RESEARCH ARTICLE

Long-term monitoring in endangered woodlands shows effects of multi-scale drivers on bird occupancy

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Abstract

Aims: The effect of spatial scale on the location and abundance of species has long been a major topic of interest in ecology. Accounting for key drivers at multiple scales is critical for rigorous description of patterns of species distribution and biodiversity change. We quantified the effects of potential drivers of bird occupancy across a geographically dispersed, but heavily disturbed and fragmented ecosystem.

Location: Threatened Box-Gum Grassy Woodlands in south-eastern Australia, which stretch across 9° of latitude (~900 km).

Taxon: Birds (Class Aves).

Methods: We grouped data from four monitoring studies of birds that spanned 10–22 years in Box-Gum Grassy Woodlands. We then employed joint species distribution modelling to investigate multi-species responses to environmental drivers measured at patch, landscape and regional scales, and selected combinations of all three.

Results: We show that in Box-Gum Grassy Woodlands: vegetation structure influences bird occupancy beyond the presence of the despotic Noisy Miner (Manorina melanocephala); woodland cover is more important than vegetation productivity and topographic position; bird occupancy is sensitive to a combination of average climate, seasonality, and summer and winter extremes; and there is limited redundancy between drivers of bird occupancy at different scales. Species differ most in their response to the presence of the Noisy Miner, high summer temperatures and nearby woodland cover.

Main Conclusions: Quantifying the influence of environmental drivers that act at different spatial scales is valuable for understanding patterns of bird species occurrence. Fine-scale studies can benefit from considering the climate and biogeographical context in which the research occurs. Conversely, large-scale studies should recognise that downscaling species occupancy projections from continental to patch scales requires careful consideration of the role of patch-scale vegetation.

Keywords
Box-Gum Grassy Woodlands, climate, eastern Australia, joint species distribution models, modified agricultural landscapes, Noisy Miner, spatial scale, statistical relationships, vegetation structure
The effect of spatial scale on the location and abundance of species has long been a major topic of interest in ecology (Levin, 1992); yet quantifying the spatial scale of effects of environmental drivers remains challenging. This is because differences in autecology, such as home range, body size, nesting and foraging requirements, suggest that each species has a particular spatial scale at which it responds to variation in the environment (Jackson & Fahrig, 2014). In addition, many individual studies have shown that different factors influence the distribution and abundance of species at different scales (Mackey & Lindenmayer, 2001; Tscharntke et al., 2012). For instance, the spatial scale of nesting site suitability (e.g. within an individual tree hollow) may be different to the spatial scale of foraging resources (Webb et al., 2017). Other key ecological processes may be influenced by yet other scales of environmental factors, such as regional-scale fluctuations in spatial levels of vegetation cover (Fahrig, 2017; Fletcher et al., 2018), the rate of change of local environmental conditions (Pinek et al., 2020) or climatic drivers (Moran-Ordonez et al., 2018).

In fragmented ecosystems, it is common practice for ecologists and landscape managers to focus research or conservation activities on patches of uncleared or remnant vegetation and their surrounding landscape (Haddad et al., 2015). This approach has a defensible scientific basis because habitat patches are critical refuges in cleared landscapes; and because patches are a logical place to focus management actions such as pest removal, grazing exclusion or revegetation (Lindenmayer, Michael, et al., 2018). However, such approaches should account for the area of habitat within the surrounding landscape (Fahrig, 2017) and there is a growing body of research that has sought to investigate how other environmental context influences patch-scale dynamics (e.g. Purvis et al., 2018). Investigating large-scale processes is particularly important where a vegetation type is sufficiently widely distributed that there is natural turnover of its dependent faunal communities across climate or latitudinal gradients. An additional challenge is that the assemblage of co-occurring fauna present at a patch, and their ecological interactions, can also impact a species’ ability to persist there (Maron et al., 2013; Westgate et al., 2021).

To gain insights into the impact on biodiversity of environmental factors at different scales, it is often necessary to collect, analyse and interpret longitudinal data measured at geographically dispersed locations (Bayraktarov et al., 2019). Where this has been achieved, studies have consistently shown that understanding processes that act at different spatial scales is critical to developing an accurate picture of the patterns and drivers of biodiversity change (Newbold et al., 2015). Yet, multi-scale studies remain comparatively rare in the literature (see Spake et al., 2019 for an example and discussion), limiting the ability to draw meaningful conclusions about key drivers of occurrence of biodiversity. This is particularly problematic for understanding the biodiversity in commodity production landscapes where remnant patches of threatened ecosystems are often widespread (increasing their exposure to large-scale gradients such as changing climates), highly fragmented (i.e. affected by fine-scale effects such as patch-level grazing) and yet retain high ecological value (Wintle et al., 2019).

To quantify species occurrence in relation to drivers at different spatial scales, here we analysed data on birds from multiple long-term studies, each of up to 22 years in duration, conducted in the endangered Box-Gum Grassy Woodlands of south-eastern Australia. Our investigation spanned long-term studies distributed across nine degrees of latitude (~90 km) and encompassed a strong climate gradient (Lindenmayer, Lane, Crane, et al., 2018), with factors like rainfall known to influence the extent of development of understorey vegetation (Specht & Morgan, 1983). Understorey, in turn, is an important factor influencing the occurrence of a range of bird species in Box-Gum Grassy Woodlands, including an array of taxa of conservation concern (Montague-Drake et al., 2009) and despotic species like the hyper-aggressive native honeyeater, the Noisy Miner (Manorina melanocephala), which can drive away other (typically smaller-bodied) species (Maron et al., 2013; Westgate et al., 2021). There are also differences in levels of woody vegetation cover in landscapes surrounding Box-Gum Grassy Woodlands—from 3% to 27% in the southern half of our study region—and this too can influence the occurrence of bird species (Lindenmayer et al., 2020). Our study is the first system-wide analysis to determine which processes are most important for which avian species across Box-Gum Grassy Woodlands. This approach is critical to ensure that conservation and management actions are being undertaken with an appropriate environmental context.

Our analyses were guided by a series of four key questions that explored relationships between bird occupancy in patches and environmental attributes that have different spatial scales (see Section S1 for a full list of models).

Q1. To what extent does vegetation structure influence bird occupancy, relative to the effect of the despotic Noisy Miner?

Vegetation structure and plant species composition are key attributes of habitat for many species of birds globally (Gill, 1995). Vegetation structure is known to vary widely across temperate woodland environments (Ikin et al., 2015) and at the outset of this investigation, we predicted that vegetation structural complexity would strongly influence the probability of bird occupancy. Furthermore, a large body of research has shown that patches occupied by the aggressive Noisy Miner support fewer birds from other species, and we expected to observe this same pattern in our study (Maron et al., 2013). However, the presence of understorey vegetation is known to be a prominent factor limiting the presence and abundance of despotic taxa like the hyper-aggressive Noisy Miner that otherwise have marked negative impacts on smaller bodied bird taxa in temperate woodlands (Maron et al., 2013; Westgate et al., 2021).

Q2. To what extent do vegetation productivity and topographic position influence bird occupancy, relative to the effect of woodland amount?

Given the findings of past research into how measures of biodiversity like species richness relate to the amount of habitat in a...
landscape (e.g. Fahrig, 2017; Fletcher et al., 2018; Smith et al., 2011), we predicted that landscapes with low coverage of woody vegetation would support fewer species than well-vegetated landscapes (Lindenmayer et al., 2020). However, a related suite of important studies have indicated that species richness (including for birds) also tends to be greater in areas of higher productivity (Gill, 1995; Huston, 1994; Storch et al., 2018; Verschul et al., 2008). Like productivity, bird occupancy may also be limited by water availability (Wright, 1983), which is partly associated with topographic position.

Q3. To what extent do climate extremes influence bird occupancy, relative to the effects of latitude and mean temperature or rainfall?

Vegetation productivity is often also reflected by patterns of average rainfall and temperatures, which have strong gradients across the temperate woodlands examined in this study (Lindenmayer, Lane, Crane, et al., 2018). Given the large spatial extent of the Box-Gum Grassy Woodlands, we predicted that bird occupancy would be sensitive both to average climate (Willig et al., 2003) and to latitude. Different portions of this spatial range suffer large variation in extreme values, however, with very cold winter temperatures in the south and very high maximum temperatures inland. Therefore, we also expected to observe an effect of summer and winter extremes on bird occurrence (Ehbrecht et al., 2021).

Q4. To what extent are environmental factors at different scales redundant in their influence on bird occupancy (Levin, 1992; Wilson et al., 2013)?

Redundancy may arise if, for example, variation in bird occupancy explained by factors at patch level was also explained by broader scale climate attributes. We would also expect to see this redundancy when there are associations between environmental factors that have different spatial scales, such as between patch vegetation structure and climatic factors. To answer this key question, we developed composite models that combined environmental factors at all spatial scales and compared these models to previous models from a single spatial scale.

2 | MATERIALS AND METHODS

2.1 | Field methods

2.1.1 | Study area

Our study encompassed an extensive part (approx. 170,000 km²) of the wheat-sheep belt of south-eastern Australia. Much of the region was formerly dominated by temperate woodland (Hobbs & Yates, 2000); the southern half of the region has been cleared of an estimated 85% of its original cover (Pressey et al., 2000). The wheat-sheep belt of south-eastern Australia is one of the most heavily modified agricultural regions worldwide (Fischer et al., 2009) and is characterised by a range of land degradation problems including secondary salinity, soil erosion, weed invasion and extensive biodiversity loss (Lindenmayer, Michael, et al., 2016). In an effort to tackle these problems, major restoration programmes have been undertaken (Lindenmayer, Lane, et al., 2016). There also has been substantial natural regeneration of temperate woodlands in parts of the study region, particularly over the past 15 years (Lindenmayer, Blanchard, et al., 2018), often as a result of changes in livestock grazing pressure (Fischer et al., 2009).

2.1.2 | Field sites

Our investigation used data from monitoring undertaken at 429 sites dominated by old growth or regrowth Box-Gum Grassy Woodlands that were located on 209 farms (Figure 1). These sites were part of four distinct studies (Section S6). The old-growth woodland stands were typically dominated by scattered large trees that were 200 or more years old (Figure 2). Regrowth woodland stands were recovering naturally after disturbance by fire, clearing or both.

Each site was 2 ha in area and comprised a 200 m long and 100 m wide transect with permanent steel post markers established at the 0, 50, 100, 150 and 200 m points along the transect. The size of our sites broadly matched the typical size of woodland patches in heavily modified agricultural areas of south-eastern Australia (Gibbons & Boak, 2002).

FIGURE 1 Field site locations (dots) in south-eastern Australia. Bird surveys and vegetation structure surveys were conducted at each site. Colours refer to the field study that each site was part of: Stewardship study (yellow); south-west slopes restoration study (green); Nanangroe plantation study (blue); Murray/Riverina biodiversity baseline study (purple). See Section S6 for information on each study.
2.1.3 | Bird surveys

Our standardised field protocols entailed 5-min point interval counts (sensu [Pyke & Recher, 1983]) at the 0, 100 and 200 m posts along each site’s transect. Time of day and approximate ordinal indications of windiness, cloudiness and temperature were recorded before starting each point-interval count. For each point-interval count, an observer recorded all bird species seen or heard within the site and the detection of each individual bird was assigned to one of several distance categories from the observer; 0–25 m, 25–50 m and >50 m. To reduce observer heterogeneity and day effects, we did not undertake surveys during poor weather (rain, high wind, fog or heavy cloud cover) (Lindenmayer et al., 2009). We were able to partially account for remaining observer heterogeneity and day effects by different highly experienced ornithologists surveying each site on two different days in spring (Cunningham et al., 1999; Field et al., 2002).

For this investigation, we included only those detections made within 50 m of the post. We did not treat individual point counts as independent samples, but rather pooled counts across the 0, 100 and 200 m plots within each site to give the presence or absence of each species at that site on any given survey day. Due to availability of woody vegetation maps (see Section 2.2), we omitted surveys conducted earlier than the year 2000 and later than 2019. We removed waterbirds (orders Caprimulgiformes, Accipitriformes, Strigiformes, Podicipiformes, Gruiformes, Pelecaniformes and Anseriformes) and species with large home ranges (order Falconiformes). To avoid overfitting in our models, we also removed species detected less than 100 times across all the surveys that we used. Removing rarely detected species is a common practise for the statistical models that we employed (Tobler et al., 2019).

2.2 | Predictor variables

Our modelling approach (see Section 2.3) used occupancy predictor variables measured at three distinct spatial scales. Information quantifying properties of individual woodland patches was considered patch scale, while variables describing the neighbourhood of a patch were considered landscape scale. Finally, we termed predictors that described the climate or latitude of a patch as regional scale.

Below, we further describe the variables we recorded for each of these scales. For detection in each bird survey, we used the average of information recorded at the start of each point-interval count: Time of day, windiness, temperature and cloudiness (see Section S3).

2.2.1 | Patch scale

The majority of our patch-scale variables contained information on vegetation structure, which we quantified during vegetation surveys at each patch. We measured understorey (<2 m in height), midstorey (plants 2–10 m high) and overstorey (>10 m high) cover by recording the percentage cover in each height class every 5 m along a 100 m transect, and calculating an average value. We used the same approach for quantifying short or ground cover, except that we recorded presence of a range of elements every metre, rather than every 5 m. For the purpose of this analysis, we summed the percentage cover of native sub-shrubs, cryptograms, native forbs/herbs/other, organic litter, exotic broadleaf plants/forbs/other and coarse woody debris, which we termed low cover. We also summed the percentage cover of exotic perennial and annual grasses, exotic sub-shrubs and exotic broadleaf plants/forbs/other, which we termed exotic cover.

Our final patch-scale variable was the presence or absence of the Noisy Miner. The Noisy Miner has been shown to strongly defend...
individual habitat patches and is widely known to influence the range of bird species that can exist at a location (Maron et al., 2013). While not strictly an environmental attribute of a patch, we follow Westgate et al. (2021) in treating Noisy Miner occupancy as an environmental attribute, rather than a response variable like other bird species. Our predictor variables also included the interaction term between Noisy Miner presence and midstorey, as the impacts of Noisy Miners can be mitigated by higher midstorey (Westgate et al., 2021).

### 2.2.2 Landscape scale

We included three variables in our analysis that described the biophysical properties of the neighbourhood surrounding each vegetation patch. We measured nearby woodland amount as the percentage woody vegetation cover within 500 m of the survey site’s centre for each year (Liao et al., 2020; data available at http://anuwald.science/tree). The amount of nearby woody vegetation canopy has been demonstrated to influence bird biodiversity in Box-Gum Grassy Woodlands (Cunningham et al., 2014), including species of conservation concern (Montague-Drake et al., 2009).

Our second variable was gross primary production (GPP) of the vegetation at the centre of a site derived from data with 500 m spatial resolution. GPP is the amount of carbon transferred from the atmosphere into plants via photosynthesis, ignoring the amount of carbon that exits plants. The data we used, 8-day satellite-derived GPP data (Yebra et al., 2015; monthly averages at 0.05° resolution available at www.wenfo.org/wald/), allowed us to explore the influence of both typical GPP and GPP at the time of the bird surveys. For each location, we used average GPP between January 2000 and December 2019 as an indication of long-term typical photosynthetic productivity. As an indication of current productivity, for each year and location, we interpolated the difference between the 8-day GPP time series and the long-term average of GPP on the days on which bird surveys occurred.

Our final landscape-scale predictor was the topographic wetness index at the centre of each site, extracted from a dataset with three arcsecond resolution (Gallant & Austin, 2012; O’Brien & Searle, 2020; data available at www.clw.csiro.au/acelp/soilandian_dscapegrid). The topographic wetness index reflects the relative moisture content within a catchment and is also an indication of relative position of points on a slope.

### 2.2.3 Regional scale

At the regional scale, we used longitude, latitude and all 19 bioclimatic variables from WORLDCLIM 1.4 at 0.5 min spatial resolution (Hijmans et al., 2005; data obtained using the raster (Hijmans, 2017) package for R (R Core Team, 2020)), which were averages over the years 1960-1990.

### 2.3 Statistical methods

#### 2.3.1 Modelling framework

We modelled bird species occurrence using Bayesian joint species distribution models as described by Tobler et al. (2019). Specifically, each model included environmental predictors for each species and accounted for imperfect detection (MacKenzie et al., 2002). Our final model also included latent variables for residual interspecies correlation (Hui et al., 2015; Warton et al., 2015). These latent variables have similarities with random effects in mixed models and are constrained to have standard Normal distribution, which allows them to be estimated (Warton et al., 2015). We modelled detection probabilities as a logistic regression, and occupancy probabilities using a probit regression. We assumed that the species occupancy at each site and year was independent of the species occupancy in other years and sites, conditional on environmental predictors. The models exploited commonalities between species by assuming that species-specific loadings of environmental predictors were drawn from a common distribution.

#### 2.3.2 Model selection

Of our 429 field site locations, we reserved 10% of the locations from each study as holdout locations. These holdout locations were selected completely randomly from within each study. We used data for these holdout locations for assessing model quality and they were not used to fit models. We termed the remaining 90% of locations in sample.

We began by developing a set of models that included terms from only a single spatial scale. That is, we included one set of models that included only those terms at the patch scale; a separate set of variables at the landscape scale; and a third set that included only regional-scale predictors. Each set contained combinations of variables chosen to represent plausible competing models about the processes acting at that scale (Section S1). We avoided collinearity among our regional-scale predictors by progressively removing predictors with highest variance inflation factors until all predictors had a variance inflation factor of 10 or lower (Zuur et al., 2010). In all cases, we fit this first round of models without latent variables and detection predictors (only species-specific detection intercepts), so as to reduce fitting time.

Although we chose each model set to be as small as practical, we then expanded each set of models using a method of stepwise addition based on Dunn–Smyth occupancy residuals (Warton et al., 2017) (for details, see Section S4.2). Specifically, when we observed systematic variation in Dunn–Smyth residuals in relation to a term already included in the model, we took that as evidence that the effect of that term should be modelled as a quadratic or logarithmic term rather than a linear term. Furthermore, if we found a systematic pattern when plotting Dunn–Smyth residuals against a term that was not yet included in the model, we used this as evidence to support including that term in the model.
We summarised model quality using the difference in a leave-one-out information criteria (LOOIC) between the model in question, and a ‘null’ model that contained only intercepts; we named this measure ‘LOOIC$_{null}$’. We computed LOOIC by Pareto smoothed importance sampling (Vehtari et al., 2017). It is a more robust version of the Watanabe–Akaike Information Criterion (Watanabe, 2010; Vehtari et al., 2017) and has mathematically convenient properties for assessing the quality of Bayesian models (Gelman et al., 2014). We stopped adding occupancy predictors to our models when the LOOIC$_{null}$ was not significantly improved, using ad-hoc 95% confidence intervals for LOOIC$_{null}$ as a guide (Vehtari et al., 2017). This process generated a set of fitted models for each group of predictors, where each group contained models with predictors from a single spatial scale.

We constructed our models that combined scales by identifying and including terms from each scale that were associated with marked improvements in fit, again as measured using LOOIC$_{null}$. We then successively added survey year, potential detection predictors (survey time of day, windiness, temperature and cloudiness) and latent variables. The robustness of this final model was examined using several diagnostic tools (Section S4.4), including a sensitivity analysis of the buffer distance for woodland amount and an inspection of residual spatiotemporal autocorrelation. Differences between the median of fitted loadings for each predictor variable and species were investigated using a principal component analysis.

3 | RESULTS

During the 4153 bird surveys at our 429 sites, we observed at total of 247 bird species. Of these species, 186 were detected in fewer than 100 bird surveys (2.4% of bird surveys) and were removed. This minimum requirement on detections was stricter than employed by Tobler et al. (2019), which was appropriate given the high number of predictors in our models. A water bird, the Australian Wood Duck (Chenonetta jubata), was also removed, leaving 60 species as model responses (listed in Section S2). Of these remaining species, five were listed as vulnerable in the administrative region covering most of our study area (Department of Environment, Energy and Science, 2021).

In total, we fitted over 30 different models (Section S1). Most models passed diagnostic tests using the occupancy and detection residuals (Section S4.2), and model comparisons were supported by tests on the holdout data (Section S4.1).

3.1 | To what extent does vegetation structure influence bird occupancy, relative to the effect of the despotic Noisy Miner?

We found that vegetation structure influenced bird occupancy beyond the presence of the Noisy Miner. From the initial three models that used patch-scale terms only (see Section S1), the midstorey led to a significant improvement in LOOIC$_{null}$ (Figure 3, top). However, additional vegetation structure terms (overstorey and low cover) did not significantly improve LOOIC$_{null}$. Quadratic forms of vegetation structure, which were suggested by occupancy residuals, also did not significantly improve LOOIC$_{null}$ (Figure S1). Furthermore, vegetation composition terms (native sub-shrub and exotic cover), which were also suggested by occupancy residuals, did not significantly improve LOOIC$_{null}$ over the Noisy Miner and midstorey model. As these extra terms did not significantly improve LOOIC$_{null}$ we did not pursue further patch-scale factors.

3.2 | To what extent do vegetation productivity and topographic position influence bird occupancy, relative to the effect of woodland amount?

We found that nearby woodland amount, as measured by woody vegetation cover within 500 m, had a much stronger relationship
with bird occupancy than either gross productivity or the topographic wetness index (Figure 3, centre). Furthermore, models using a combination of landscape-scale terms did not have significantly better LOOIC\textsubscript{null} relative to the woodland amount model. Residuals did not suggest a need for additional landscape-scale terms, and we therefore did not fit any additional models.

### 3.3 To what extent do climate extremes influence bird occupancy, relative to the effects of latitude and mean temperature or rainfall?

Bird occupancy was substantially more sensitive to the combination of average climate, summer and winter extremes, and latitude than the individual climate attributes (Figure 3, centre). We constructed the combined climate model by starting with all terms from the average climate, seasonality, aridity, cold limit, latitude and longitude models (Section S1) and removing terms using variance-inflation factors (see Methods). The combined climate model performed similarly well to the model that was constructed by selecting terms from all 19 bioclimatic variables, latitude and longitude, using variance-inflation factors (see Methods). In fact, the combined climate model performed similarly well to our models using patch-scale predictors, and markedly better than the models that used landscape-scale predictors only (Figure 3).

The latitude-only model (see Section S1) performed the poorest of all models that used regional-scale terms. The latitude and longitude model, the average model and the cold limit model, all performed similarly well to each other (Figure 3). The average climate and seasonality model performed significantly better, but not as well as the combined model. No additional models were fitted as inspection of residuals did not suggest additional terms.

### 3.4 To what extent are environmental factors at different scales redundant in their influence on bird occupancy?

There was limited redundancy between the different scales of environmental factors. In our final modelling stage, we fitted models using all the best drivers from each spatial scale. Specifically, we fitted models that used the presence of the Noisy Miner, midstorey cover, woody vegetation cover, annual precipitation, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation seasonality, latitude and survey year. For detection, the final model used survey time of day and windiness.

The final model passed several diagnostic assessments, although there was some indication of overfitting (Section S4.4). Visual assessments of the empirical spatiotemporal variogram of average Dunn–Smyth occupancy residuals suggested that there was no residual spatiotemporal autocorrelation (Figure S3). The final model did not fail a goodness of fit test ($p = 0.07$) based on expected detections across all species and had the largest p-value of all models (Section S4.3). Furthermore, an analysis of sensitivity to the buffer distance for the woodland amount variable confirmed that a 500 m buffer distance was a good choice (Figure S4).

The only predictor that became redundant in the final model was the interaction between midstorey vegetation cover and presence of the Noisy Miner; the loadings for this predictor were credibly zero (95% highest posterior density interval) for all species except the Black-Faced Cuckoo-Shrike (Coracina novaehollandiae) (Figure 4). Relative to our earlier models, the final model showed more species with credibly-zero responses to midstorey vegetation cover and minimum temperature of the coldest month, suggesting some redundancy between these two predictors for some species (Section S5). Similarly, four species (Buff-rumped Thornbill—Acanthiza reguloides, Crimson Rosella—Platycercus elegans, Weebill—Smicornis brevirostris, and White-throated Gerygone—Gerygone olivacea) showed marked changes in loadings for woody vegetation cover and the presence of the Noisy Miner, suggesting further redundancy between these variables. Indeed, median loadings for most variables were lower in the final model than in earlier models that contained fewer effects (Figure 4).

The most important predictors, as measured by average median loading size across all 60 species, were the presence of the Noisy Miner, woodland amount and maximum temperature of the warmest month. The median loadings of these predictors also had the largest range between species (Figure S6). Conversely, on average, the smallest effect sizes were for midstorey cover, minimum temperature of the coldest month and survey year, with most species having a credibly zero loading for minimum temperature of the coldest month.

### 3.5 Differences between species

To better visualise patterns among species associations with the full set of predictor variables in our final model, we used principal component analysis of the median fitted variable loading. We found that species were distinguishable primarily by their response to the presence of the Noisy Miner on the horizontal axis, and the maximum temperature of the warmest month on the vertical axis (Figure 5a). Bird taxa mapped against the first and second principal components (Figure 5b) show a set of species that can persist given presence of the Noisy Miner on the left, while species in the bottom-right are...
associated with hot summer climates. Species at the top-right of (Figure 5b) were associated with greater nearby woodland amounts (a landscape-scale attribute), an absence of Noisy Miners (a patch-scale attribute) and cooler summer temperatures (regional-scale attribute).

4 | DISCUSSION

Quantifying associations between animal occurrence and factors at multiple scales can be difficult due to interspecific differences in responses, including differences in the scales at which they are sensitive to the environment. Nevertheless, efforts to quantify scale effects are critical for ensuring effective conservation and resource management strategies (Chase et al., 2020). We constructed a suite of statistical models to answer four key questions associated with potential drivers of bird occupancy at a patch scale, landscape scale or regional scale, and a combination of scales (Section S1). In the remainder of this section, we discuss the value of modelling the effects of drivers that have different spatial scales on species occurrence patterns, discuss potential threats to bird biodiversity (as suggested by our final model) and discuss explanations for the modelled attributes for which we did not find support.

4.1 | Spatial scale

An unexpected outcome of our study was that regional-scale drivers had a similar level of influence on bird assemblages as patch-scale drivers and that there was little redundancy between the best drivers of each of the three scales we examined. Furthermore, combining these scales appeared to be more important than accounting for detection effects such as time of day and windiness (which resulted in very limited improvement to LOOIC_null, see Figure 3), despite detection effects being widely considered as critical for the interpretation of species occurrence datasets (e.g. Kellner & Swihart, 2014).
Together, our results suggest that accounting for environmental drivers with different scales is extremely important in understanding patterns of occurrence of biodiversity.

The high degree of complementarity (i.e. low redundancy) we found among different spatial scales provides an interesting perspective into longstanding problems experienced by researchers focusing solely on single spatial scales. At fine scales, for example, it is common to report a high degree of context specificity or inconsistency among field studies in different locations (e.g. Fraser et al., 2015 showed that the term 'woodland bird assemblage' was applied unevenly across studies). This context specificity can make it difficult to create summaries that apply to a whole ecosystem, which can complicate management recommendations. According to our work, this context specificity might be expected due to species turnover across a single woodland ecosystem. Conversely, it is widely known that downscaling large spatial scale species distribution models to make patch-scale predictions about species assemblages is fraught (an issue known as the 'range porosity problem'; Hurlbert & White, 2005). Indeed, we witnessed this issue in the difference in LOOIC_null between the best model using regional-scale drivers and the combined scales model (Figure 3).

Our findings concur with existing literature showing that accounting for processes that act at multiple scales can be important when seeking to understand patterns of species occurrence (e.g. Jackson & Fahrig, 2014; Webb et al., 2017). We were able to achieve this by combining data from multiple studies that shared a common design. Our approach differs from the more traditional meta-analytic method, which groups statistical summaries across studies (e.g. Doherty et al., 2020), and is instead more closely related to projects that produce aggregated analyses based on raw data from a diverse set of monitoring studies (e.g. Chase et al., 2020; Newbold et al., 2015).

More widespread adoption of data aggregation and re-analysis depends on greater support for the generation, standardisation and sharing of biodiversity monitoring data (Bayraktarov et al., 2019). Our approach also required common field survey methods between studies; differences between field survey methods that are not accounted for can lead to spurious predictions about the status and drivers of biodiversity. As the amount of data shared from individual ecological studies grows, it should be possible to expand the general approach applied in this investigation to a broader range of ecosystems and taxa, providing rich insights at the fine spatial scales that are often needed for effective conservation.

4.2 Threats to biodiversity

Of the drivers we investigated, the presence of the Noisy Miner had the single greatest effect on occurrence of other bird species, followed by woodland amount, and then the maximum temperature of the warmest month. The effects of the Noisy Miner and woodland amount were often mutually opposing, with 27 species responding negatively to the Noisy Miner and positively to woodland amount, although the converse was true for six species (Figure 4). There were also 12 species negatively associated with Noisy Miners that appeared to have limited association with woodland amount. These findings support previous observations that the Noisy Miner—and an associated set of large-bodied bird species—are able to thrive in cleared landscapes (Maron et al., 2013) and support previous calls to use revegetation as a mechanism for bird conservation in Box-Gum Grassy Woodlands (Begg et al., 2019; Lindenmayer, Blanchard, et al., 2018). Our results further suggest that there are at least 12 species which may be impacted by Noisy Miners but which may not benefit from revegetation. The inclusion of climate in our model showed that different species will benefit from revegetation.
in areas characterised by different climatic conditions across the extent of the Box-Gum Grassy Woodlands. Specifically, our results suggest that the Yellow-rumped Thornbill (A. chrysorrhoa), Yellow-faced Honeyeater (Lichenostomus chrysops) and Striated Thornbill (A. lineata) have most to gain from revegetation in regions with cooler summers (Figure 4), whereas the Jacky Winter (Microeca fascinans), Little Friarbird (Philemon citreogularis), Noisy Friarbird (P. corniculatus) and Grey Shrike-thrush (Colluricinclla harmonica) will benefit most in regions with warmer summers (Figure 4). Given the known increase in populations of the Noisy Miner and expected changes in future climate, some species (in the top-right of Figure 5b) may be at risk of declines under future conditions, including the Yellow-faced Honeyeater, Striated Thornbill, Grey Fantail (Rhipidura fuliginosa) and Rufous Whistler (Pachycephala rufiventris).

4.3 | Hypotheses not supported by our results

We did not find strong empirical support for seven of the potential explanatory variables that we tested (Section S1). Topographic position (as measured by the topographic wetness index), gross productivity and latitude had only weak influences on bird occupancy. Similarly, the inclusion of overstorey and low cover, gross productivity deviation and survey year led to only limited improvement in model quality.

The limited influence of survey year was particularly surprising as previous findings have showed marked declines in some species, in some portions of their range (Lindenmayer, Lane, Westgate, et al., 2018). Species decline may have been accounted for by other environmental factors in the model, such as Noisy Miner presence and woodland amount, or declines in one place being offset by increases in another place. Another possibility is that bird occupancy did not decline monotonically: during our study period there were two prolonged drought periods, separated by an intermediate wet period between 2009 and 2012. Given these potential confounding effects, we suggest caution before interpreting our results as evidence that birds in our study ecosystem are not at risk of decline.

5 | CONCLUSIONS

We compared potential drivers of bird species occupancy on a long-term ecosystem-wide bird survey dataset. These empirical comparisons provide welcome confirmation of ecological theories by involving many species and multiple spatial scales. Our results provide answers to key questions on environmental drivers:

1. Vegetation structure substantially influenced bird occupancy beyond the presence of the despotic native bird species, the Noisy Miner;
2. Gross primary productivity and topographic position had little association with bird occurrence relative to woodland amount;
3. Average temperature and rainfall, summer extremes and winter extremes each explained a similar amount of species occupancy, with species occupancy better explained by a combination of all these climatic factors;
4. There was limited redundancy between environmental drivers at different scales.

Our results showed that quantifying the influence of drivers that act at different spatial scales is valuable for understanding patterns of bird species occurrence across a broadly distributed ecosystem type. Fine-scale studies can benefit from considering the climate and biogeographical context in which the research occurs. Conversely, large-scale studies should consider that it may be unsafe to ignore processes acting at finer spatial scale when making species occupancy projections.

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CONFLICT OF INTEREST

No conflict of interest is declared.

DATA AVAILABILITY STATEMENT

The data used in our statistical models, after standardisation, are available on Dryad (doi:10.5061/dryad.tqjq2bw08). Random noise was added to the latitude and longitude values to avoid identifying individual farms.

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REFERENCES

Bayraktarov, E., Ehmke, G., O’Connor, J., Burns, E. L., Nguyen, H. A., McRae, L., Possingham, H. P., & Lindenmayer, D. B. (2019). Do big unstructured biodiversity data mean more knowledge? Frontiers in Ecology and Evolution, 6, 1–5.
Beggs, R., Tulloch, A. I. T., Pierson, J., Blanchard, W., Crane, M., & Lindenmayer, D. (2019). Patch-scale culls of an overabundant bird defeated by immediate recolonization. Ecological Applications, 29, e01846.
Chase, J. M., Blowes, S. A., Knight, T. M., Gerstner, K., & May, F. (2020). Ecosystem decay exacerbates biodiversity loss with habitat loss. Nature, 584, 238–243.
Cunningham, R. B., Lindenmayer, D. B., Crane, M., Michael, D. R., Barton, P. S., Gibbons, P., Ikin, K., & Stein, J. A. R. (2014). The law of diminishing returns: Woodland birds respond to native vegetation cover at multiple spatial scales and over time. Diversity and Distributions, 20, 59–71.
Cunningham, R. B., Lindenmayer, D. B., Nix, H. A., & Lindenmayer, B. D. (1999). Quantifying observer heterogeneity in bird counts. *Australian Journal of Ecology, 24*, 270–277.

Department of Environment, Energy and Science. (2021). *Species found in the grassy woodlands formation*. New South Wales Department of Environment.

Doherty, T. S., Balouch, S., Bell, K., Burns, T. J., Feldman, A., Fist, C., Garvey, T. F., Jessop, T. S., Meiri, S., & Driscoll, D. A. (2020). Reptile responses to anthropogenic habitat modification: A global meta-analysis. *Global Ecology and Biogeography, 29*, 1265–1279.

Ehbrecht, M., Seidel, D, Annighöfer, P., Kreft, H., Köhler, M., Zemp, D. C., Puettmann, K., Nilus, R., Babweteera, F., Willim, K., Stiers, M., Soto, D., Bohemer, H. J., Fischelli, N., Burnett, M., Juday, G., Stephens, S. L., & Ammer, C. (2021). Global patterns and climatic controls of forest structural complexity. *Nature Communications, 12*(1), 519. https://doi.org/10.1038/s41467-020-20767-z

Fahrig, L. (2017). Ecological response to habitat fragmentation per se. *Annual Review of Ecology and Systematics, 48*, 1–23.

Field, S. A., Tyre, A. J., & Possingham, H. P. (2002). Estimating bird species richness: How should repeat surveys be organized in time? *Austral Ecology, 27*, 624–629.

Fischer, J., Stott, J., Zerger, A., Warren, G., Sherren, K., & Forrester, R. I. (2009). Reversing a tree regeneration crisis in an endangered ecoregion. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 10386–10391.

Fletcher, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., Holt, R. D., Gonzalez, A., Pardini, R., Damschen, E. I., Melo, F. P. L., Ries, L., Prevedello, J. A., Tschhartke, T., Laurance, W. F., Lovejoy, T., & Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? *Biological Conservation, 226*, 9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Fraser, H., Garrard, G. E., Rumpff, L., Hauser, C. E., & McCarthy, M. A. (2015). Consequences of inconsistently classifying woodland birds. *Frontiers in Ecology and Evolution, 3*, 1–8.

Gallant, J. & Austin, J. (2012). Topographic wetness index derived from 1″ SRTM DEM-H.v2. CSIRO. Data collection. https://doi.org/10.4225/08/57590B59AA08

Gelman, A., Hwang, J., & Vehtari, A. (2014). Understanding predictive information criteria for Bayesian models. *Statistics and Computing, 24*, 997–1016.

Gibbons, P., & Boak, M. (2002). The value of paddock trees for regional conservation in an agricultural landscape. *Ecological Management & Restoration, 3*, 205–210.

Gill, F. B. (1995). *Ornithology* (2nd ed.). W.H. Freeman and Company.

Haddad, N. M., Brudvig, L. A., Colbert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances, 1*(2), https://doi.org/10.1126/sciadv.1500552

Hijmans, R. J. (2017). Raster: Geographic data analysis and modeling. R package. https://cran.r-project.org/package=raster

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology, 25*, 1965–1978.

Hobbs, R. J., & Yates, C. J. (2000). *Temperate eucalypt woodlands in Australia: Biology, conservation, management and restoration*. Surrey Beatty & Sons.

Hui, F. K. C., Taskinen, S., Pledger, S., Foster, S. D., & Warton, D. I. (2015). Model-based approaches to unconstrained ordination. *Methods in Ecology and Evolution, 6*, 399–411.

Hurlbert, A. H., & White, E. P. (2005). Disparity between range map- and survey-based analyses of species richness: Patterns, processes and implications. *Ecology Letters, 8*, 319–327.

Huston, M. A. (1994). *Biological diversity - the coexistence of species on changing landscapes*. Cambridge University Press.

Ikin, K., Mortelliti, A., Stein, J., Michael, D., Crane, M., Okada, S., Wood, J., & Lindenmayer, D. (2015). Woodland habitat structures are affected by both agricultural land management and abiotic conditions. *Landscape Ecology, 30*, 1387–1403.

Jackson, H. B., & Fahrig, L. (2014). Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography, 24*, 52–63.

Kellner, K. F., & Swihart, R. K. (2014). Accounting for imperfect detection in ecology: A quantitative review. *PLoS One, 9*, e111436.

Levin, S. A. (1992). The problem of scale and pattern in ecology: The Robert H. MacArthur Award lecture. *Ecology, 73*, 1943–1967.

Liao, Z., Van Dijk, A. J. M., He, B., Larraondo, P. R., & Scharf, P. F. (2020). Woody vegetation cover, height and biomass at 25-m resolution across Australia derived from multiple site, airborne and satellite observations. *International Journal of Applied Earth Observation and Geoinformation, 93*, 102209.

Lindenmayer, D. B., Blanchard, W., Crane, M., Michael, D., & Florance, D. (2018). Size or quality. What matters in vegetation restoration for bird biodiversity in endangered temperate woodlands? *Austral Ecology, 43*, 798–806.

Lindenmayer, D. B., Blanchard, W., Foster, C. N., Scheele, B. C., Westgate, M. J., Stein, J., Crane, M., & Florance, D. (2020). Habitat amount versus connectivity: An empirical study of bird responses. *Biological Conservation, 241*, 108377.

Lindenmayer, D. B., Lane, P. W., Barton, P. S., Crane, M., Ikin, K., Michael, D., & Okada, S. (2016). Long-term bird colonization and turnover in restored woodlands. *Biodiversity and Conservation, 25*, 1587–1603.

Lindenmayer, D. B., Lane, P. W., Crane, M., Florance, D., Foster, C. N., Ikin, K., Michael, D., Sato, C. F., Scheele, B. C., & Westgate, M. J. (2018). Weather effects on birds of different size are mediated by long-term climate and vegetation type in endangered temperate woodlands. *Global Change Biology, 25*, 675–685.

Lindenmayer, D. B., Lane, P. W., Westgate, M., Scheele, B. C., Foster, C., Sato, C., Ikin, K., Crane, M., Michael, D., Barton, P., O’Loughlin, L. S., & Robinson, N. (2018). Tests of predictions associated with temporal changes in Australian bird populations. *Biological Conservation, 222*, 212–221.

Lindenmayer, D. B., Michael, D., Crane, M., Florance, D., & Burns, E. (2018). *Restoring farm woodlands for wildlife*. CSIRO Publishing.

Lindenmayer, D. B., Michael, D., Crane, M., Okada, S., Barton, P., Ikin, K., & Florance, D. (2016). *Wildlife conservation in farm landscapes*. CSIRO Publishing.

Lindenmayer, D. B., Wood, J. T., & MacGregor, C. (2009). Do observer differences in bird detection affect inferences from large-scale ecological studies? *Emu - Austral Ornithology, 109*, 100–106.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droegue, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology, 83*, 2248–2255.

Mackey, B. G., & Lindenmayer, D. B. (2001). Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography, 28*, 1147–1116.

Maron, M., Grey, M. J., Catterall, C. P., Major, R. E., Oliver, D. L., Clarke, M. F., Loyin, R. H., Mac Nally, R., Davidson, I., & Thomson, J. R. (2013). Avifaunal disarray due to a single despotic species. *Diversity and Distributions, 19*, 1468–1479.

Montague-Drake, R. M., Lindenmayer, D. B., & Cunningham, R. B. (2009). Factors affecting site occupancy by woodland bird species of conservation concern. *Biological Conservation, 142*, 2896–2903.

Moran-Ordóñez, A., Briscoe, N., & Wintle, B. A. (2018). Modelling species responses to extreme weather provides new insights into constraints on range and likely climate change impacts for Australian mammals. *Ecography, 41*, 308–320.

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Chouimes, A., Collen, B., Day, J., De
Palma, A., Díaz, S., Echeverría-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., ... Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545), 45–50. https://doi.org/10.1038/nature14324

O’Brien, L. & Searle, R. (2020). Slga: Data access tools for the soil and landscape grid of Australia. R package version 1.1.1. https://cran.r-proje ct.org/package=slga

Pinek, L., Mansour, I., Lakovic, M., Ryo, M., & Rillig, M. C. (2020). Rate of environmental change across scales in ecology. *Biological Reviews*, 95, 1798–1811.

Pressey, R. L., Hager, T. C., Ryan, K. M., Schwarz, J., Wall, S., Ferrier, S., & Creaser, P. M. (2000). Using abiotic data for conservation assessments over extensive regions: Quantitative methods applied across New South Wales, Australia. *Biological Conservation*, 96, 55–82.

Purvis, A., Newbold, T., De Palma, A., Contu, S., Hill, S. L. L., Sanchez-Ortiz, K., Phillips, H. R. P., Hugson, L. N., Lysenko, I., Böger, L., & Scharlemann, J. P. W. (2018). Chapter five - Modelling and projecting the response of local terrestrial biodiversity worldwide to land use and related pressures: The PREDICTS project. In D. A. Bohan, A. J. Dumbrell, G. Woodward, & M. Jackson (Eds.), *Advances in ecological research next generation biomonitoring: Part 1* (pp. 201–241). Academic Press.

Pyke, G. H., & Recher, H. F. (1983). Censusing Australian birds: A summary of procedures and a scheme for standardisation of data presentation and storage. In S. J. J. F. Davies (Ed.), *Methods of censusing birds in Australia* (pp. 55–63). Department of Conservation and Environment.

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Smith, A. C., Fahrig, L., & Francis, C. M. (2011). Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography*, 34, 103–113.

Spake, R., Bellamy, C., Graham, L. J., Watts, K., Wilson, T., Norton, L. R., Wood, C. M., Schmucki, R., Bullock, J. M., & Eigenbrod, F. (2019). An analytical framework for spatially targeted management of natural capital. *Nature Sustainability*, 2, 90–97.

Specht, R. L., & Morgan, D. G. (1983). The balance between the foliage projective covers of oversorey and understorey in Australian vegetation. *Australian Journal of Ecology*, 6, 193–202.

Storch, D., Bohdalová, E., & Okie, J. (2018). The more-individuals hypothesis revisited: The role of community abundance in species richness regulation and the productivity-diversity relationship. *Ecology Letters*, 21, 920–937.

Tobler, M. W., Kéry, M., Hui, F. K. C., Guillera-Arroita, G., Knaus, P., & Sattler, T. (2019). Joint species distribution models with species correlations and imperfect detection. *Ecology*, 100, e02754.

Tschanntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, 87(3), 661–685. https://doi.org/10.1111/j.1469-185x.2011.00216.x

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27, 1413–1432.

Verschul, J. P., Hansen, A. J., McWethy, D. B., Sallabanks, R., & Hutto, R. L. (2008). Is the effect of forest structure on bird diversity modified by forest productivity? *Ecological Applications*, 18, 1155–1170.

Warton, D. I., Blanchet, F. G., O’Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2014). So many variables: Joint modeling in community ecology, *Trends in Ecology & Evolution*, 30, 768–779.

Warton, D. I., Stoklosa, J., Guillera-Arroita, G., MacKenzie, D. I., & Welsh, A. H. (2017). Graphical diagnostics for occupancy models with imperfect detection. *Methods in Ecology and Evolution*, 8, 408–419.

Watanabe, S. (2010). Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research*, 11, 3571–3594.

Webb, M. H., Terauds, A., Tulloch, A., Bell, P., Stoianovic, D., & Heinsohn, R. (2017). The importance of incorporating functional habitats into conservation planning for highly mobile species in dynamic systems. *Conservation Biology*, 31, 1018–1028.

Westgate, M. J., Crane, M., Florange, D., & Lindenmayer, D. B. (2021). Synergistic impacts of aggressive species on small birds in a fragmented landscape. *Journal of Applied Ecology*, 58, 825–835.

Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, 34, 273–309.

Wilson, J. W., Sexton, J. O., Todd Jobe, R., & Haddad, N. M. (2013). The relative contribution of terrain, land cover, and vegetation structure indices to species distribution models. *Biological Conservation*, 164, 170–176.

Wintle, B. A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen, A., Gordon, A., Lentini, P. E., Cadenehd, N. C. R., & Bekessy, S. A. (2019). Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences*, 116, 909–914.

Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, 41, 496–506.

Yebra, M., Van Dijk, A. I. J. M., Leuning, R., & Guerschman, J. P. (2015). Global vegetation gross primary production estimation using satellite-derived light-use efficiency and canopy conductance. *Remote Sensing of Environment*, 163, 206–216.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

**Biosketch**

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