TITLE: Distribution and abundance of large herbivores in a northern Australian tropical savanna: a multi-scale approach

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ABSTRACT: Australian mammals have exhibited exceptionally high rates of decline since European settlement 230 years ago with much focus on small mammals in northern tropical savannas. In these systems, little scientific attention has been given to the suite of grazing macropods, family Macropodidae, (common wallaroo [Osphranter robustus], antilopine wallaroo [O. antilopinus] and agile wallaby [Notamacropus agilis]). These species may be impacted by feral herbivores and contemporary fire regimes, two threats linked to small mammal declines. A multi-scale approach using aerial surveys, road surveys and camera trapping was utilised to determine the effects of feral cattle and fire on the distribution and abundance of large macropods in the North Kimberley bioregion. Feral cattle density and biomass exceeded that of macropods regardless of survey technique. Density estimates for cattle were up to 125 times higher (0.3-10.0 km^{-2}) than estimates for macropods (0.08-0.49 km^{-2}). Cattle biomass, based on the aerial survey estimates (corrected for perception bias), were 15 and 95 times higher than macropods for infertile (279 versus 19 kg km^{-2}) and fertile savannas (518 versus 5 kg km^{-2}), respectively. Proximity to the nearest pastoral station was a significant predictor of the aerial sightings of feral cattle ($p \leq 0.05$). Abundance and foraging activity of cattle were positively associated ($p \leq 0.05$) with recently burnt areas. In contrast, camera trapping showed agile wallaby and wallaroo occurrence and foraging were associated with longer unburnt areas ($p \leq 0.05$). Agile wallaby and wallaroo were negatively associated with cattle ($p \leq 0.05$) and showed substantial diurnal and seasonal separation consistent with an antagonistic interspecific interaction. Results also suggest that the agile wallaby is the primary prey of the dingo, not wallaroo. Collectively, this study suggests that recent landscape changes such as altered fire regimes and introduced herbivores have negatively impacted large grazing macropod species.

KEYWORDS: feral cattle, fire, landscape ecology, macropods, wildlife surveys

INTRODUCTION

Australian mammals have exhibited an exceptionally high rate of decline comprising almost 30% of all the world's known mammal extinctions since 1600 AD (Baillie et al. 1996; McKenzie et al. 2007). Around 10% of Australian endemic mammal species have gone extinct since European colonisation 230 years ago (Woinarski et al. 2015). Much of the recent focus has been on "critical weight range" mammals, marsupials and rodents with small body mass (35 – 5500g), in the northern tropical savannas declines are linked to introduced predators, competition and habitat degradation by feral and domestic livestock, and the increased frequency, size and severity of landscape fires following the decline of Aboriginal patch burning (Woinarski et al. 2001; Pardon et al. 2003; Legge et al. 2008; Woinarski et al. 2010; Woinarski et al. 2014). Notably, land clearance, which is a threatening process for many species globally, is not implicated in the northern Australian small mammal declines, reflecting that most northern savannas remain free of agricultural development (Woinarski et al. 2007; Bradshaw 2012).

Compared to the small mammal declines, little attention has been given to the conservation status of Australia's larger mammals (Ziembicki et al. 2015). Unlike the tropical savannas of Africa, the native Australian large herbivore assemblage now lacks megaherbivores (> 1,000 kg) and has few species greater than 20 kg. The large native herbivores with a widespread range across the savannas of northern Australia are all macropods (i.e. members of the marsupial family Macropodidae, including kangaroos and wallabies): common wallaroo (Osphranter robustus), antilopine wallaroo (O. antilopinus) and agile wallaby (Notamacropus agilis). These species occur in varied assemblages, with biogeographic patterns strongly controlled by terrain and climate (Ritchie and Bolitho 2008; Ritchie et al. 2008), often with other smaller macropods (e.g. rock-wallabies [Petrogale spp.] and northern nail-tail wallaby [Onychogalea unguifera]). A suite of marsupial megaherbivores became extinct in the late-Pleistocene, coincident with human colonisation (Johnson 2006; Johnson 2016). European settlers introduced large ungulate grazing animals (e.g. cattle [Bos sp.], water buffalo [Bubalus bubalis], wild horses [Equus caballus] and donkeys [E. asinus]), starting in the 1820s, at various places in northern Australia (Letts 1962). These species subsequently established feral (wild) populations, rapidly expanding and achieving higher densities than in their native ranges and predictions based on the body-size population density relationship (Freeland 1990). Lack of predation is likely a contributing factor to the success exhibited by introduced large herbivores since Australia’s largest predator, the dingo (Canis lupus dingo), is not large enough to kill adult individuals. Feral bovine success also suggests that introduced herbivores may be occupying an ecological niche that became vacant following the Pleistocene extinctions (Bowman et al. 2010; Reid et al. 2020).

Compared to the largest northern grazing macropods (55kg) bovines are much larger (> 10 times), are generalist bulk feeders, utilising both grass and browse, and have fundamentally different digestive systems (ruminant vs. nonruminant foregut fermenters; Sanson 1989; Bowman et al. 2010). Hence the dietary breadth of bovines and macropods is different in terms of forage quality and quantity, whereby macropods can utilise phytomass more efficiently than bovines, which are better able to adjust to fluctuating forage quality (Brown 1996; Poisot et al. 2011) by including browse (Bowman et al. 2010; Reid et al. 2020). In semi-arid and arid rangelands used for cattle and sheep production, the provision of water points, control of dingoes and promotion of pasture has led to population irruptions of red (O. rufus) and grey kangaroos (Macropus fuliginosus, M. giganteus) indicating that, in some settings, large populations of both groups can co-exist at high densities (Caughley et al. 1980; Calaby and Grigg 1989). However, in tropical savannas introduced herbivores especially feral bovines (cattle and water buffalo) can negatively affect native herbivore abundance directly by competing for high-quality forage, water and habitat, or indirectly by degrading the habitat (Taylor and Friend 1984; Petty et al. 2007; Bowman et al. 2011; Eldridge et al. 2016).

Surveys across Australia’s tropical savannas suggest some macropods (antilopine wallaroo) are declining (Ritchie 2007) although the ubiquity of this decline and drivers are poorly understood. Higher temperatures and more intense dry seasons associated with climate change may become a threatening process to large macropod populations in northern Australia (Ritchie et al. 2008) but are unlikely to have seriously affected population dynamics in the recent past. Introduced predators that have been linked to small mammal declines, feral cat (Felis catus) and European red fox (Vulpes vulpes), are unlikely to impact large macropods. The range of the European red fox does not extend into the tropics and feral cats are not known to predate adult large macropods. Although large macropods are predated by dingoes and wild dogs (C. lupus familiaris and C. l. dingo x C. l. familiaris) and previous studies, conducted primarily in the arid zone, have shown dingo abundance to impact macropod distribution and abundance (Letnic et al. 2012).

Similar to small mammals, changed fire regimes have been implicated in macropod declines in tropical savannas (Woinarski et al. 2014). The strongly seasonal rainfall pattern of the monsoon tropics leads to rapid production of tall grass during the wet season followed by desiccation during the dry season creating a high biomass of combustible grass with low nutritional quality. This annual 'boom-bust' cycle of forage quantity and quality, and the relatively weathered, infertile soils characteristic of Australian savannas, has been posited as the reason for low biomass of herbivorous mammals (Mott et al. 1985) when compared to the rest of the world's savannas (Calaby 1980). Aboriginal people used patch burning to provide nutritious 'green pick' for herbivores by setting numerous small fires throughout the dry season (Crawford 1982; Braithwaite 1991; Saint and Russell-Smith 1997; Murphy and Bowman 2007). This management approach is a form of pyric herbivory, an ecological process whereby herbivores follow post-fire nutritious resprouting grasses resulting in a patch mosaic of vegetation caused by differential grazing pressure (Fuhlendorf and Engle 2001). The Aboriginal socio-ecological tradition of patch burning drastically changed after European settlement (Russell-Smith 2001; Vigilante 2001; Edwards et al. 2003; Fisher et al. 2003; Russell-Smith et al. 2003; Legge et al. 2011b) shifting to large, high intensity fires burning predominantly in the late dry season in unmanaged landscapes (Vigilante 2001).

Introduced large herbivores may also be a potential driver of macropod decline. Experiments have shown that cattle stocking can be increased via nutrient supplementation and strategic patch burning during the dry season (Mott et al. 1981; Winter 1987). It is therefore possible that cattle and macropods compete for green pick, or that the combination of altered fire regimes and introduced large herbivores have reduced landscape productivity (Burbidge and McKenzie 1989). Indeed, some Aboriginal Traditional Owners show growing concern over the negative impact of inappropriate fire regimes and feral species on populations of large macropods (Wunambal Gaambera Aboriginal Corporation 2010).

The Uunguu Indigenous Protected Area (Uunguu IPA), in the North Kimberley bioregion of Western Australia, is an ideal location to study the interactions between macropods and feral bovines because it has never been used for pastoralism or experienced large-scale vegetation clearing, is little affected by economic development and has highly diverse savannas on both fertile and infertile substrates (Fig. 1). The feral herbivore assemblage is dominated by cattle, that have only recently spread from adjoining pastoral leases, with much smaller populations of wild horses and donkeys. Although modes of Aboriginal fire management were disrupted in the 1930s with the nearby establishment of Kalumburu Mission, the Uunguu IPA is currently managed by its Aboriginal Traditional Owners in a way intended to replicate the historical fire regime. In this setting we used a variety of survey methods to address three linked questions:

1) How do the density and biomass of native and non-native herbivores (macropods and cattle, respectively) differ?
2) Do the occurrence and abundance of macropods and cattle have similar environmental correlates, especially relating to time since fire?
3) Do macropods and cattle show competitive exclusion in space and time?

These questions are approached using a range of different methods applied at varying spatial and temporal scales (Fig. 2). At the landscape-scale, aerial and vehicle-based surveys were used to provide snapshot estimates of herbivore density and examine environmental correlates impacting landscape distribution of herbivores. Camera traps were used to gauge site-level environmental correlates of herbivore diversity, abundance and foraging on fertile and infertile substrates and evidence of on-going interspecific associations. These methods allow us to evaluate the hypothesis that cattle and macropods occupy separate niches and examine how both groups are influenced by fire. Dingo predatory impacts were considered when data were available.

METHODS

Study Area

This study was undertaken in the North Kimberley bioregion of Western Australia on the Uunguu Indigenous Protected Area (approximately 8,000 km^2), declared in 2011 and managed by the Wunambal Gaambera Aboriginal Corporation (WGAC, the Uunguu IPA is an IUCN category VI protected area; Fig. 1a). The vegetation is dominated by eucalypt (Eucalyptus and Corymbia spp.) savanna with a physiognomy of woodland and open forest with an understorey of hummock and tussock grasses on infertile soils and a mixture of perennial and annual tussock grasses on more fertile soils. The climate is defined by a monsoonal wet–dry seasonal cycle with mean annual rainfall of 1100-1700 mm across a steep latitudinal gradient (Fig. 1b; BMA 2018). Approximately 90% of annual rainfall occurs during the 5-month wet season (December-April), greatly impacting the availability of fresh water throughout the middle of the year.

Much of the landscape burns each dry season. Most fire ignitions are anthropogenic but lightning storms concentrated in the transition between the dry and wet season (October-December) can start fires. The mean fire return interval for the Uunguu IPA during this study was 2.5 years with 73% of fires occurring in the early dry season (before 1 August) and fires ranged in size from less than 1 to 21,500 ha, averaging 320 ha. Significant changes to the historical fire regime occurred around the mid-1900s because the Wunambal Gaambera people, the Aboriginal people of the region, had moved to nearby settlements and as a result traditional fire management ceased in most areas. A small community was re-established at Mitchell Plateau in the 1980s but fire management was limited in scale (Vigilante et al. 2004). Historical fire regimes have been better replicated in recent decades with the establishment of Aboriginal fire management programs (Vigilante et al. 2004; Vigilante et al. 2017).

The large macropod populations known to occur on the Uunguu IPA are the antilopine wallaroo, common wallaroo and agile wallaby. Macropods are an important traditional food resource for Wunambal Gaambera people, and culturally significant animals. Fire is used to manage forage and habitat mosaics for macropods and, less commonly today, to facilitate hunting them (Vigilante et al. 2009). Pastoral leases adjacent to the Uunguu IPA were established in the 1900s and cattle grazing intensified in the 1950s and 1960s, such that these leases became a major source of feral cattle dispersal. Johnstone and Burbidge (1991) documented the arrival of cattle at Mitchell Plateau in 1976 while some coastal peninsulas have remained cattle free due to exclusion fencing and rugged terrain (McKenzie and Belbin 1991). The Western Australian state government carried out an aerial shooting program at Mitchell Plateau from 2007 to 2017, initially targeting all cattle and subsequently only bulls (Corey et al. 2013). Although annual culls of up to 30% of the total cattle population occurred within the Uunguu IPA during the study period, cattle have a high maximum population rate of increase (0.17; Bayliss and Yeomans 1989b) resulting in only a modest population decline (13%). In addition, there is a high likelihood that cattle migrate into the Uunguu IPA from surrounding properties. All cattle in the study area are considered feral.

Aerial Survey

Aerial surveys were conducted in June 2016 and August 2017 to determine macropod and cattle distribution and abundance across the Uunguu IPA in the dry season (Fig. 1c). The survey methodology was based on established aerial survey techniques for wildlife populations (Caughley and Grice 1982; Bayliss and Yeomans 1989b; Marsh and Sinclair 1989). Overall there were 26 transects (17 in 2016 and 9 in 2017), on average 6.5 km apart and orientated east-west (except on peninsulas), with a mean length of 43 km, resulting in a coverage of 5.2% of the property. Surveys were conducted up to 3 h after sunrise or 3 h before sunset to capture daylight times of highest macropod activity.

A fixed-wing aircraft was flown at a mean altitude of 76 m (250 ft) above ground level and an average ground speed of 204 km h^{-1} (110 kn). Fiberglass rods were attached to aircraft wing struts to delineate a 200 m wide transect on each side. Each survey had three observers seated in the starboard middle and rear and port rear. Each observer rotated through the seat positions such that all combinations of two observers sat on a side together for a portion of the survey allowing for correction of perception bias described by the double-count technique (Caughley and Grice 1982). Two observers remained constant for the 2015 and 2016 surveys, but the third observer differed. Species (cattle or macropod), number of individuals and transect zone (inside, low, high, outside as marked by wing struts) were recorded for each sighting on digital voice recorders. Flight paths were logged using a handheld global positioning system (GPS) recording latitude, longitude, and date and time every 30 s which was divided into six intervals to provide estimated location every 5 s. Sighting location was determined by matching the date and time from the observer log with the flight path log, and the midpoint of the recorded transect zone. Error associated with sighting locations could be from estimated time lag between observation and nearest GPS record (up to 280 m, i.e. the distance travelled in 5 s at 204 km h^{-1}) and location within the transect zone (up to 50 m, i.e. the maximum distance from transect zone midpoint to edge of zone). Environmental data was collected at the start of each transect including air temperature at flying height, cloud cover percent and light conditions (bright or dull). Survey conditions averaged 28.7 ˚C, 8% cloud cover and 86% bright light conditions.

Population estimates

Perception bias correction factors for starboard and port side observations were 3.08 and 10.00 and 1.87 and 3.14, for macropod and cattle, respectively; these values were averaged across observers and habitats. Uncorrected and corrected (for perception bias only) population estimates were calculated using the ratio method for unequal transects in Caughley (1979b) following the method of Edwards et al. (2004) that was adapted from Caughley (1979a), Marsh and Sinclair (1989) and Caughley and Sinclair (1994). Observations outside the transect were removed for population estimates but included in the habitat association analysis. Correction factors for habitat or species were not applied because validated correction factors for both macropods and cattle within the study region do not exist. Densities were calculated based on transect area and herbivore biomass estimates were calculated using an average of 450 kg for cattle, the slaughter weight of shorthorn steers (DEDJTRV 2018), and 32 kg for macropods, the average of female and male weight limits for antilopine wallaroo, common wallaroo and agile wallaby (Menkhorst and Knight 2010).

Joint species distribution modelling

Aerial transect observations were further analysed with binomial Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al. 2017) to determine if herbivore groups (cattle, macropods) were associated with specific habitat characteristics and to examine species-to-species association. We used the 'HMSC' package in R (Blanchet 2018) that provides significance of environmental correlates for each species as well as the amount of variation each correlate accounts for in species occurrence. This package is a Bayesian joint species distribution model that allows for the examination of signals of environmental filtering and biotic filtering and was chosen for its ability to handle both joint species and single species distribution modelling within a single package. Only 2016 data were used for joint species modelling (macropod and cattle) because no macropods were sighted in the 2017 survey and there was concern that it was due to the varying conditions between 2016 and 2017 surveys including moisture conditions and different observers. Data from both the 2016 and 2017 surveys were utilised to model cattle distribution.

Pseudo-absences were randomly generated (n = 1000) within the aerial transects and added to aerial sighting data for analyses. Using the location of each animal sighting or pseudo-absence, a geographic information system (GIS) was used to associate time since fire, fertility, distance to perennial water and distance to nearest pastoral tenure. These variables were included in the model along with a species co-occurrence matrix (joint species on the 2016 survey) or cattle occurrence (cattle only from the 2016 and 2017 surveys). Convergence of parameters for all models was evaluated by visual inspection of the Markov chain Monte Carlo trace plots to ensure a representative sample from the posterior distribution before further evaluation of model outputs. The 95% central credible interval was used to assess the level of statistical relationship of cattle and macropods with a given environmental covariate. If the credible interval does not include zero, it can be concluded that this covariate relates positively or negatively (according to if the credible interval is above or below zero) to occurrence with this level of statistical support. The 'HMSC' package outputs include significance between each species and environmental covariates, percent variability associated with each covariate and a species-to-species correlation matrix assessing associations amongst species after accounting for all environmental correlates.

Land system pasture potential

A pastoral potential classification map was obtained from the Department of Agriculture and based on CSIRO land system mapping assessments (Speck et al. 1960), and overlaid with the Uunguu IPA boundaries. Each of the five pasture potential categories had a range of carrying capacity densities (e.g. very low: 1 – 2.5 animals km^{-2}), the minimum density was used to calculate a weighted average pasture potential for the entirety of the Uunguu IPA.

Road Survey

Seven transects were surveyed between 2015 and 2016 during the dry season months July-September following the approach of Ritchie et al. (2008; Fig. 1d). Transects were selected along existing road networks and based on dominant savanna fertility, fertile (n = 5) and infertile (n = 2), fire management and proximity to camera trap monitoring sites. Repeat surveys for each 5 km transect were conducted at each sampling period between one and three consecutive days consisting of two morning surveys (05:30-07:30 hrs) and two afternoon surveys (17:00-18:30 hrs) with an average of 3.6 ± 1.1 repeat surveys. Surveys were conducted with a vehicle moving 10-15 km h^{-1} while three observers visually scanned the surrounding area. Cattle or large macropod species, group size, burn status and GPS location on each transect were recorded for each sighting. A laser rangefinder was used to estimate visibility every 1000 m on each side of the road; with an average visibility of 88.7 ± 26.6 m. Average density estimates were calculated using transect length and average visibility for width using the mean of repeat surveys at each sampling period. Herbivore biomass estimates were calculated as above. No dingoes were sighted during road surveys.

Remote Camera Trapping

Site establishment and data acquisition

Monitoring sites (n = 11; 3-5 ha each) were selected to span geological formations that yield comparatively fertile soils (n= 7; Carson Volcanics) and relatively infertile soils (n = 4; King Leopold Sandstone and Colluvium and Alluvium; Fig. 1d) based on geological classifications (Geoscience Australia 2012; DMP 2010). These soils are some of the dominant soils across the Uunguu IPA and are representative of woodlands on fertile and relatively infertile uplands. The fertile sites are characterised by gently undulating to hilly terrain with shallow stony soils dominated by a mixture of perennial and annual tussock tall grasses; infertile sites are characterised by gently undulating sandstone terrain with sandy soils of variable depth dominated by a mixture of hummock grasses in the endemic Australian genus Triodia and perennial and annual tussock grasses. Sites were selected based on fire management and utilisation by both large macropods and feral cattle. Aboriginal Traditional Owners located sites in recently burnt and unburnt areas known to be historically good macropod habitat and areas were searched for macropod scat and cattle dung to confirm presence of both herbivore groups. Distance to nearest perennial freshwater source was calculated for each site (DLAWA 2003; Crossman and Li 2015). Fire history of each site for the duration of the project (2015-2017) and one-year previous (2014) was constructed from observations and a satellite-derived (MODIS) fire history (NAFI 2018). See supplementary material (S1) for detailed site descriptions.

Five cameras (RECONYX PC800 Hyperfire, RECONYX, Inc., Holmen, USA) were deployed across each site at various periods between 2015-2017 ranging from 31 to 294 trap nights (Fig. 1d). Camera trap records have been significantly related to macropod faecal pellet deposition in foraging areas (Morgan et al. 2018) so cameras were arranged to maximise visual coverage of potential foraging areas, without overlapping the fields of view. Areas around the cameras (~25 m^2) were cleared with a brush-cutter and cameras were attached to robust trees 1 m above the ground for fire protection and to reduce false triggers due to wind blowing the grass. Clipping the grass was necessary but likely to stimulate localised new growth if moisture conditions were suitable, however, we assume that a small area within a larger unburnt area would not be drawing in animals that were not already in the vicinity. Cameras were set to trigger mode with motion sensor on medium/high sensitivity, three photos per trigger with a 1 s interval between photos and a 1 min quiet period between triggers.

Images were classified as containing cattle, dingo or macropod species (if identifiable), number of individuals and behaviour. Due to the difficulty of positively identifying antilopine and common wallaroos in the night-time black and white photos these two large-bodied, closely related and morphologically similar species (Menkhorst and Knight 2010) were lumped together and are referred to as “wallaroos,” agile wallabies were separate, and a further category for unknown macropods was created for macropods unidentifiable to species (e.g. a blurred macropod hopping through the frame or a body part without identifying features). Behaviour was defined as foraging if the animal was clearly chewing or had its head down to the forage below, all other activities were lumped together. A measure of abundance of the top predator, the dingo, which may influence herbivore distribution was calculated per site based on monthly sightings. Date, time and temperature were automatically recorded for each photo. Temperature represents herbivore activity period as it is a continuous variable closely linked to time of day which was expected to show a divergent pattern for cattle and macropods; Julian date represents seasonal dryness. Distance to perennial water, site fertility, time since fire and a measure of dingo abundance (calculated as a monthly ratio of dingo photos to trap nights by site) were determined for each photo trigger.

Herbivore abundance

Across all sites, animal detections per trap night was compiled to provide an index of activity. Differences amongst species were tested using analysis of variance (ANOVA) and Tukey HSD for multiple comparisons where the overall ANOVA was significant ($p \leq 0.05$). Data were checked for normality and heteroscedasticity and log transformed prior to analysis.

The total number of individuals detected for each species at each site during each 2-week period that cameras were deployed was determined. The midpoint of each 2-week period was used to establish time since fire and Julian date to model total individuals detected. We also determined presence or absence of agile wallabies, wallaroos, unidentified macropods and cattle to calculate the total (native and non-native combined) herbivore species richness in each 2-week period. Unidentified macropods were only included if no other macropod group had been counted so that total species present ranged from 0-3; the unidentified macropod data were not included in any other analyses. Data were analysed using generalised linear mixed modelling to determine if effects of time since fire, site fertility, dingo abundance, and season on the total number of individuals of each species was similar to significant environmental correlates for basic detection data used in joint species modelling. This analysis was also utilised to examine a suspected interaction between substrate fertility and time since fire on herbivore abundance. Normal probability and residual plots were examined to determine appropriate distribution families. Total individuals detected per species were modelled using a negative binomial distribution in the 'glmmTMB' package in R (Brooks et al. 2017). Total trap nights per 2-week period per site was used as an offset for all models to account for incomplete 2-week periods and camera malfunction; site was included as a random variable.

Joint species distribution modelling

Camera trap detection/non-detection data were further analysed using binomial Hierarchical Modelling of Species Communities to determine environmental factors affecting presence (cattle, agile wallaby, wallaroos and dingo) and foraging behaviour (cattle, agile wallaby and wallaroos) and to examine species-to-species association and species-to-species effects on foraging. Model evaluation and interpretation as described in "Aerial Survey-Joint species distribution modelling" section.

Diurnal patterns of cattle, macropods and dingo

Diurnal activity profiles for cattle, agile wallaby, wallaroos and dingo were examined to determine the level of overlap in species at camera sites using the 'overlap' package in R to provide a non-parametric kernel density estimate using the default smoothing parameters recommended by Ridout and Linkie (2009).The coefficient of overlap, Δ, ranging from 0, no overlap, to 1, exact overlap, was calculated (Ridout and Linkie 2009).

RESULTS

Density and biomass of native and non-native herbivores

Landscape-scale: aerial survey and pasture potential estimate

A total of 96 animal group sightings were recorded during the 2016 and 2017 aerial surveys (72 cattle groups and 24 macropod groups). Mean group size (± SE) for cattle and macropod sightings was 2.4 ± 0.26 and 1.4 ± 0.12, respectively. Only groups recorded inside the transects were used for density estimates: 140 cattle in 54 groups and 33 macropods in 23 groups. The corrected (for perception bias only) population estimates for the Uunguu IPA (7,815 km^2) were 6,096 ± 1, 603 for cattle and 3,845 ± 1,343 for macropods, yielding densities of 0.78 and 0.49

km^{-2}, respectively. These represent a conservative estimate of the species' populations. Population estimates for cattle were 1.6 and 4.3 times higher than macropod population for corrected and uncorrected estimates with a precision of 24% and 26% for cattle (corrected and uncorrected estimates, respectively) and 27% and 35% for macropods. Cattle and macropod densities based on corrected population estimates were similar for infertile savannas (0.62 and 0.59 km^{-2}) but 6.8 times higher for cattle than macropods in fertile savannas (1.15 and 0.17 km^{-2}). Biomass estimates of cattle were 15 and 95 times higher than macropods for infertile and fertile savannas, respectively (Fig. 3). The pasture potential estimate based on land system mapping assessments for the Uunguu IPA was 1.45 animals km^{-2}.

Medium-scale: road survey

For all transects and sample periods there was only a single macropod sighting, two antilopine wallaroos, yielding an overall density estimate of 0.08 km^{-2}. Cattle were 125 times more abundant and had approximately 1800 times the biomass of macropods. A total of 164 cattle were sighted, yielding a density of 10.0 km^{-2} (Fig. 3).

Site-scale: remote camera trapping

Across all sites, a total of 3,703 triggers were recorded for cattle and macropods during 20,591 trap nights. Cattle had the highest total abundance (0.23 individuals night^{-1} vs. 0.07 and 0.08 night^{-1} for wallaroos and agile wallabies, respectively) as measured by detections per trap night ($p \leq 0.05$; Fig. 3).

Environmental correlates of occurrence and foraging of large herbivores

Landscape-scale: aerial survey

The joint species distribution model using 2016 aerial survey data showed that the greatest variability (38%) in macropod occurrence was associated with substrate fertility with a significant ($p \leq 0.05$) association with infertile savanna. Macropods were significantly ($p \leq 0.05$) associated with greater distance to the nearest pastoral lease, accounting for an additional 30% of variability in occurrence (Table 1). Cattle occurrence was not significantly ($p > 0.05$) related to any of the correlates (substrate fertility, time since fire, distance to perennial water and nearest pastoral station).

The single species distribution model for cattle occurrence showed significant ($p \leq 0.05$) effects of close proximity to pastoral stations, recently burnt areas and increased distance from perennial water, correlates explaining respectively 60%, 21% and 15% of the variation (Table 1).

Site-scale: remote camera trapping

Herbivore species occurrence and abundance

The joint species distribution model based on presence data of agile wallaby, wallaroo, cattle and dingo showed that the random variable (site) accounted for approximately 50% of variation for all species except dingo (Table 1). Agile wallaby occurrence was significantly ($p \leq 0.05$) associated with longer time since fire, cooler temperatures and the late dry season/early wet season ($R^2 = 0.22$). Wallaroo occurrence was significantly ($p \leq 0.05$) associated with longer time since fire, increased distance to perennial water and cooler temperatures and had the best fit of all species in the model ($R^2 = 0.57$). Cattle occurrence was significantly ($p \leq 0.05$) associated with recently burnt areas, proximity to perennial water, warmer temperatures, the late wet season/early dry season and low dingo abundance ($R^2 = 0.31$). Dingo occurrence was significantly ($p \leq 0.05$) associated with fertile savannas, proximity to perennial water and cooler temperatures ($R^2 = 0.13$).

Large herbivore abundance (total number of individuals per species per bi-weekly camera trapping period) was examined with single species GLMMs and was positively related to seasonal dryness for all species ($p \leq 0.05$) meaning that total individuals detected increased towards the end of the dry season/beginning of the wet season (Tables 2 and S2). Agile wallaby and cattle abundance were positively associated with dingo abundance in contrast to analyses using presence/absence data suggesting that higher dingo numbers are associated with areas with higher numbers of their potential prey species. The number of individual cattle was higher on recently burned areas whereas the number of agile wallaby increased in longer unburnt areas ($p < 0.05$) in agreement with joint species distribution analysis. An interaction between site fertility and time since fire was significant ($p < 0.05$) for the abundance of wallaroo. Total number of wallaroo decreased with time since fire on infertile sites and increased with time since fire on fertile sites until approximately 1.5 years post-burn, then declined (Fig. 4).

Foraging behaviour

Joint species distribution model results for wallaroo and cattle showed that site accounted for over 50% of variation in detection of foraging behaviour, with time since fire explaining an additional approximately 25% (Table 1). Observed wallaroo foraging was significantly ($p \leq 0.05$) associated with infertile savannas, longer time since fire, cooler temperatures, the late dry season/early wet season and higher dingo abundance and had the best fit of all species in the model ($R^2 = 0.51$). Observed cattle foraging was significantly ($p \leq 0.05$) associated with recently burnt areas, warmer temperatures and the late wet season/early dry season ($R^2 = 0.17$). Variation in agile wallaby foraging was largely explained by temperature (35%) and site fertility (24%) and significantly associated ($p \leq 0.05$) with infertile savannas, longer time since fire, increased distance to perennial water, cooler temperatures and the late dry season/early wet season ($R^2 = 0.20$; Table 1).

Interspecific relationships

Landscape-scale: aerial survey

There was no significant association between macropods and cattle sightings detected by the aerial surveys.

Site-scale: remote camera trapping

After accounting for environmental covariates, both agile wallaby and wallaroo were negatively associated with cattle ($p \leq 0.05$; Fig. 5a). Dingo and agile wallaby were positively associated ($p \leq 0.05$), and cattle and dingo were negatively associated ($p \leq 0.05$). Agile wallaby and wallaroo foraging had a significantly negative relationship after accounting for environmental covariates ($p \leq 0.05$) while cattle foraging was unrelated to either agile wallaby or wallaroo foraging (Fig. 5b).

Camera derived activity profiles show a distinct separation in activity period between species (Fig. 6). Cattle were active primarily during mid-afternoon and before sunrise. Agile wallaby were active during the night with peak activity before sunrise overlapping 73% with cattle while wallaroo were primarily active from before sunset and throughout the night without a distinct peak and a 57% overlap with cattle. The dingo activity profile was similar to the agile wallaby with 78% overlap during a 24-hour period.

DISCUSSION

This study was framed around three questions concerning (a) abundance (b) distribution and environmental controls, and (c) interspecific relationships of native and non-native large herbivores in a monsoonal eucalypt savanna using a range of methods that span local to landscape scales. We found that the density, abundance and biomass of feral cattle exceeded that of macropods, regardless of survey technique utilised (aerial survey, road survey, remote camera trapping). Cattle were most abundant in close proximity to pastoral stations while macropods were more abundant further from pastoral stations and on infertile, sandstone substrates. As expected by the pyric herbivory model, cattle occurrence and observed grazing were significantly associated with recently burnt areas, yet, contrary to the model, agile wallaby and wallaroo occurrence and foraging were associated with longer unburnt areas. Consistent with competitive exclusion, joint species distribution models revealed that macropods occurred with cattle less frequently than expected by chance, and temporal separation is evident both diurnally and seasonally. Below we contextualise our findings in light of previous studies of cattle and macropod abundance and distribution, their responses to landscape fire and theories of herbivore niche separation.

Abundance of cattle and macropods

Our landscape-wide estimate of cattle density was 0.78 cattle km^{-2} (aerial survey corrected for observer bias) though differing between fertile and infertile substrates (1.15 and 0.62 km^{-2}). This density estimate is slightly lower than the cattle density of 1.38 km^{-2} (uncorrected for observer bias or habitat) reported by an aerial survey conducted in 2008 covering approximately 10% of the Uunguu IPA, centred on infertile substrates that abutted a large area of fertile savanna (Corey et al. 2013). This is also similar to the minimum estimated cattle density (1.36 km^{-2}) derived from pasture potential based on land system mapping assessments for the same area (Speck et al., 1960). Our density estimate based on the aerial survey is around half (54%) of the minimum pasture potential estimate (1.45 km^{-2}) for the Uunguu IPA. Our density estimate is also lower than the typical carrying capacity of 1-3 cattle units km^{-2} for northern Western Australian pastoral lands (DPIRDWA 2018). This most likely reflects that the Uunguu IPA is not being managed for cattle production and that the feral cattle populations have been recently culled so are unlikely to have reached carrying capacity.

Our density estimates are broadly comparable to feral bovine densities recorded in other eucalypt savannas outside the study area using similar aerial and ground survey techniques, with ground surveys consistently producing higher estimates (Fig. 7; Ridpath et al. 1983; Bayliss and Yeomans 1989a; Koenig et al. 2003; Bayliss et al. 2006; Saalfeld 2006; Gorman et al. 2007; Australian Wildlife Services 2010; Eldridge 2012). Our density estimates are similar to those available for introduced bovines of similar size (Bos bateng and Bulbalus bubalis) in their native habitats (Hoogerwerf 1970; Eisenberg and Seidensticker 1976). Cattle biomass, based on the corrected aerial survey estimates, was estimated to be 351 kg km^{-2}, less than half the previously reported ungulate biomass for northern Australian monsoon tallgrass (Mott et al. 1981) and an order of magnitude less than large herbivore biomass estimates for some African savannas (8427 kg km-2; Damuth 1982). The success of feral cattle is likely, in part, due to a lack of natural predators and supports the view that the empty megaherbivore niche (bulk-feeding herbivores) in Australian savannas can be effectively filled by introduced bovines (Freeland, 1990; Bowman et al., 2010; Reid et al. 2020).

Macropod densities found in our study were much lower than those reported for pastoral landscapes in South Australia and central and southern Queensland (Caughley and Grigg 1981; Caughley and Grigg 1982; Caughley et al. 1985; Pople et al. 1998), where land management, including provision of artificial water points and dingo control, compensate for the competitive effects of high cattle densities (Fig. 8). Our macropod density estimates were also lower than less intensely managed tropical savannas in Western Australia, the Northern Territory and Queensland (Fig. 8; Croft 1987; Ritchie et al. 2008; Ritchie et al. 2009). For instance, ground-based surveys in the mesic savannas of the Northern Territory in the early 1980s provided substantially higher densities (up to 325 times higher) than this study (Croft 1987). One exception is the study of Koenig et al. (2003) that reported a very low (0.023 km^{-2}) uncorrected aerial survey macropod density (Osphranter robustus, O. antilopinus, O. bernardus) in Arnhem Land. Aside from land management, it is possible that soil infertility in the North Kimberley and Arnhem Land is the primary reason for macropod scarcity. However, there is some evidence that macropods are also declining. Ritchie (2007) provides anecdotal evidence of decline and road surveys during 2003-2005 in the North Kimberley, including our study area, reported a higher total density of antilopine wallaroos than this study (4 km-2 vs. 0.08 km-2; Ritchie et al. 2008) although whether this points to a trend in declining macropod densities in northern Australia's tropical savannas is unclear and highlights the need for further surveys. Such surveys must use a diversity of methods, as we have done, because of the variable sightability of macropods. For instance, using camera traps we found common wallaroos were abundant, yet this species was not sighted on our road surveys.

Regardless of the survey technique utilised (aerial survey, road survey, remote camera trapping) we have shown that the biomass of a large non-native herbivore (cattle) is much higher than the native herbivore biomass in the Uunguu IPA by 1 and 2 orders of magnitude (based on corrected aerial surveys) for infertile and fertile savannas, respectively. This pattern is even more pronounced in Arnhem Land where the biomass of non-native cattle and buffalo is 98 and 725 times higher than macropods, respectively (based on densities reported by Koenig et al. 2003). It is important to acknowledge that because habitat correction factors could not be applied for cattle and macropod density estimates, these differences may be exaggerated. Nonetheless, even when macropod densities are higher than cattle, the non-native herbivores still have higher total biomass. For example, on a pastoral lease in arid central Australia where the density of red kangaroos (*M. rufus*; 0.91 km^{-2}) is higher than cattle (cattle estimates were not corrected for visibility so represent a minimum population; Australian Wildlife Services 2010), non-native herbivore biomass is at least 1.2 times higher than that of red kangaroos. The vast difference in biomass between native and non-native large herbivores highlights the need to convert density measurements to have a more realistic understanding of feral herbivore abundance.

Distribution and environmental correlates

Cattle occurrence, abundance and foraging were influenced by both season and time of day (as represented by temperature). Cattle detections were less frequent at the camera trap sites towards the end of the dry season/beginning of the wet season but the number of total individuals detected was higher, suggesting larger group sizes later in the year possibly due to limited water resources towards the end of the dry season. Daily activity was associated with warmer temperatures and daylight hours, consistent with other studies (Borchard and Wright 2010).

Landscape distribution of feral cattle was closely associated with pastoral stations and post-burn regrowth and inconsistently associated with water points. Importance of proximity to historical distribution points suggests that bovines are opportunistically expanding from pastoral properties that border the Uunguu IPA. Geographic complexity across the property such as rugged sandstone may impede northward movement especially in the west and distribution is periodically being altered by aerial shooting programs designed to limit the spread and density of feral cattle. Landscape-scale occurrence and site-scale occurrence, abundance and foraging of cattle were all significantly associated with recently burnt areas consistent with multi-scale pyric herbivory, whereby herbivores are attracted to the nutritious regrowth following a fire event (Fuhlendorf and Engle 2001). Though it is well established that water points strongly influence bovine landscape distribution (Koenig et al. 2003; Allred et al. 2011), our analyses did not reveal such clear-cut relationships, most likely because of the persistence of ephemeral water sources into the dry season. Site-scale cattle occurrence was linked to perennial water but foraging was not, suggesting recently burnt areas are a stronger driving force (Allred et al. 2011).

In contrast to cattle, the landscape-scale distribution of macropods was associated with greater distance to adjacent pastoral properties suggesting macropods may be geographically displaced northwards as feral cattle expand from the south into the Uunguu IPA. We also found substrate fertility affects the distribution and abundance of macropods. Camera trapping suggests common wallaroo are common in infertile sandstone habitats, possibly on fertile substrates as well, whereas antilopine wallaroo are more strongly associated with fertile substrates (Ritchie et al. 2008). We found wallaroo occurred further from perennial water bodies while agile wallaby foraging was associated with proximity to water, corroborating previous literature on differences in physiological tolerance of dryness between wallaroo and the agile wallaby (Ritchie et al. 2009; Stirrat 2009). However, the ranges of the two wallaroo species are thought to be differentiated in part by their tolerance of water scarcity (Croft 1981; Letnic et al. 2014) where antilopine wallaroo require access to permanent water (Ritchie et al. 2008; Ritchie et al. 2009). Our inability to reliably differentiate the two wallaroo species prevented us identifying the environmental factors that differentiate these macropods across the study area.

Contrary to the pyric herbivory model, macropod occurrence, abundance and foraging were not simply associated with recently burnt areas and patterns varied between species. For the two wallaroo species, we found an interaction between fertility and time since fire whereby abundance was highest on recently burnt areas in infertile savanna and abundance increased in fertile savanna sites up to 1.5 years after a fire. Interactions between habitat and time since fire have been previously reported for both cattle and macropods (Vermeire et al. 2004; Murphy and Bowman 2007; Ritchie et al. 2008; Ritchie et al. 2009). The cause of this interaction could be related to avoidance of cattle on recently burnt fertile areas and the ability of macropods, with more selective feeding ecology, to utilise the smaller and more sparsely distributed amounts of green pick available on infertile substrates (Dawson 1995). Common wallaroo abundance has been previously linked to low fire frequency but antilopine wallaroo abundance has been shown to increase with late dry season fires (Ritchie et al., 2008, Ritchie et al., 2009) highlighting the importance of maintaining or reintroducing the seasonal heterogeneity of the historical Aboriginal fire regime known to affect macropod abundance (Murphy and Bowman, 2007). Fire management programs in the North Kimberley in recent years have reduced late dry season fires by 50% (Corey et al. 2016) in efforts to better control late dry season wildfires and generate carbon credits with the abatement of greenhouse gas emissions. Current carbon credit programs penalise participants for fires occurring after 31 July encouraging fire management programs to focus on early dry season burning (Carbon Credits 2018) which may have unintended ecological consequences (Corey et al. 2019). Such a management regime of only early dry season burning may be disadvantaging species that are highly dependent on grasses (including the antilopine and common wallaroo [Reid et al. 2020]) whereas incorporating mid-dry season and late dry season burning, if moisture conditions are appropriate to allow for green pick emergence, could produce new forage throughout the dry season. The spatial pattern of fire is also likely an important influence on macropod species abundance. For instance, in arid central Australia Codding et al. (2014) found common wallaroo scat densities were higher in early seral (recently burnt) patches with emerging green pick and mid-seral patches with longer time since fire where fruits and herbaceous browse had recovered. Ritchie et al. (2008) and Telfer et al. (2008) also note the nexus between fire mosaics and the abundance of common wallaroo.

Macropod activity was also linked to seasonal shifts and diurnal cycles. In contrast to cattle activity patterns, macropods were more abundant and foraged more frequent at study sites at the end of the dry season/beginning of the wet season and were detected and foraged more frequent in cooler temperatures linked to night-time or crepuscular activity, a result found previously for the common wallaroo and agile wallaby (Ealey 1967; Kaufmann 1974; Stirrat 2004). Green-Barber and Old (2018) similarly found that macropod occurrence and behaviour were dictated by season and time of day with feeding occurring most often at night and early morning in the summer and early morning to mid-afternoon in winter.

Interspecific relationships

Our findings of spatial and temporal partitioning of landscape resources between macropods and cattle may be a result of competition. Consistent with previous studies, we found cattle mostly foraged during the day while macropods foraged at night (Ealey 1967; Kaufmann 1974). Although we found no association between cattle and macropod presence with the aerial survey data, we did find a significant negative association at the site-level using camera trapping. Previous work across northern Australia has suggested cattle abundance was not an important factor for predicting wallaroo distribution (Ritchie et al. 2008; Ritchie et al. 2009). Elsewhere, competitive relationships between cattle and macropods is mixed and context-specific. Non-native and native herbivore interactions can be affected by habitat quality (Dudzinski et al. 1982; Daskin and Pringle 2016). For example, in Arnhem Land, feral herbivores are most strongly associated with more fertile habitat and native species with less fertile habitats (Koenig et al. 2003). In less productive semi-arid ranglelands, cattle production can be adversely affected by large macropod abundance (Kutt et al. 2012; Frank et al. 2016) but on improved pastures, there can be a positive association between cattle and macropods (eastern grey kangaroo) with little evidence of competition (Payne and Jarman 1999). Despite competition with higher densities of cattle, pastoral lands can sustain very high macropod populations in response to provision of water points and reduced predation by dingoes (Caughley et al. 1985). Herbivorous species have a higher potential for competition when resources are limiting (Dudzinski et al. 1982), especially with independent evolutionary histories (Davis et al. 2017). Although much of Australia's tropical savannas have high pasture productivity associated with the wet season, by the end of the dry season they can become nutrient deserts if there have been no fires to initiate new growth. Thus, it is possible that the most intense competition between cattle and macropods occurs at the end of the dry season and is strongly influenced by fire, or lack thereof. In addition to competition for food resources, predation by dingoes may be more heavily skewed towards macropods than cattle, given the positive association of dingo and agile wallaby and negative association with cattle, potentially impacting macropod landscape utilisation. Interactions between dingoes and macropods should be further studied to elucidate impacts of these predator-prey relationships.

Agile wallaby and wallaroo exhibited no antagonism in general occurrence, however, their foraging exhibited statistical spatial separation. The negative relationship between agile wallaby and wallaroo foraging is possibly due to fine-scale vegetation characteristics not accounted for in the model that relate to dietary niche separation between the species where wallaroo species would be expected to forage in areas with more grass and agile wallaby in areas with grass, browse and herbs (Croft 1987; Stirrat 2002; Murphy et al. 2007; Reid et al. 2020).

CONCLUSION

Using a multi-scale survey approach, we have found that feral cattle, a non-native herbivore, are more abundant in terms of density and biomass than the largest native herbivores in a little-modified Australian tropical savanna. Further, there is some evidence suggestive of population declines of macropods, which may be related to a contemporary fire regime of early dry season burning that has replaced the traditional Aboriginal practice of burning throughout the dry season, as well as competition with cattle for the highest quality forage resources. This study provides evidence to support cattle management/removal for the benefit of native macropods on conservation lands in savanna ecosystems. Multi-scale monitoring as applied in this study is essential to determine if large macropods are declining across northern Australia because camera trapping can record macropod species and behaviours that are often unidentifiable using aerial and road surveys. The ecological cause of putative macropod declines, including the nexus of soil fertility and season of burning, warrants further investigation.

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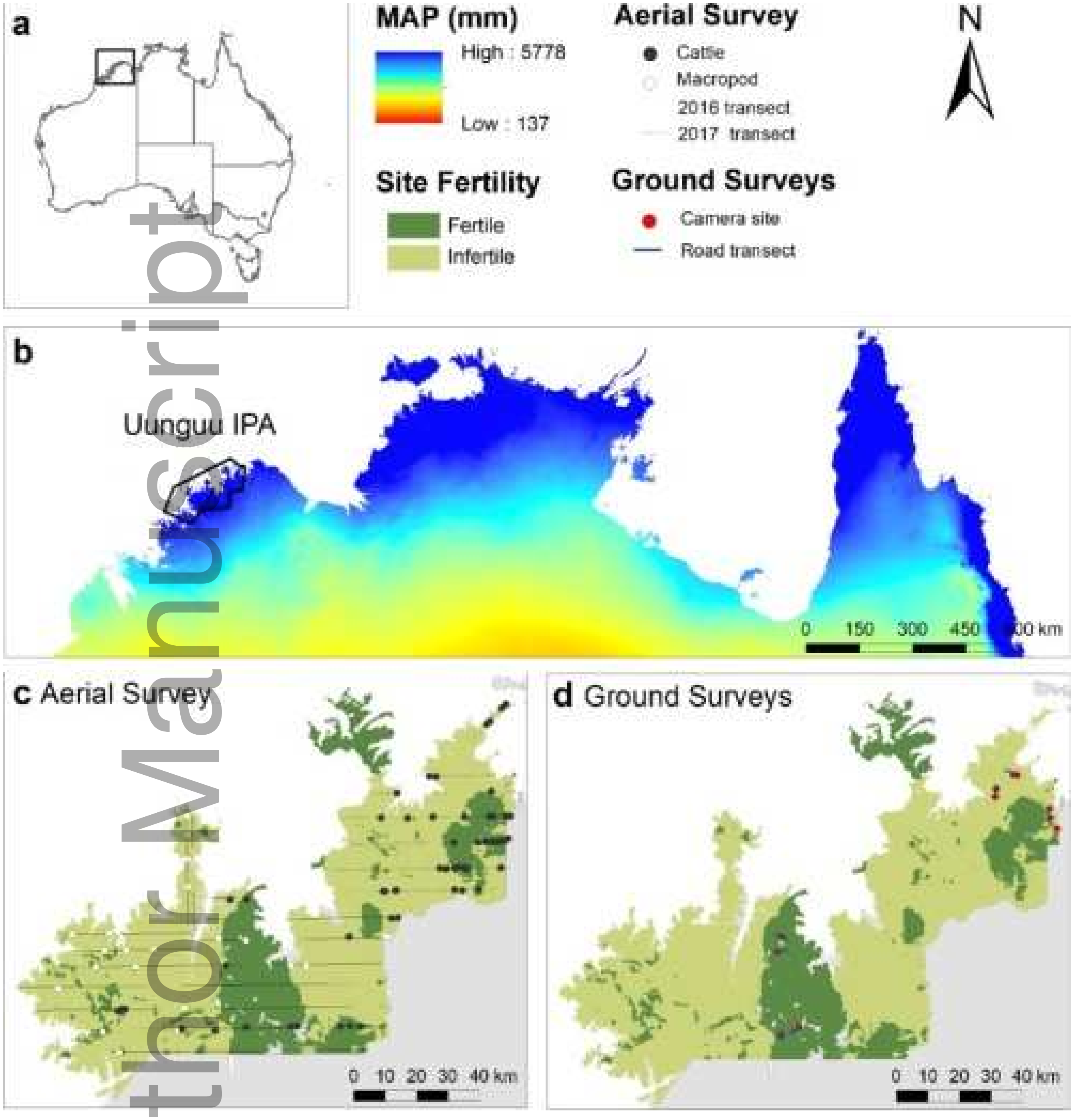
Table 1. Species distribution modelling results for variance partitioning and environmental correlate significance from four models: 1) landscape occurrence from 2016 aerial survey records for cattle and macropods, 2) landscape occurrence from 2016 and 2017 aerial survey records for cattle, 3) occurrence and 4) foraging behaviour from 2015-2017 camera trap records for cattle, agile wallaby, and a combined category for wallaroo (antilopine and common). Models 3 and 4 include site as a random variable. Values in the table represent the amount of variance each correlate accounts for in each model. Correlates with significant positive relationships are in bold and significant negative relationships are in bold italics for all models as determined by the 95% central credible intervals.

Scale	Method	Model	Species	Fertility	TSF	Water	Pastoral
Landscape	Aerial	1	Cattle	0.09	0.39	0.18	0.34
			Macropods	**0.38**	0.06	0.25	**0.32**
		2	Cattle only	0.04	**0.21**	**0.15**	**0.60**

Scale	Method		Species	Fertility	TSF	Water	Temp	Julian	Dingo	Site
Site	Camera-Occurrence	3	Cattle	0.10	**0.12**	**0.18**	**0.09**	**0.00**	**0.02**	0.49
			Agile	0.10	**0.16**	0.07	**0.17**	**0.02**	0.00	0.49
			Wallaroo	0.02	**0.33**	**0.10**	**0.03**	0.00	0.01	0.51
			Dingo	**0.11**	0.01	**0.44**	**0.04**	0.00	**0.28**	0.12
	Camera-Foraging	4	Cattle	0.05	**0.23**	0.07	**0.08**	**0.01**	0.00	0.56
			Agile	**0.24**	**0.16**	**0.12**	**0.35**	**0.01**	0.01	0.12
			Wallaroo	**0.10**	**0.26**	0.02	**0.02**	**0.00**	**0.02**	0.57

TSF: time since fire; Water: distance to perennial water; Pastoral: distance to nearest pastoral station; Temp: temperature; Julian: Julian date; Dingo: dingo abundance index

Table 2. Model fit of generalised linear mixed models for total number of individuals detected for agile wallaby, wallaroo, cattle and dingo from camera traps established at 11 sites from 2015-2017 in the Uunguu IPA, North Kimberley, Western Australia. Correlates with significant ($p < 0.05$) positive relationships are in bold and significant negative relationships are in bold italics for all models.



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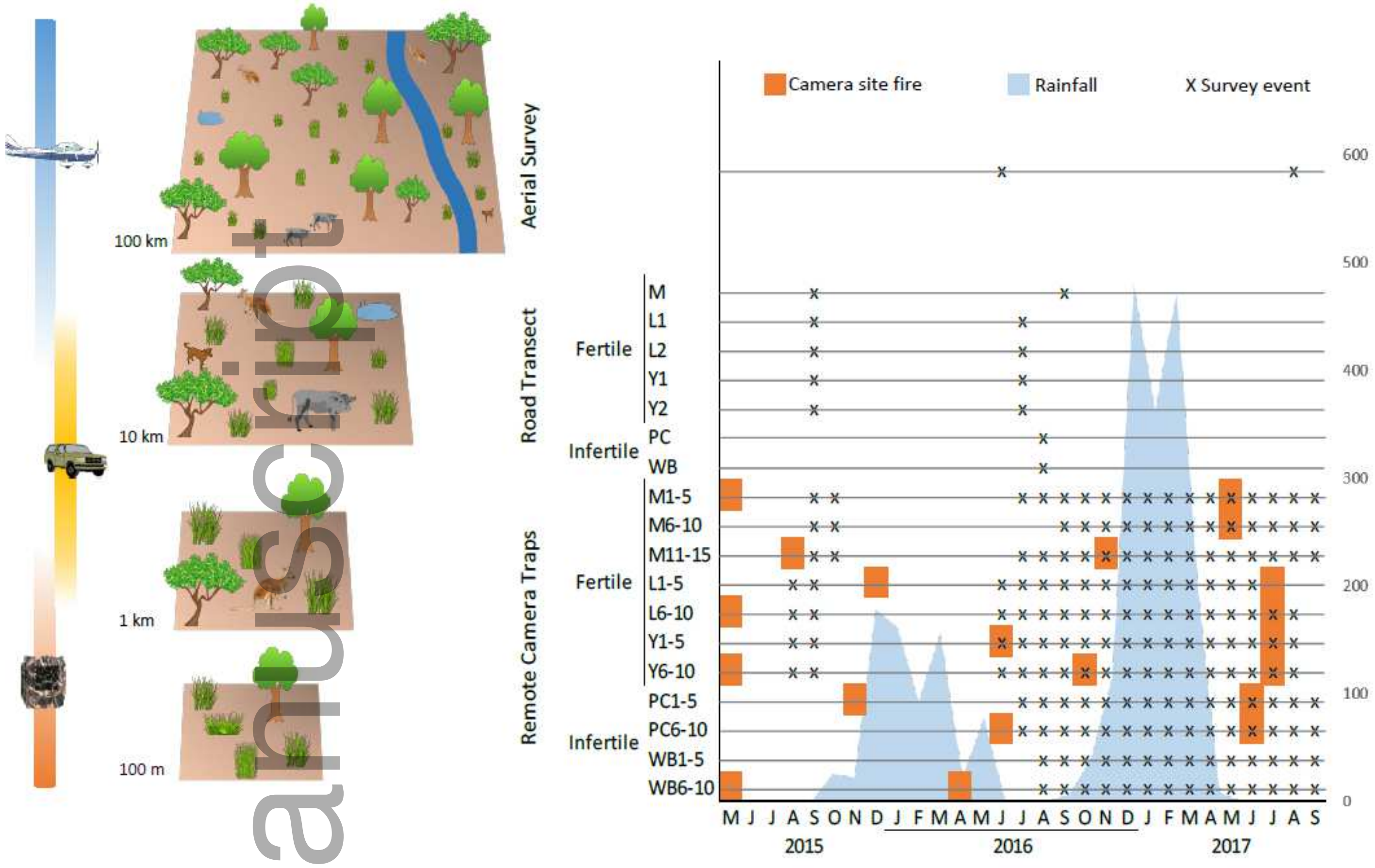

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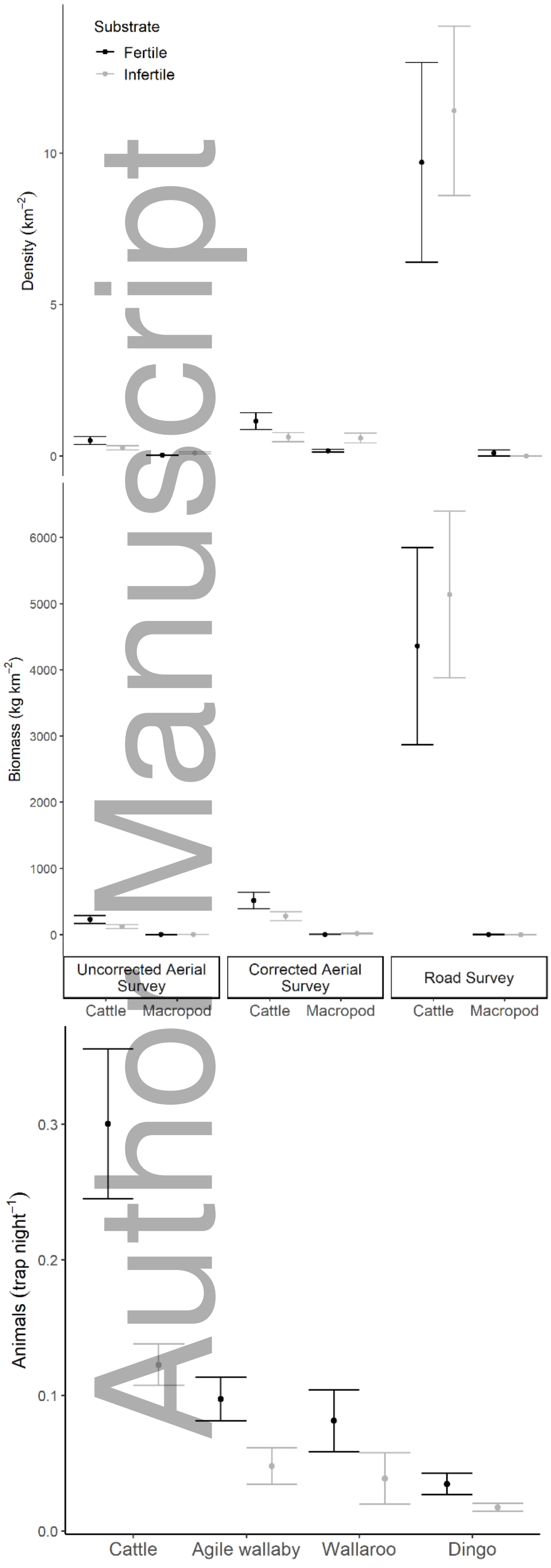
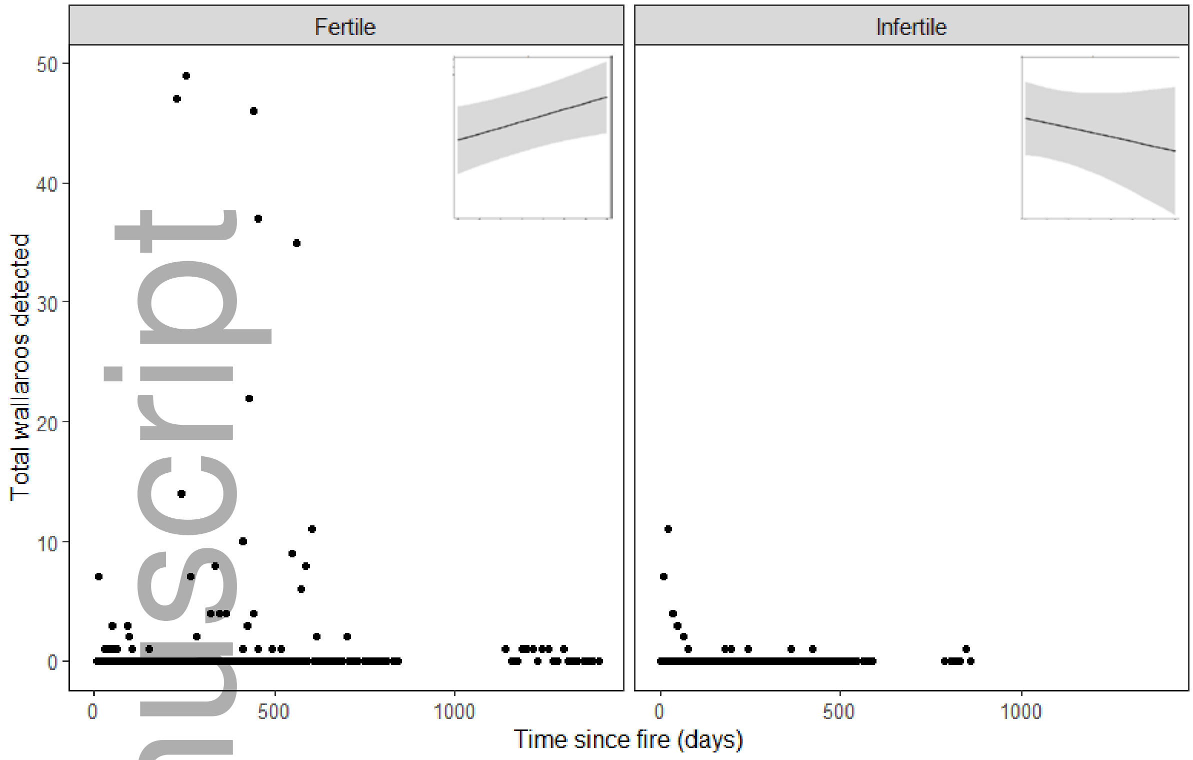
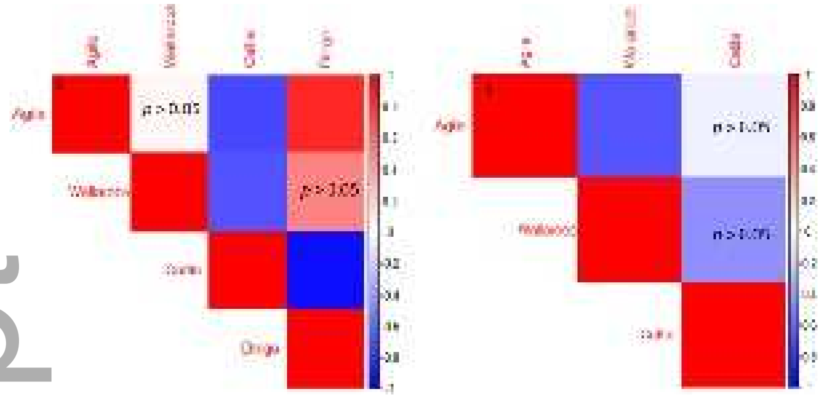



Fertile
Infertile
Total wallaroos detected
0
10
20
30
40
50
0
500
1000
0
500
1000
Time since fire (days)



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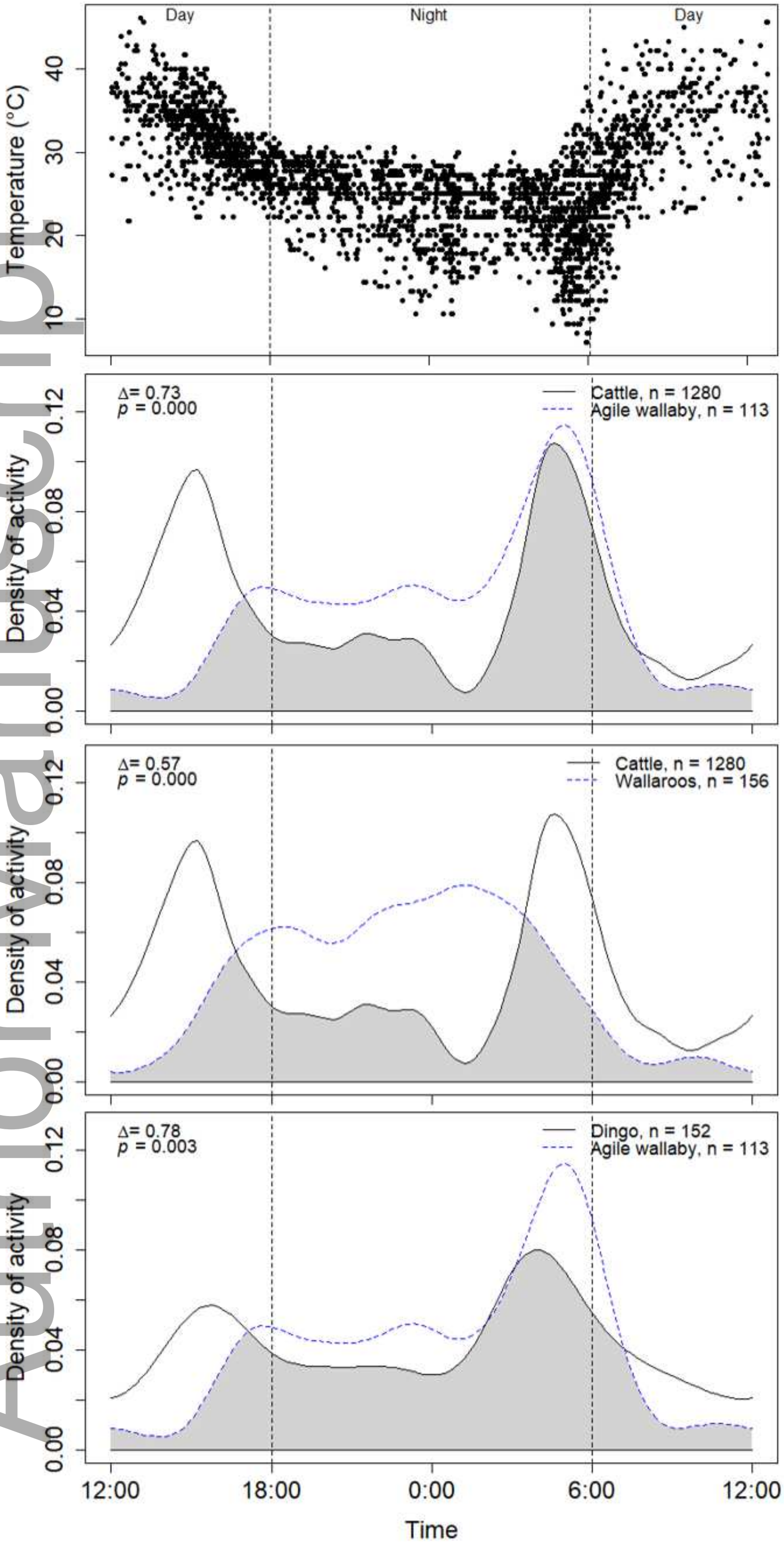

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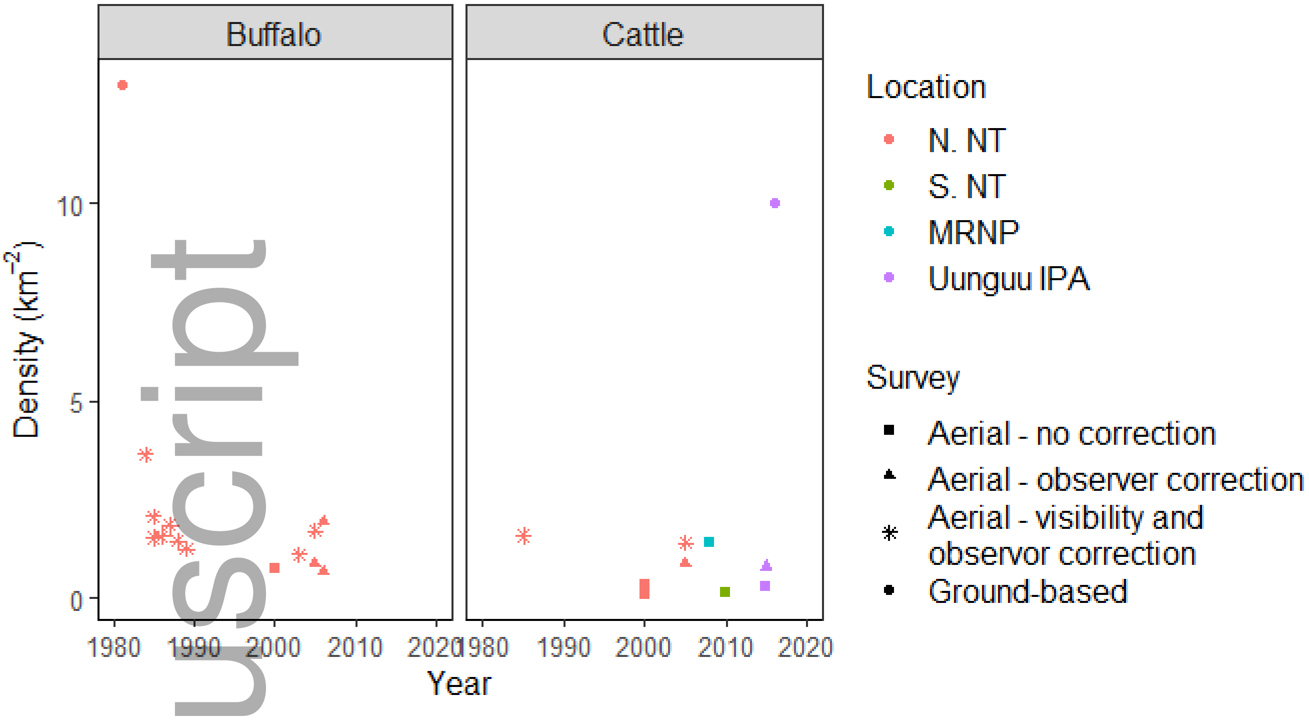

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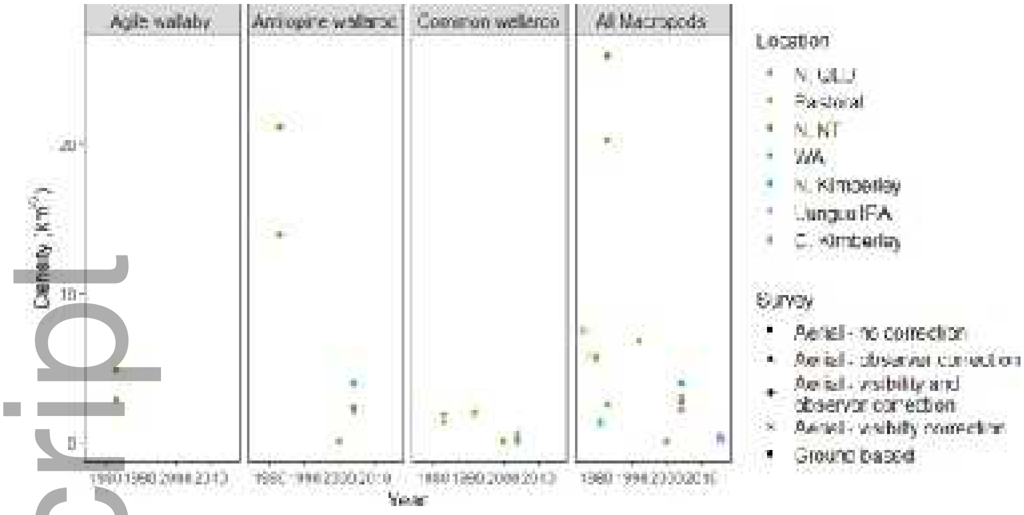

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