human activity change on the condition and functioning of ecosystems.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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