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ORIGINAL RESEARCH

Protected area coverage has a positive effect on koala occurrence in Eastern Australia

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Abstract
Protected areas (PAs) are crucial conservation tools implemented worldwide to conserve biodiversity. Although PAs can positively impact wildlife populations, their ecological outcomes vary substantially depending on PA management and governance. Recent calls have highlighted the need to better assess the role of area-based conservation in preventing biodiversity loss. This is crucial to improve PA effectiveness in order to meet global biodiversity goals. Here we take advantage of a unique dataset composed of 2230 surveys conducted with koala detection dogs across Eastern Australia, to assess how protection status affected the occurrence of a threatened specialist folivore. We assessed if coverage of protected forest influenced koala presence or absence at two spatial scales (1 and 3 km), for (i) strictly and (ii) all protected areas. We also investigated if PA effects were explained by differences in habitat composition (percentage of secondary forest) between protected and unprotected areas. Taking confounding factors into account, we showed that forest protection (all IUCN categories) had a significant positive effect on koala occurrence, which increased by ~10% along the forest protection gradient. Contrarily, koala occurrence was not affected by strictly protected areas. In addition, adding the percentage of secondary forests in our models did not modify the statistical effect of PAs on koala occurrence, suggesting that forest composition is not the driver of the observed difference along the protection gradient. Our results contribute to a broader understanding of the effects of PAs on a threatened marsupial and call for further attention to assessments of PA effectiveness in Eastern Australia, a global biodiversity hotspot.

Keywords Protected area effectiveness · Threatened species · Impact evaluation · IUCN management categories · Conservation policy · Forest quality

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Introduction

Protected areas (PAs) are crucial policy instruments in halting ongoing biodiversity loss resulting from the global anthropogenic alteration of ecosystems. The importance of PAs for conservation has been demonstrated in both marine and terrestrial ecosystems across biological systems (Andam et al. 2008; Duckworth and Altwegg 2018; Edgar et al. 2014; Zupan et al. 2018). For example, Gray et al. (2016) showed that PAs harbor higher species richness and abundance than unprotected areas. Threatened species are often the main target of conservation actions and are expected to benefit from land protection and management actions associated to protected area status. For instance, Cazalis et al. (2020) showed that PAs located in tropical forests are effective at retaining bird species at greater risk of extinction (Threatened or Near Threatened categories). Protected areas can positively influence wildlife distribution and abundance through different pathways, by preventing habitat loss and fragmentation (Jones et al. 2018), preserving or enhancing habitat quality inside their boundaries or through additional effects of management actions, e.g. limiting poaching, human disturbance or predation by commensal predators (Kearney et al. 2018).

Six different categories of PAs have been defined by the International Union for Conservation of Nature (IUCN) with different management objectives and protection levels, from access restricted areas (category I) to areas where sustainable extractive activities are allowed (category VI) (IUCN & VCMC, 1994). Differences in conservation outcomes between IUCN categories have been shown, with low protection categories being less efficient at avoiding forest loss (Leberger et al. 2020) or at conserving larger and more threatened wildlife species (Ferreira et al. 2020). Similarly, Jones et al. (2018) found a strong effect of protection status (IUCN PA category) on mammal species richness and encounter rates of the most common species in forests of Tanzania.

However, available evidence indicates that despite an increase in the total area covered by PAs worldwide and the reported positive effects of land protection (Gray et al. 2016), biodiversity continues to decline globally, highlighting a paradox (Maxwell et al. 2020). Recent research has shown that ecological effectiveness of PAs can vary substantially depending on a variety of socio-economic factors. Local governance, funding, national development indices or external pressures (e.g. human density in the periphery of PAs) can have adverse effects on biodiversity inside PAs (Barnes et al. 2016; Eklund & Cabeza-Jaimejuan 2017; Amano et al. 2018; Geldmann et al. 2019; Veldhuis et al. 2019). This is related to addressing key threats to species of concern, which are mostly limited to PAs with sufficient resources (Coad et al. 2019). Ultimately, for optimal ecological outcomes, PAs need to be strategically located in order to protect high-quality habitat, which is not the norm in most parts of the world (Venter et al. 2018). As a result, the effectiveness of PAs in terms of wildlife conservation is sometimes hard to predict, and recent studies have recorded counterintuitive effects of PAs in several taxa: similar densities inside and outside PAs (no PA effect) or even negative population trends inside PAs (Kiffner et al. 2020; Terraube et al. 2020; Bayraktarov et al. 2021).

Yet, studies assessing the outcomes of PAs for wildlife conservation and identifying the drivers of PA effectiveness (IUCN categories, external factors or poor local management) remain too rare. This is despite it having been recently identified as an urgent priority for the long-term success of area-based conservation (Maxwell et al. 2020). Under the post-2020 global biodiversity framework, attention is increasingly focusing beyond quantity (total PA coverage) and including the quality of PAs (Visconti et al. 2019), providing targets that are often more important for species occurrence and persistence.

The koala (*Phascolarctos cinereus*) is a specialist arboreal marsupial distributed across eastern and southern Australia. Populations in Queensland (QLD) and New South Wales (NSW) have been declining steeply over the last decades (Adams-Hosking et al. 2016). Consequently, the species status has been up-listed to Vulnerable by the IUCN in 2012 and to Endangered in three Australian states in 2022. Pressure is rising to further up-list the species to globally Endangered (Lam et al. 2020). Habitat loss and fragmentation due to deforestation is the main threat to this species (McAlpine et al. 2015). Diseases, dog predation and vehicle collisions are other additive mortality factors threatening koala populations (Beyer et al. 2018). In addition, the impacts of climate change are multiple and likely increasing, a recent example are the mega-fires that have impacted Eastern Australia during the summer of 2019–2020 (Phillips et al. 2021; Ward et al. 2020a) estimated that the species has lost 11% of its total habitat area following these unprecedented fires.

Despite the precarious status of this species, the effect of PAs on koala populations, e.g. occurrence and abundance, is poorly understood across its distribution (Tisdell et al. 2017). Here we take advantage of a substantial dataset of >2000 surveys conducted across QLD and NSW to provide the first assessment of how PAs influence koala occurrence. We assessed whether forest protection (i.e. the percentage of forest cover under protection) had an effect on koala occurrence at several spatial scales, while considering potential confounding factors that are likely to cause biases in PA effectiveness studies (ecological and anthropogenic variables potentially influencing koala occurrence). We also aimed to identify (i) the effects of IUCN categories on the relationship between forest protection and koala occurrence and (ii) if this relationship was driven by variations in forest composition between protected and unprotected areas.

Materials and methods

Study area

Koala surveys were carried out in eight local government areas (hereafter councils) distributed across South-East Queensland (SEQ): Sunshine Coast, Noosa shire, Gympie, Toowoomba, Moreton Bay, Redlands City, Fraser Coast and Stradbroke Island (Fig. 1). Surveys were also carried out in the Northern Tablelands in New South Wales (NSW). The climate in Queensland is temperate to subtropical, with habitats ranging from open dry sclerophyll forests, acacia and callitris dominated forests, and patchy rainforests. The Northern Tablelands are temperate characterized by higher altitude, and cooler temperatures. The region consists of a mixture of lowland plains, and tablelands dominated by a mixture of dry eucalyptus forests and grasslands. Native vegetation across both regions is fragmented by the agricultural expansion for cattle and crop, and urban settlements. Koalas within our study area inhabited a variety of habitats, including remnant and non-remnant forest patches surrounded by an agricultural matrix or even suburban settlements with low tree cover that could be generally characterized as low-quality habitat for koalas.

Protected areas in Eastern Australia

Each protected area was categorized using IUCN classification (Dudley and Phillips 2006) based on the protected area's management strategies. Protected areas in IUCN management categories I through to IV are strict PAs primarily managed for biodiversity conservation, while other IUCN management categories allow sustainable use of natural resources and light extractive activities (UNEP-WCMC and IUCN, 2018).

Currently, according to the World Database on Protected Areas, nationally designated PAs located in SEQ, cover around 10.2% of its terrestrial area, while designated PAs located in New-South Wales (Northern Tablelands), cover around 19.4% of its terrestrial area. Of this total protected area, strict PAs in IUCN management categories I-IV cover about 7.8% of SEQ terrestrial area and 15.3% of the Northern Tableland total area (Fig. 1; Table 1 in Supplementary Material).

Koala occurrence

Given koalas are cryptic and often difficult to find, we used detection dogs to find evidence of koala presence (i.e., scat; Cristescu et al. 2020). A team consisting of a handler and detection dog specifically trained to detect koala scats were deployed across the study area between 2015 and 2021 for different purposes (e.g. koala habitat mapping, genetic sampling).

All surveys were conducted in the same manner with no prerequisite in terms of habitat type. Each survey began once the detection dogs were motivated to find the target scent and ended when the handler found the target scent or when the area was thoroughly searched. The dogs were only prompted by the handler to ensure the target area was covered or moved down-wind to benefit from wind direction. Based on previous surveys, in koala-positive sites, this survey method is highly efficient in confirming koala presence (Cristescu et al. 2020). If a detection dog indicated on a target scent, the handler identified the scat to species level (Triggs 2004) and recorded koala scat location using a handheld Garmin GPS (Alpha ® 100, Garmin Ltd., Olathe). We classified a site as used by koalas if koala scats were found, and not used when scats were not found during the survey. The teams also recorded the total search time to account for survey effort.

We conducted a total of 2230 surveys. We filtered our data to remove potential biases as follows. Regarding surveys conducted with detection dogs specially trained to find specific scents (i.e., very fresh scats or individual koalas) we only included surveys that were positive and removed negative surveys. Indeed, negative surveys with fresh scat or koala detection dogs cannot be interpreted as evidence of koalas not using the area, only as koalas not being there on that day ('koala' dog) or the few days prior ('fresh scat' dog). As a result, a total of 1463 surveys were used for subsequent analyses: koalas were detected in 861 of them and were absent from the remaining 602 surveys.

Environmental variables

Variables were extracted at two different buffer scales: (i) 1 km and (ii) 3 km. If a site was positive, variables were extracted for every first scat found across the survey. If the site was negative, variables were extracted from the survey's starting point as the area covered by

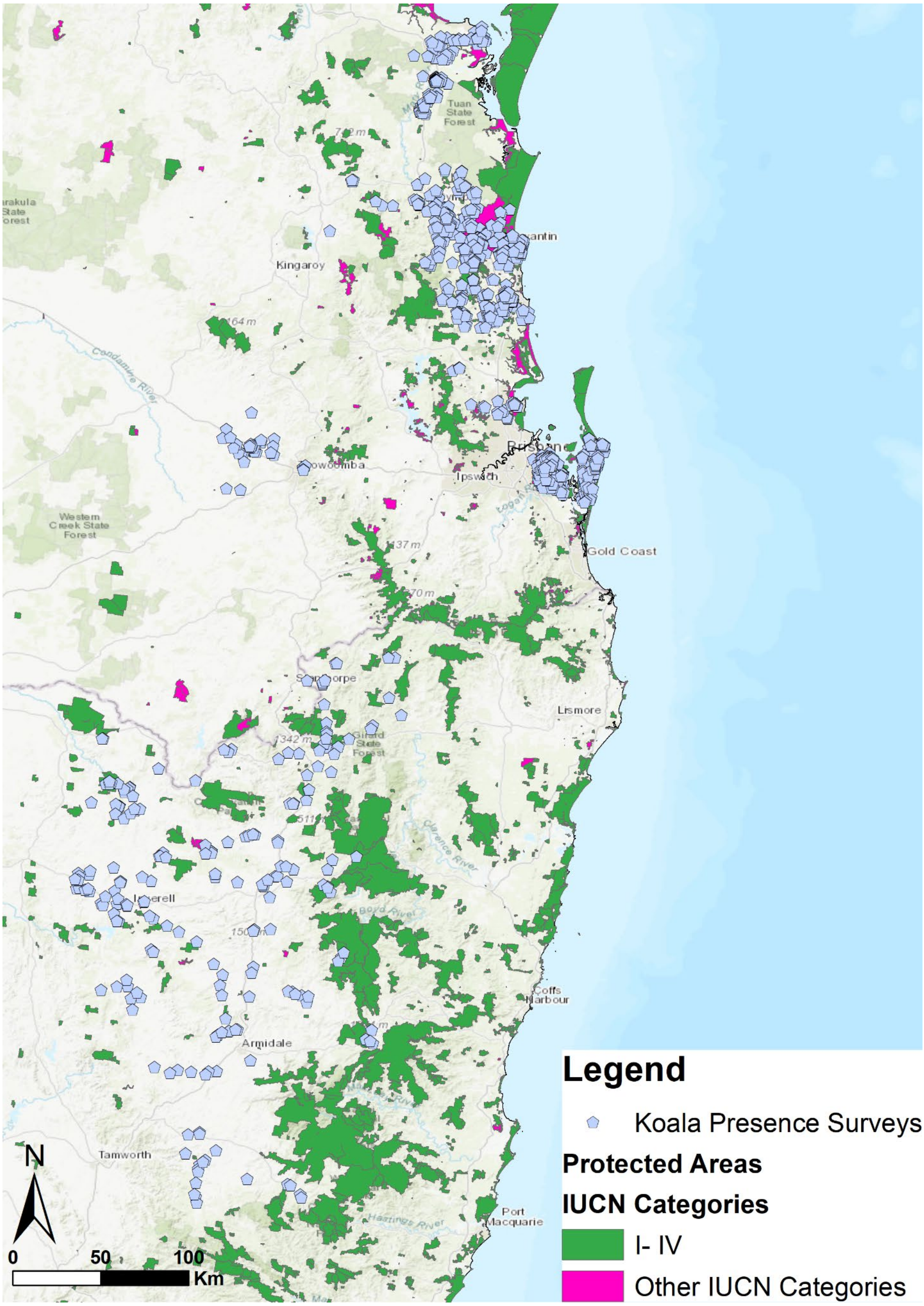

Fig. 1 Location of koala surveys, strict and all protected areas across the study area. Blue symbols represent the location of all koala surveys performed in nine councils across Queensland and New-South Wales. Strict protected areas are highlighted in green while other protected areas are presented in pink on the map

detection dogs during casual surveys is not linear but rather has a circular shape from the starting point. Koala home ranges and dispersal distances can vary significantly depending on region and individuals (Dique et al. 2003). Therefore, size of the different buffers was chosen according to previous research on koala ecology to reflect home range size and dispersal of koalas across the landscape (McAlpine et al. 2006, 2008; Rhodes et al. 2008).

We extracted both potential confounding factors (forest extent, distance to road, total water area, phosphorous levels in soil, average rainfall and amount of non-remnant *Eucalyptus* forest) and the variable of interest (percentage of protected forest) at these two spatial scales in ArcGIS (10.8) as follows:

Data sources

- i Forest extent: We used the *Forests of Australia* 2018 dataset created by the *Australian Bureau of Agricultural and Resource Economics and Sciences* (data.gov.au), with a 1-hectare resolution. Given koalas are considered specialist folivores of the *Eucalyptus* genus, we aggregated and clipped forest type layers and calculated the extent of *Eucalyptus* forest in each buffer size.
- ii Protection status: We assessed the amount of *Eucalyptus* forest that was classified under protection within each buffer. For this, we calculated the percentage of intersection between each buffer area with a Protected Area from the World Database of Protected Areas (WPDA, 2020). For subsequent analyses, we calculated this percentage both for (i) PAs under strict protection (IUCN categories I-IV) and (ii) PAs from all IUCN categories (IUCN categories I-IV and IUCN category VI). Of note, areas protected at the Council level (such as reserves) are not classified as protected under IUCN categories.
- iii Distance to the closest road: to account for anthropogenic disturbance, we calculated the distance to the closest major primary road using the *Near* tool. Data was extracted from spatial layer *Global Roads Inventory Project dataset* (globio.org).
- iv Total water area: the total water area in each buffer was used as a proxy for leaf water content and / or forest resilience to drought, as the presence of water was shown to be an important driver of occurrence for populations at the edge of their range (Gordon, 1988, Davies et al. 2013). We extracted the area of water from the *National Surface Hydrology* spatial layer (ga.gov.au). We excluded water bodies classified as 'foreshore flats' as these are associated to beaches and likely to include saltwater bodies which have no positive influences on koala habitat.
- v Soil phosphorous: Phosphorous is considered important for the health of *Eucalyptus* forests and previously highlighted as a contributor to koala presence (Ullrey et al. 1981; Thomas et al. 2006; DES, 2021). We extracted mean mass fraction of total phosphorous in soil by weight (%) within topsoil layers of 0–5 cm from the *Soil and Landscape Grid National Soil Attribute* (data.csiro.au) at the survey start (for negative surveys) or evidence of presence (for positive surveys).
- vi Average rainfall levels: We collected rainfall statistics from weather stations in the closest towns to our survey points, calculating average rainfall recorded from the year prior to conducting surveys. This was obtained from the *Bureau of Meteorology* (bom.gov.au).

vii Habitat composition (% of secondary forest): We assessed the amount of *Eucalyptus* forest that was classified as secondary habitat (original vegetation has been removed and has less than 50% cover remaining) within each buffer. Note that primary (i.e. old growth) vegetation is classified as woody vegetation that is undisturbed with more than 50% forest cover. This variable was available only for Queensland surveys. *Eucalyptus* forest within buffers was intersected with primary versus secondary classification variables from the regional ecosystem mapping 2019 (Queensland Spatial https://qldspatial.information.qld.gov.au/).

Statistical analyses

We assessed whether the percentage of protected *Eucalyptus* forest affected koala occurrence considering other potential confounding factors at two different spatial scales (1 and 3 km buffer scales) and for two levels of protection (strict PAs/all PAs). In the end, we removed all surveys from NSW as habitat composition variables were not available for this state and we therefore performed the following analyses on 1164 surveys. The analyses followed a two-step approach at both spatial scales. First, we used Generalized Linear Mixed Models (GLMMs) with a binomial distribution (logit link function) to evaluate the effect of forest protection status on the occurrence of koalas, then we aimed at understanding if the protected area effect could be explained by differences in habitat composition associated to protection status.

i) Effect of forest protection status on koala occurrence.

Models contained eleven fixed effects: (i) the variable of interest: percentage of protected forest out of total forest area available per buffer (only *Eucalyptus* species); (ii) potential confounding factors influencing koala occurrence in the wild: percentage of forest out of total buffer area; average rainfall one year prior to survey; distance to closest major road; proportion of water area out of total buffer area; elevation; phosphorous mass; and (iii) total search time (seconds) for each survey. The latter aimed at controlling for the potential effect of difference in survey length on the probability of detection for koalas. We used council as a random effect and year as a random effect nested within council to account for repeated observations in each council over the years (as surveys were never conducted twice at the exact same location). We also added dog ID as a random factor to account for individual differences in detection ability. However, in this case the model residuals were non-linear and heteroscedastic. Considering that the results of the model were not affected by the inclusion or not of dog ID as a random effect (see Table 11 in the Supplementary Material) and that the model with a simpler structure had the best goodness of fit, we decided to include only year nested within council as a random effect. Longitude and latitude of surveys were also added as covariates in the models to describe latitudinal/longitudinal gradients across the study area.

ii) Role of habitat composition in explaining PA effect on koala occurrence.

Second, we wanted to understand if the effect of protected areas was caused by differences in habitat composition along the gradient of forest protection. To achieve this we added a covariate to the set of four models described previously: the ‘percentage of secondary forest out of total forest area available per buffer’ (*Eucalyptus* species only). We hypothesized that differences in the percentage of primary and secondary habitat between protected and unprotected areas could explain the potential effect of PAs on koala occurrence. Therefore, by incorporating the amount of secondary forest in our models, we tested whether the statistical effect of protected areas on koala occurrence would change.

As a result, we built a total of eight different models including two estimates of percentage of protected forests, (i) for all protected area categories (IUCN categories I-VI) and (ii) only for strictly protected areas (IUCN categories I-IV), for each buffer size (1.5 and 3 km), with and without the additional ‘habitat composition’ covariate (see Table 1 for the structure of the eight models).

Table 1 Structure of the eight different models built in this study

Models	Model structure
Model 1–4 – Buffer of 1 km	
1-	Occur. ~ **% Prot. Forest1km_AllIUCNCat.** + % Forest areas1km + Dist. Roads + % Water areas1km + Rainfall$_{-1}$ + Elevation + Phosphorus + Long + Lat + Search time + (1| Council/Year)
2-	Occur. ~ **% Prot. Forest1km_AllIUCNCat.** + % Forest areas1km + **% secondary Forest1km** + Dist. Roads + % Water areas1km + Rainfall$_{-1}$ + Elevation + Phosphorus + Long + Lat + Search time + (1| Council/Year)
3-	Occur. ~ **% Prot. Forest1km_StrictIUCNCat.** + % Forest areas1km + Dist. Roads + % Water areas1km + Rainfall$_{-1}$ + Elevation + Phosphorus + Long + Lat + Search time + (1| Council/Year)
4-	Occur. ~ **% Prot. Forest1km_StrictIUCNCat.** + % Forest areas1km + **% secondary Forest1km** + Dist. Roads + % Water areas1km + Rainfall$_{-1}$ + Elevation + Phosphorus + Long + Lat + Search time + (1| Council/Year)
Model 5–8 – Buffer of 3 km	
5-	Occur. ~ **% Prot. Forest3km_AllIUCNCat** + % Forest areas3km + Dist. Roads + % Water areas3km + Rainfall$_{-1}$ + Elevation + Phosphorus + Long + Lat + Search time + (1| Council/Year)
6-	Occur. ~ **% Prot. Forest3km_AllIUCNCat** + % Forest areas3km + **% secondary Forest3km** + Dist. Roads + % Water areas1km + Rainfall$_{-1}$ + Elevation + Phosphorus + Long + Lat + Search time + (1| Council/Year)
7-	Occur. ~ **% Prot. Forest3km_StrictIUCNCat** + % Forest areas3km + Dist. Roads + % Water areas3km + Rainfall$_{-1}$ + Elevation + Phosphorus + Long + Lat + Search time + (1| Council/Year)
8-	Occur. ~ **% Prot. Forest3km_StrictIUCNCat** + % Forest areas3km + **% secondary Forest3km** + Dist. Roads + % Water areas3km + Rainfall$_{-1}$ + Elevation + Phosphorus + Long + Lat + Search time + (1| Council/Year)

We also repeated the analyses on a dataset where presence-only data were removed (surveys conducted with ‘koala dogs’ and ‘fresh scat dogs’) in order to check that these data did not introduce a bias in our dataset in terms of habitat selection.

All covariates were standardized. Multicollinearity among explanatory variables was evaluated using the variance inflation factor (VIF), where variables with VIF values > 5 were removed. All covariates had VIF < 3.5. All statistical analyses were performed using the software R 4.0.0. We used package *lme4* for all GLMMs and the package *MUMIn* to calculate the proportion of variance in koala occurrence explained by the fixed effects and both fixed and random effects in the eight different GLMMs. Goodness-of-fit of the models were assessed using residual diagnostics following the procedures described in the DHARMa package (Hartig 2020). All the results of the different GLMMs (parameter estimates, confidence intervals, z and p values, conditional and marginal coefficients of determination) are presented in the Results section or in the Supplementary Material.

Results

All IUCN categories

Our analysis revealed a significant effect of PAs on koala occurrence across our study at 1 km (estimate = 0.292; CI = 0.085;0.499; z = 2.772; p = 0.005) and 3 km (estimate = 0.274; CI = 0.039; 0.508; z = 2.292; p = 0.021), when considering forests protected by all IUCN management categories (see Fig. 2; Tables 2 and 6 in Supplementary material). The positive effect of forest protection was consistent across spatial scales and robust to the inclusion of other environmental confounding factors (see below). Our results showed that koala occurrence increases by ~ 10% along the forest protection gradient (see Fig. 3). We also calculated the marginal (R^2m) and conditional (R^2c) coefficients of determination for the two Generalized Mixed Models mentioned above: (i) GLMM_AllIUCNcat_1km: R^2m = 0.169; R^2c = 0.544; (ii) GLMM_AllIUCNcat_3km: R^2m = 0.177; R^2c = 0.544.

Strictly protected areas

The percentage of strictly protected forest had no significant effect on koala occurrence at 1 km (estimate=-0.054; CI=-0.217; 0.108; z=-0.657; p = 0.511) and 3 km (estimate=-0.077; CI=-0.011; 0.007; z=-0.854; p = 0.393) (see Fig. 2; Tables 4 and 8 in the Supplementary Material). We calculated the marginal (R^2m) and conditional (R^2c) coefficients of determination for the two Generalized Mixed Models mentioned above: (i) GLMM_StrictIUCNcat_1km: R^2m = 0.169; R^2c = 0.565; (ii) GLMM_StrictIUCNcat_3km: R^2m = 0.181; R^2c = 0.566.

Therefore, for models including all PAs and only strictly protected areas, our results show that > 35% of the variance in koala occurrence across our study area was explained by the nested random effect (‘Year’ nested within ‘Council’).

Confounding factors

Search time had a strong effect on the probability of koala occurrence (see Fig. 2; Tables 3a and 3c) in all models at both 1 and 3 km buffer scale. The amount of rainfall one year prior

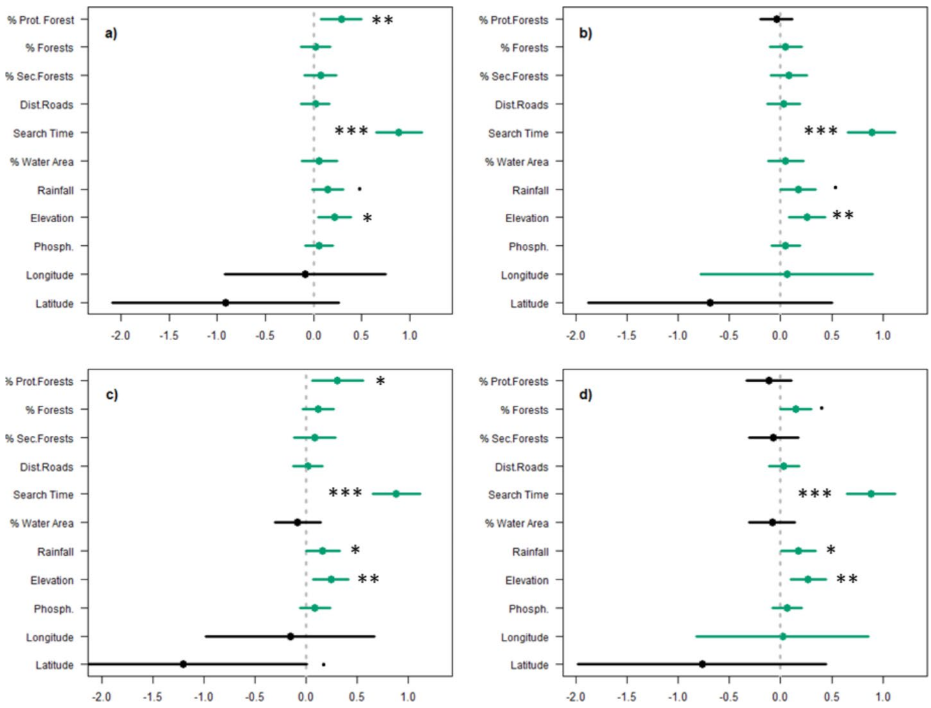

Fig. 2 Regression coefficients (dots) and 95% confidence intervals (arrows) from Generalized linear mixed models (GLMMs) for the impacts of the percentage of protected forest (as well as additional confounding covariates) on koala occurrence at (a) 1 km buffer scale, for all PAs ; (b) 1 km buffer scale, only strictly protected areas (I-IV categories) ; (c) at 3 km buffer scale, all protected areas and (d) at 3 km buffer scale, only strictly protected areas (I-IV categories). Parameter estimates are in log-odds ratios. Estimates of covariates having a positive effect on koala occurrence are represented in green and estimates of covariates having a negative effect on densities are represented in black). Asterisks indicate statistical significance

to scat collection and elevation also had a consistent positive effect on koala occurrence in all models at 1 and 3 km buffers, although the effect of rainfall was weaker at 1 km buffer scale. In other words, koalas were more likely to be detected during surveys conducted at higher elevation and in areas with higher rainfall. A trend for a negative latitudinal effect was detected in models including all PAs at 3 km buffer scale, meaning that southernmost sites had higher koala occurrence across our study area. We also detected a trend for a positive effect of the percentage of *Eucalyptus* forest cover in models including strictly PAs at 3 km scale (see Tables 3e and 3 g in Supplementary material).

Effect of habitat composition on the relationship between forest protection and koala occurrence

Adding the 'percentage of secondary forest' covariate did not significantly modify the effect size or the statistical significance of the '% of protected forest' covariate in any model (for both scales and types of PAs considered). The addition of this covariate did not impact either the marginal coefficient of determination of any model presented in this study. This result

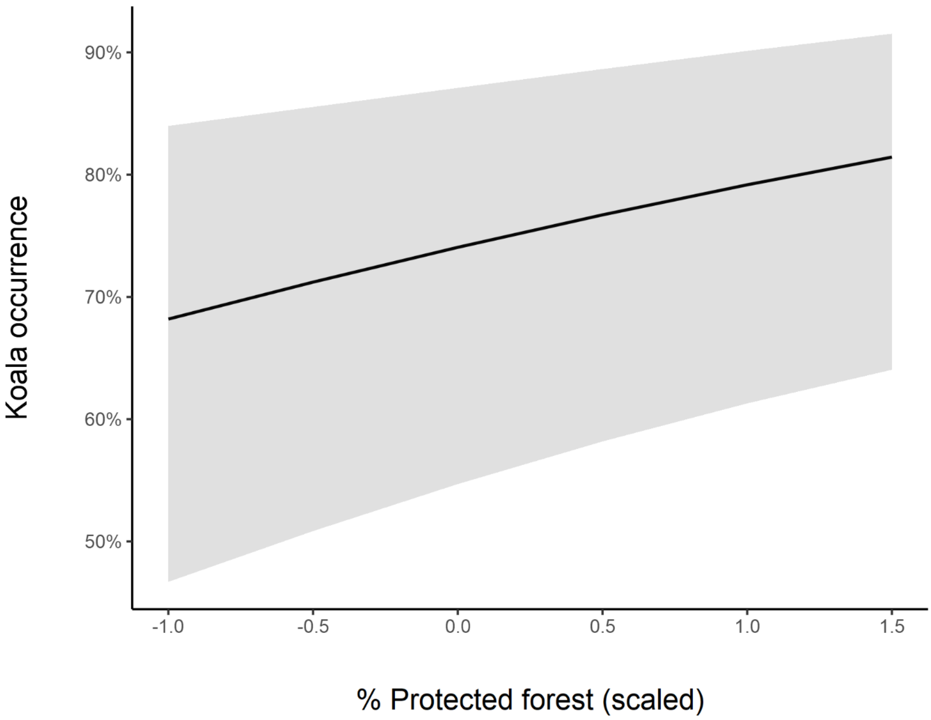

Fig. 3 Predicted values and 95% confidence intervals of koala occurrence in relation to the percentage of protected forest areas at 1 km scale (all IUCN management categories)

suggests that the effect of forest protection on koala occurrence highlighted earlier is not driven by differences in the percentage of secondary forest along the protection gradient (see Tables 3, 5, 7 and 9 in Supplementary material).

Analyses performed on the datasets excluding specifically trained dogs (in which presence-only data had been removed) showed similar results than the analyses performed on the complete dataset (see Table 10 in Supplementary Material).

Discussion

Effects of forest protection on koala occurrence

We identified a positive impact of PAs on koala occurrence (~10% increase in occurrence along the protection gradient). Both habitat quality and quantity (total forest extent) have been shown to play an important role in determining koala abundance and distribution (McAlpine et al. 2006; Callaghan et al. 2011; Phillips and Callaghan 2011). Therefore, one could expect the effect of PAs on koala occurrence to be mediated by the conservation of patches of high-quality *Eucalyptus* forests. However, our results suggest that the effect of protection on koala occurrence is independent of habitat amount or composition, although the landscape categories used here might not allow us to capture small-scale variations in habitat quality between protected and unprotected areas, e.g. foliar palatability (Moore et al. 2010) and soil fertility (Dargan et al. 2019).

The positive effect of forest protection on koala occurrence could be linked to specific management actions that have been shown to positively impact koala populations (e.g. disease management, predator control or active restoration of main food tree species, e.g. Beyer et al. 2018). Yet, to the best of our knowledge these conservation actions are rather limited inside PAs in Eastern Australia. Low anthropogenic disturbance inside PAs could still explain this positive effect of forest protection on koala occurrence.

The overall limited effect of strict PAs is surprising but could be linked to the spatial structure of our dataset (limited number of surveys inside strictly protected areas, see limitations section below). Overall Australian PAs are thought to conserve poorly threatened forest specialists such as koalas. Historically, Australian PAs had been created on unproductive lands at higher elevation and with low human population density (Watson et al. 2009), far from the high-quality forests in lowlands that are optimal habitat for koalas (Smith 2004) but also preferred land for agricultural development (Bradshaw et al. 2012). These areas on private land generally have more fertile soils, which is hypothesized to favour trees with higher nitrogen and lower formylated phloroglucinol compounds (FPCs) that are linked to foliage palatability (Moore et al. 2004). Therefore, previous research has underlined that most National Parks and State Forests occurring on low fertility soils at high elevation do not provide optimal habitat for koalas, arguing that koalas are mainly dependent on the optimal management of private lands (Crowther et al. 2009). Yet, more recent research has also shown high habitat suitability for koalas in large reserves located on public land and at mid-elevation (Law et al. 2017; Whisson et al. 2023). Our results build on this evidence and highlight a consistent positive effect of elevation and forest protection on koala occurrence suggesting that nowadays this species might be confined to sub-optimal forests at higher elevation in certain areas of Eastern Australia, see the 'refugee species concept', (Kerley et al. 2012). This indicates that, although koala conservation in anthropized lowlands is crucial, protected sites located at mid-or high elevation may play a role in koala conservation (e.g. as climate refugia).

Further research is needed to decipher the linkages between protection status, management actions and koala occurrence.

Interestingly, a large part of the variance in koala occurrence was explained by the random effect used in our models (year nested within council), suggesting that large-scale climate variability might have a strong effect on koala population dynamics, particularly in areas located further from the coast (Seabrook et al. 2011).

Limitations of the methodological approach

We identified several limitations in this study. First, the percentage of Eucalyptus forests and the percentage of secondary habitat included in our analyses may not capture small-scale variations in forests quality (e.g. abundance of main food trees or nutritional value of trees, Moore and Foley 2005; Au et al. 2019), that are important drivers of koala occurrence at the local scale. The available landscape categories could thus be too simplistic to assess accurately drivers of koala occurrence in modern ecosystems (Cristescu et al. 2019; Mitchell et al. 2021). Second, strictly protected areas (categories I-IV) primarily aimed at protecting biodiversity cover in average only 8.63% of the 1 km buffers analyzed in this study (versus 38.01% for all protected areas categories, n=1164 surveys). This means that a higher proportion of koala surveys were conducted in protected areas where extractive activities (categories V-VI) are allowed than in strictly protected areas despite strict PAs covering a higher proportion of terrestrial areas in the different councils considered here (Table 1, Supplementary Material). Lack of representativeness of surveys conducted inside strictly protected areas in our dataset may explain the low effect size of PAs on koala occurrence found in this study. Third, Australia's protected area coverage could be inclusive of a wide range of levels of designation, management and condition as reported recently in the UK (Starnes et al. 2021). As a result, even PAs of the highest IUCN management categories may not be effectively protected for nature in Eastern Australia (Craigie and Pressey 2022), blurring effectiveness assessments of PAs. Fourth, dog ID would account for a large proportion of the variance in our models given that the surveys used in this study were pooled from dogs trained on different target scent (dogs trained to search for koala scats of any age, dogs trained to search for fresh scats, and dogs trained to search for the koala itself). In terms of survey design, dogs trained on fresh scats are deployed where koalas are known to occur, whereas dogs trained to search for koala scats of any age are deployed in areas with no prior knowledge (Cristescu et al. 2020). However, this survey design does not affect the robustness of our results as shown previously.

Implications for PA management and conservation planning

Further monitoring of koala occupancy using a structured sampling design (similar habitats inside and outside PAs) and cost-efficient survey methods such as detection dogs and passive acoustic monitoring (Hagens et al. 2018) would help estimating fine-scale effects of PAs on koala occurrence and would guide PA management plans and prescribed actions at local scale. Utilizing fresh scats to obtain koala abundance and genetic diversity estimates was limited by sample size in this study but would provide an important assessment of the effects of PAs on these parameters, which is crucial for holistic conservation management. Finally, we highlighted the low coverage of strictly protected areas across our study area (average cover=15.72%, n=9 councils), which could have serious consequences in terms of wildlife occupancy and abundance across the PA network, although our results suggest that multiple-use PAs can have a positive impact on koala occupancy which deserves further attention. The establishment of strictly protected areas focused on conserving high-quality forests for koalas should continue to be a priority. Yet, establishing new PAs in high-priority lowland areas is particularly challenging throughout Eastern Australia as remnants of high-quality forests overlap with private lands where agriculture expansion and development projects are the priority. Engaging private land holders and First Nations communities into regional conservation efforts and increasing conservation status around PAs could partially solve this challenge (Ivanova and Cooke 2020; Belote and Wilson 2020). Finally, koalas have been recently highlighted as an efficient umbrella species and conservation actions targeting main threats that this species faces will likely benefit many Australian threatened species (Ward et al. 2020b).

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Author contributions JT and CF conceived the ideas; RG, KH and RC collected the koala occurrence data; RG and KH extracted the spatial data; JT led the statistical analyses; JT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Declaration

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