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1 **TITLE:** Mistletoes could moderate drought impacts on birds, but are themselves susceptible to
2 drought-induced dieback.

3 **RUNNING TITLE:** Drought impacts on mistletoes and birds.

4 **AUTHORS:** Ross Crates¹, David M Watson², Greg Albery³, Timothée Bonnet⁴, Liam Murphy¹,
5 Laura Rayner¹, Dejan Stojanovic¹, Chris Timewell⁵, Beau Meney⁵, Mick Roderick⁵, Dean Ingwersen⁵,
6 Robert Heinsohn¹

7 1. Fenner School of Environment and Society, Australian National University, Linnaeus Way, Acton,
8 Canberra, Australia 2601.

9 2. School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Albury,
10 New South Wales, Australia.

11 3. Department of Biology, Georgetown University, Washington DC, USA.

12 4. Research School of Biology, Australian National University, Linnaeus Way, Acton, Canberra,
13 Australia 2601.

14 5. BirdLife Australia, Carlton, Melbourne, Australia.

15 ¶ Corresponding author: ross.crates@anu.edu.au

16 **ABSTRACT:** Mistletoes are hemiparasitic plants and keystone species in many ecosystems globally.
17 Given predicted increases in drought frequency and intensity, mistletoes may be crucial for
18 moderating drought impacts on community structure. Dependent on vascular flow of hosts, mistletoes
19 can succumb to water stress when moisture availability falls, making them susceptible to mortality
20 during climatic extremes. We counted mistletoe at 2,111 sites across >350,000 km² of south-eastern
21 Australia. At 1,218 sites, we conducted standardised bird surveys between 2016 and 2021, spanning a
22 major drought event in 2018-19. We aimed to identify predictors of mistletoe abundance and
23 mortality and determine whether mistletoes might moderate drought impacts on woodland birds. Live
24 mistletoe abundance varied with tree species composition, land use and presence of mistletoebirds- a
25 specialist frugivore. Mistletoe mortality was widespread, consistent with high 2018/19 summer

26 temperatures, low 2019/20 summer rainfall and the interaction between summer temperatures and
27 rainfall in 2019/20. The positive association between surviving mistletoes and woodland birds was
28 greatest in the peak drought breeding seasons of 2018/19 and 2019/20, particularly for small residents
29 and insectivores. Paradoxically, mistletoes could moderate drought impacts on birds, but are
30 themselves vulnerable to drought-induced mortality. An improved understanding of the drivers and
31 dynamics of mistletoe mortality is needed to address potential cascading trophic impacts associated
32 with mistletoe die-off.

33 **INTRODUCTION:** Mistletoes—five families of flowering plants in the order Santalales—are
34 hemiparasites with over 1600 species distributed globally¹. Given their well-documented ecological
35 roles in nutrient cycling, forest stand dynamics, food and nest substrate provisioning, mistletoes are
36 keystone species in many ecosystems². In addition to providing abundant resources and boosting
37 heterogeneity in productivity via nutrient subsidies, these plants depend on a network of other
38 organisms, including pollinators, seed dispersers and host plants. Consequently, mistletoe health and
39 abundance serve as important bioindicators of broader ecosystem health³⁻⁵.

40 Although population-scale impacts of climate change on mistletoes have not been quantified, several
41 aspects of their life-history and physiology pre-dispose them to acute sensitivity to sudden changes in
42 water availability. Lacking roots and storage organs, mistletoes use high transpiration rates to
43 maintain vascular flow from hosts^{6,7}. By retaining cations in semi-succulent foliage, mistletoes
44 maintain water balance by passively drawing down a concentration gradient^{8,9}. While this enriches
45 tissues, increases water flux and likely within-canopy humidity¹⁰, their limited control over stomatal
46 closure makes mistletoes sensitive to sudden reductions in moisture availability⁷, with increased
47 evapotranspiration from prolonged hot/dry conditions associated with mistletoe mortality^{11,12} (Zweifel
48 et al. 2012; Greibel et al. 2022a).

49 In Australia, flowering mistletoes provide high quality nutritional resources for many animals¹³. In
50 addition to being the principal food source for several nectarivorous bird species^{14,15}, many other
51 species rely on mistletoe fruits for carbohydrates, fats, amino acids and water^{2,16}. Annual flowering
52 and fruiting phenology of mistletoes is typically more regular than that of their host trees¹³. Sympatric

53 mistletoe species often exhibit complementary periods of peak flowering and fruiting, thereby
54 extending the period of nectar and fruit availability in a given location¹⁷. Consequently, mistletoes
55 provide predictable and reliable resources during droughts when ecosystem productivity such as
56 eucalypt flowering is otherwise low¹⁶. Lush, dense foliage of healthy mistletoes are a key browsing
57 resource for arboreal mammals and create microclimates that moderate temperature extremes^{18,10},
58 making mistletoe favourable nesting and roosting sites for many bird species⁹. With predicted
59 increases in the frequencies of prolonged droughts and severe heatwaves under climate change^{19,20},
60 more species may depend on live mistletoe to survive such events in coming decades.

61 There is some evidence that mistletoe mortality events have occurred in south-eastern Australia in
62 recent years^{21,22}. Potential drivers of mistletoe mortality in Australia's woodlands include the 2019/20
63 megafires²³ (Wintle et al., 2020) and drought-induced eucalypt dieback associated with the 2018/2019
64 drought event^{24,25}. Three widespread species potentially affected by drought are box *Amyema miquelii*,
65 long-flowered *Dendrophthoe vitellina* and needle-leaf mistletoe *Amyema cabbageii*. These species
66 provide key breeding resources for many threatened species including the Critically Endangered
67 regent honeyeater *Anthochaera phrygia*^{26,27}. In particular, needle-leaf mistletoes provide nectar
68 resources in riparian zones that function as important drought refugia²⁸. If mistletoe mortality is
69 widespread, it could have knock-on impacts across food webs, interrupting nutrient returns,
70 microclimatic buffering and food availability². However, current monitoring data available to quantify
71 the causes, extent and potential impact of mistletoe mortality in woodland ecosystems are limited in
72 extent, hindering current capacity to address threats through conservation actions.

73 Here we address some current shortfalls in our knowledge of the predictors of mistletoe abundance,
74 mistletoe mortality and the importance of mistletoe in sustaining biodiversity at higher trophic levels
75 during climate extremes. We generated a baseline dataset to monitor long-term mistletoe population
76 dynamics and associated woodland bird abundance. With these data, we aimed to answer two
77 questions:

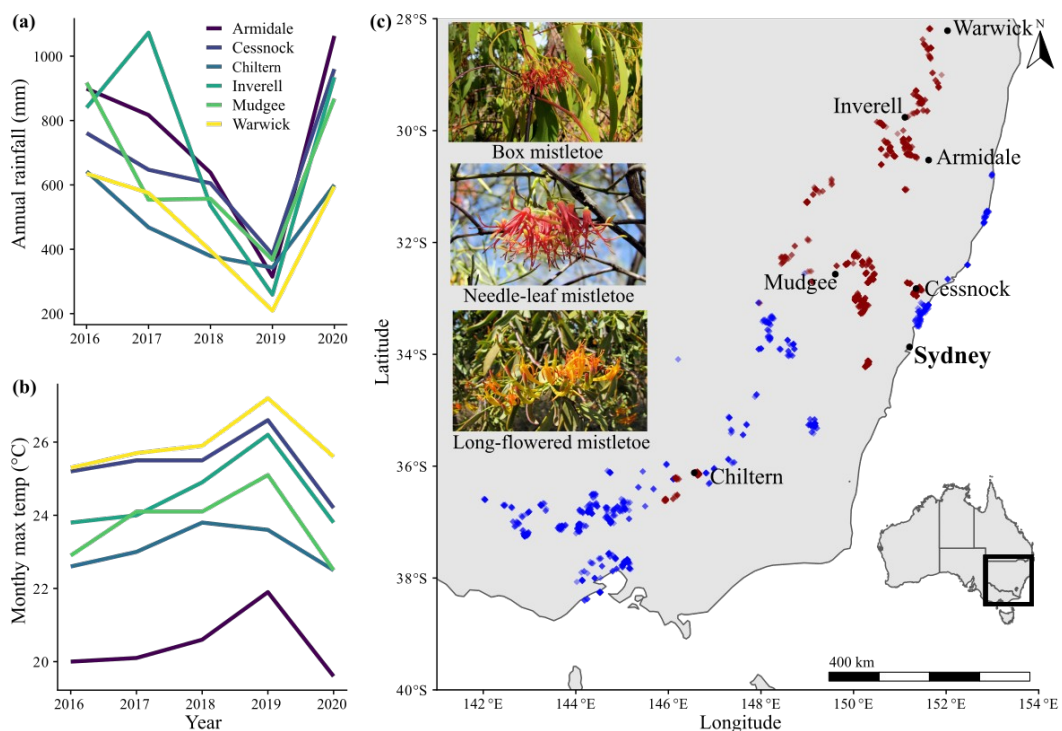
78 *Question 1:* What are the predictors of mistletoe abundance and the drivers of mistletoe mortality?

79 Question 2: What is the relationship between live mistletoe abundance and woodland bird abundance,
80 and how does this relationship change during drought?

81 METHODS

82 Habitat assessments and mistletoe counts

83 During 2019/20, we conducted habitat assessments at 2,111 monitoring sites spanning over 300,000
84 km² of south-eastern Australia (Figure 1). We selected monitoring sites in areas of woodland habitat
85 deemed suitable for two Critically Endangered bird species: the regent honeyeater and swift parrot
86 *Lathamus discolor*. We used a combination of MaxEnt habitat suitability models (Figures S1 and S2),
87 expert field searches and the location of previous sightings to inform site locations. Since both bird
88 species are habitat specialists²⁹, our sampling encompasses the highest quality remaining woodlands
89 in south-eastern Australia.



90

91 **Figure 1:** (a - b) Annual rainfall and mean monthly maximum temperature data for weather stations
92 spanning the spatial and temporal extent of the bird monitoring dataset. (c) Distribution of both
93 woodland bird and mistletoe (red) and mistletoe only (light blue) monitoring sites in south-eastern
94 Australia. Top left inset: box *Amyema miquelii*, long-flowered *Dendrophthoe vitellina* and needle-leaf

95 *Amyema cambageii* mistletoe species included in the study. Bottom right inset: study range on a
 96 national scale. Place labels (excluding Sydney) show the location of the summary climate data
 97 presented in (a - b). Rainfall and temperature data are shown to summarise annual variation in the
 98 climate surface data used in mistletoe models, sourced from the Australian Bureau of Meteorology
 99 <http://www.bom.gov.au/climate/data/>, accessed 9/3/2021.

100 Each monitoring site was a 50m radius (0.79 hectares) around a fixed GPS location to two metres
 101 accuracy. During one visit to each site in 2019/20, we recorded the habitat fixed effects detailed in
 102 Table 1. Our mistletoe counts focussed on the three most abundant mistletoe species (Family
 103 Loranthaceae) in the study range: box, needle-leaf and long-flowered. We conducted a 360° search of
 104 the canopy from each site centroid, deviating from this point where necessary to count accurately the
 105 number of live and dead mistletoe clumps present.

106

107 **Table 1:** Site-level and visit-level fixed effects obtained for identifying predictors of mistletoe
 108 abundance and health and to model the effect of mistletoe abundance on woodland bird abundance.
 109 For further information on the fixed effects, see Table S1.

Level	Fixed effect	Description
Site-level	Spatial location	WGS84 decimal latitude longitude to 2m accuracy.
	Region	10-level factor defining regional clusters of monitoring sites. Included as a random term in mistletoe and bird models.
	Land use	9-level factor: Primary land use.
	Canopy cover	Percentage canopy cover to the nearest 5%.
	Tree species PC1 & PC2	Principal component axes 1 & 2 of tree species composition (see Figure S3).
	Tree age	Proportion of trees present with a diameter at breast height >80cm.
	Tree health	Proportion of trees in the site that are healthy or only mildly stressed per Briggs & Taws ³⁰ .
	Shrub cover	Percentage shrub cover (vegetation 30cm to 2m) to the nearest 5%.
	Live mistletoe	Total number of clumps of live mistletoe across all three species.
	Dead mistletoe	Total number of clumps of dead mistletoe across all three species.
	Distance to permanent or semi-permanent water source	5-level factor: 1 = water present within site, 2 = water within 100m, 3 = water within 300m, 4 = water >300m away, 5 = distance to water unknown.
	Mistletoebird presence	Presence/absence of mistletoebirds detected during ≥ 1 bird survey per site.

	Noisy miner abundance	Mean abundance of noisy miners (a hyperabundant and colonial native bird that excludes other songbirds from habitats they occupy) detected during repeat bird surveys at each site (mistletoe models), or abundance per site visit (bird models).
Visit-level	Breeding Season	Annual Austral breeding season August to January.
	Hours since dawn/to dusk	Hours from 6am (morning) or hours to 7pm (afternoon).
	Observer	7-level factor: bird surveyor / habitat assessor. Random effect in bird models.
	Blossom	5-level factor: site-level blossom abundance (including both eucalypts and mistletoes): 0 = no blossom; 1 = light blossom- few flowers in a small number of trees; 2 = moderate blossom- few flowers in many trees or moderate flowering in a few trees; 3 = heavy blossom- profuse flowering in few trees or moderate flowering in multiple trees; 4 = very heavy blossom- multiple profusely-flowering canopies.
	Max summer temperature	Mean monthly maximum summer temperature November to Feb.
	Max summer rain	Mean maximum monthly summer rainfall November to Feb.

110

111 *Bird surveys*

112 We conducted 9,012 point-count surveys at a total of 1,218 monitoring sites in the Austral
113 spring/summer breeding season (August to January) between 2016 and 2021 (Table S2). Each survey
114 was conducted by one of 15 professional ornithologists, with 86% of surveys completed by seven
115 observers. Our rapid (5-minute) census, involving one minute of regent honeyeater song broadcast,
116 was designed to maximise the detectability of such rare, nomadic habitat specialists by increasing the
117 spatial extent of surveys without compromising detectability³¹. We recorded the maximum count of all
118 bird species detected visually or aurally within a 50m radius of the fixed-point location during each
119 site visit, along with a blossom score for each site. Observers remained at the site centroid as much as
120 possible, but deviated where necessary to identify individual birds to species level or to obtain
121 accurate counts of birds occupying heavily-flowering trees near site boundaries. We did not include
122 transient birds flying through or over study sites in the counts. The blossom score was a five-level
123 factor (Table 1); a simple way of modelling variation in blossom abundance on nomadic species
124 occupancy patterns³². To account for intra-seasonal variation in flowering phenology and associated
125 changes in woodland bird distribution/abundance³³, we surveyed as many sites as possible (77%)

126 twice; once in spring between August and October and again in early summer between November and
127 January.

128 *Climate data*

129 We sourced climate data from the Australian National University Climate surface database
130 (ANUCLIM v6.1³⁴). We obtained national monthly maximum temperature and rainfall measures
131 between 2017 and 2020, and derived these measures for each of our monitoring site locations from a
132 250m national raster. See Supplementary file S1 for further information on derivation of the climate
133 data. For mistletoe analysis, we calculated annual mean maximum rainfall and temperature measures
134 averaged across the summer months of November to February, when mistletoes are most susceptible
135 to drought impacts³⁵.

136 *Statistical analysis*

137 We used R v3.4.3³⁶ for all statistical analyses. We first checked for spatial autocorrelation in mistletoe
138 abundance and mortality data using correlograms of Moran's I via package *ncf* v1.2-5³⁷. To check for
139 cross-correlation between covariates, we used *GGally* v1.4.0³⁸, but no covariates showed consistent
140 strong positive or negative correlation with others.

141 To account for interspecific variation in the suitability of tree species as mistletoe hosts³⁹, we ran a
142 centred and scaled Principal Component Analysis (PCA) of the proportional contribution of each tree
143 species to canopy cover across sites using *stats* v3.6.2 in base R. The first two Principal Component
144 axes, which we included in subsequent mistletoe and bird models (Tree species PC1 & PC2), together
145 explained 9% of the total variation in tree species composition. Because the proportion of total
146 variation explained by the PCA was relatively low, we also conducted a separate analysis of the
147 association between individual tree species and live mistletoe abundance (Supplementary file S2).

148 To account for spatial autocorrelation in the mistletoe and bird data, we fitted a series of Integrated
149 Nested Laplace Approximation (INLA) Generalised Linear Mixed Models (GLMMs) via package
150 *INLA* v21.02-23⁴⁰. The INLA models included a Stochastic Partial Differentiation Equation (SPDE)
151 random term that calculates the distances between the spatial location of monitoring sites using

152 Matern covariance^{41,42}. We selected the best models as those with the lowest Deviance Information
153 Criterion (DIC) value and assessed their goodness of fit based on conditional R^2 values⁴³.

154 To answer question 1 *What are the predictors of mistletoe abundance and the drivers of mistletoe*
155 *mortality?* we first used live mistletoe counts as the response in a GLMM with a negative binomial
156 error structure. The model included as fixed effects: Land use, canopy cover, tree species
157 composition, tree health, tree age and distance to standing water, with region included as a random
158 term (Table 1). To assess the association between mistletoebird presence (the key disperser of
159 mistletoe fruits¹⁵) and noisy miner abundance (a key driver of mistletoebird distribution⁴⁴) on
160 mistletoe abundance, we re-ran the model on the subset of sites where we conducted bird surveys
161 (Figure 1) and included mistletoebird presence and noisy miner abundance as fixed effects in the
162 saturated model.

163 We replaced live mistletoe abundance with dead mistletoe abundance as the response measure to
164 identify the predictors of mistletoe mortality. To the fixed effects included in the live mistletoe model
165 described above, we added live mistletoe abundance, mean maximum monthly summer (Nov-Feb)
166 temperature and summer rainfall for 2017/18, 2018/19 and 2019/20, as well as the annual interaction
167 between these temperature and rainfall measures.

168 To answer question two *What is the relationship between live mistletoe abundance and woodland*
169 *bird abundance, and how does this relationship change during drought?* we calculated four woodland
170 bird abundance response measures, based on overall bird abundance, body size, residency status and
171 feeding guild (Tables 2 and S2). We excluded noisy miners from bird abundance measures due to
172 their impacts on woodland bird abundance⁴⁴, and instead included noisy miner abundance as a fixed
173 effect in the woodland bird models (Table 1). The response measures were counts of birds described
174 in Table 2. Fixed effects included overall blossom score, breeding season, noisy miner abundance,
175 canopy and shrub cover extent, tree species composition, land use, distance to standing water, survey
176 time, and live mistletoe abundance (log + 1 transformed). We included observer and region as random
177 terms. To examine how the relationship between woodland birds and mistletoes changed during

178 drought, we included in the woodland bird models the interaction term *live mistletoe abundance* ×
 179 *breeding season*. For all bird models we used a Poisson error structure.

180 **Table 2:** Bird response measures used in models to answer question 2: *What is the relationship*
 181 *between live mistletoe abundance and woodland bird abundance, and how does this relationship*
 182 *change during drought?* Note the species composition of bird response measures are not mutually
 183 exclusive. See table S3 and the raw dataset available via the Dryad digital repository.

Bird response	Description	Justification
Total bird abundance	Total abundance of all bird species detected, excluding noisy miners.	Overall bird abundance is the ultimate measure of bird community response to mistletoe health and abundance ⁴⁵ .
Small resident bird abundance	Abundance of all birds with mean body mass less than 60g considered not to be migratory or nomadic.	60g is the mean mass of noisy miners, which exclude smaller birds from habitats they occupy. Excluding migratory and nomadic species accounts for high spatio-temporal variability of such species, independent of any effects of mistletoe abundance on bird abundance ^{27,44} .
Nectarivores	Total abundance of all nectarivorous birds.	Feeding guilds will differ in the extent to which they depend on mistletoe abundance. Nectarivores predicted to be most dependent on mistletoes as a direct feeding substrate ⁴⁶ .
Insectivores	Total abundance of all insectivorous birds.	Insectivores predicted to be less dependent on mistletoes than nectarivores, but through potential impacts of mistletoe on insectivore abundance, insectivores may be more dependent on mistletoe than granivores ^{14,15} .

184

185 **RESULTS**

186 Live mistletoe was present at 1,267 of 2,111 sites. Where present, the median number of live clumps
 187 per site was 10 (s.d. = 22). Dead mistletoe was present at 1,008 sites and where present, the median
 188 number of dead mistletoe clumps per site was 4 (s.d. = 12). The proportion of dead mistletoe was
 189 highly variable and substantial in some areas— even where total mistletoe abundance was high (Figure

190 S4). There was positive spatial autocorrelation in the proportion of dead mistletoe present at
191 monitoring sites out to 100 km, but was greatest as the local scale from 0–6 km (Figures S4-S5).

192 *Question 1: What are the predictors of live mistletoe abundance and mistletoe mortality?*

193 Models including data from all habitat monitoring sites found mistletoe abundance was positively
194 associated with the proportion of trees present with a DBH exceeding 80cm, but negatively associated
195 with canopy cover (Figure 2a). Relative to within national parks and nature reserves, mistletoe
196 abundance was lower in areas where land uses were predominantly private and ungrazed, travelling
197 stock reserves, recreational parks / reserves or peri-urban. Mistletoe abundance was negatively
198 associated with both the tree species composition measures (Principal Components 1 and 2),
199 suggesting a higher abundance in plant community types dominated by white box *Eucllyptus albens*,
200 yellow box *E. melliodora*, river she-oak *Casuarina cunninghamiana* and mugga ironbark *E.*
201 *sideroxylon*, relative to communities dominated by swamp mahogany *E. robusta*, paperbarks
202 *Melalauca spp.*, smoothed barked apple *Angophora costata* and other gum species (Figure S3).
203 Supplementary analyses reinforced such relationships to the individual mistletoe and host tree species
204 level (Figure S6). Presence of mistletoebirds was the dominant explainer of high mistletoe abundance
205 at sites in which bird surveys were conducted. Despite their despotic impact on small woodland birds,
206 there was no negative effect of mean noisy miner abundance on mistletoe abundance (Figure S8).
207 Dead mistletoe abundance was associated negatively with summer temperatures in 2018/19 and with
208 summer rain in 2019/20 (i.e. peak drought). There was also a weak positive interaction between
209 summer rainfall and maximum temperatures on mistletoe mortality in 2019/20 (Figure 2a). The
210 spatial term showed a latitudinal trend in dead mistletoe abundance, with higher mortality in northern
211 regions of south-eastern Australia (Figure 2c). For all three response measures, the inclusion of the
212 SPDE effect substantially improved model fit: live mistletoe ΔDIC (from models excluding SPDE
213 term) = -556, conditional $R^2 = 0.74$; live mistletoe (birds) = $\Delta\text{DIC} -66$ $R^2 = 0.35$; dead mistletoe =
214 $\Delta\text{DIC} = -195$, $R^2 = 0.79$.

215

(a) Forest plot showing fixed effect estimates for various factors. The y-axis lists factors: Tree age, Tree health, Canopy cover, Land use: Travelling Stock Reserve, Land use: Peri-urban, Land use: Recreational park/reserve, Land use: Private ungrazed, Mistletoebird presence, Tree species PC1, Tree species PC2, Total live mistletoe, Temperature summer 2018/19, Rainfall summer 2019/20, and Summer temperature x rainfall 2019/20. The x-axis is 'Estimate' ranging from -2 to 2. A vertical dashed line is at 0. Three series are shown: Live mistletoe (cyan), Live mistletoe (bird monitoring sites) (red), and Dead mistletoe (purple). Significant effects are those where the 95% credibility interval does not overlap zero.

(b) Live mistletoe: Spatial map of live mistletoe abundance. Y-axis: Latitude (28°S to 38°S). X-axis: Longitude (142°E to 152°E). Color scale: Mean (0.94 to -3.63).

(c) Live mistletoe (bird monitoring sites): Spatial map of live mistletoe abundance including bird data. Y-axis: Latitude (28°S to 36°S). X-axis: Longitude (146°E to 152°E). Color scale: Mean (0.17 to -1.17).

(d) Dead mistletoe: Spatial map of dead mistletoe abundance. Y-axis: Latitude (28°S to 38°S). X-axis: Longitude (142°E to 152°E). Color scale: Mean (0.62 to -1.44).

216

217 **Figure 2:** (a) Fixed effect estimates of the association between environmental, biotic and climatic effects and mistletoe abundance and mortality. Land use factorial effects are
 218 relative to Land use: National park/Nature reserve. Points denote the posterior means and the error bars denote the 95% credibility intervals for the effects. Only significant
 219 fixed effects or factor levels (where estimates \pm 95% credibility intervals do not overlap zero) from the top model, based on lowest DIC, are shown. See figure S7 for the full
 220 model. (b-d): Spatial fields for the SPDE random effect of response variables of live mistletoe abundance (b), live mistletoe abundance including bird data (c), and dead
 221 mistletoe abundance (d), based on habitat (b & d) or bird (c) monitoring point locations (see Figure 1). Predictions are derived using the *ggField* function from the
 222 PointPolygon package v0.1.0⁴⁷. See Table 1 and Supplementary File S1 for further information on the fixed effects and factor levels.

223 Question 2: What is the relationship between live mistletoe abundance and woodland bird abundance, and how does
224 this relationship change during drought?

225 Total live mistletoe abundance was not retained as a single term in the top model of overall bird abundance or any
226 models of the bird functional sub-groups (Figure 3a). Bird abundance was primarily driven by blossom abundance,
227 with the greatest association with nectarivores and the weakest association with insectivores (Figure 3a). There was
228 substantial annual variation in bird abundance, primarily in nectarivores and insectivores. Noisy miner abundance had
229 a negative association with overall bird abundance, primarily driven by impacts on small residents and nectarivores
230 (Figure 3a). Bird abundance was broadly, but weakly, positively associated with both tree species composition
231 measures (Tree species Principal Components 1 & 2). Effects of vegetation structure in the form of canopy and shrub
232 cover extent were nominal. Relative to within national parks and nature reserves, overall bird abundance was lower in
233 state forests and recreational parks/reserves and higher in travelling stock reserves and private ungrazed property. Bird
234 abundance tended to decrease with increasing distance from a water source and time since dawn or dusk (Figure 3a).

235 The association between the abundance of remaining live mistletoes and woodland birds varied annually, and was
236 most strongly positive during the peak drought breeding seasons of 2018/19 and, in particular, 2019/20 (Figure 4).

237 Associations with the abundance of live mistletoe increased most substantially during the drought for small residents
238 and insectivores (Figure 4). Inclusion of the SPDE term again improved the fit of all four bird models: all birds Δ DIC
239 (from models without SPDE term) = -2642, $R^2 = 0.71$; small residents Δ DIC = -1228, $R^2 = 0.53$; nectarivores Δ DIC =
240 -3935, $R^2 = 0.87$; insectivores Δ DIC = -1685, $R^2 = 0.40$.

241

(a) Forest plot showing fixed effect estimates for various factors. The y-axis lists factors: Blossom light, Blossom moderate, Blossom heavy, Blossom very heavy, Water distance <100m, Water distance <300m, Water distance >300m, Land use: Travelling Stock Reserve, Land use: State forest, Land use: Recreational park / reserve, Land use: Roadside crown land, Land use: Private ungrazed, Tree species PC1, Tree species PC2, Noisy miner abundance, Hours since dawn / hours to dusk, Breeding season 2017/18, Breeding season 2018/19, Breeding season 2019/20, and Breeding season 2020/21. The x-axis is 'Estimate' from -1 to 2. Points represent posterior means, and error bars represent 95% credibility intervals. A vertical dashed line is at 0. The legend indicates: All birds (cyan), Small residents (red), Nectarivores (purple), and Insectivores (yellow).

(b) Spatial map for 'All birds' showing mean values across a region from 28°S to 36°S latitude and 146°E to 152°E longitude. The color scale ranges from -6.49 (yellow) to 0.84 (dark blue).

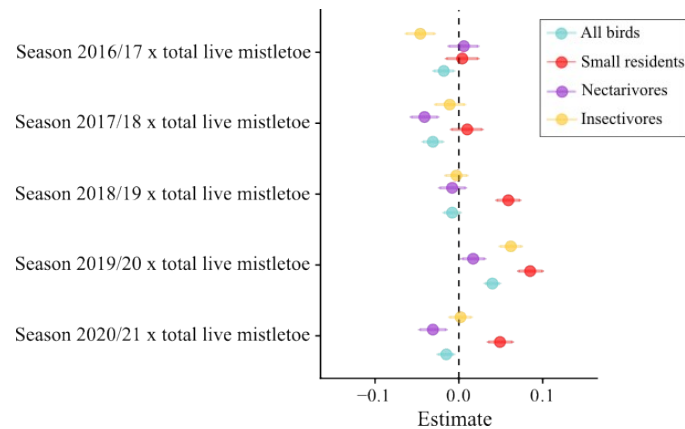
(c) Spatial map for 'Small residents' showing mean values. The color scale ranges from -4.45 (light pink) to 0.63 (dark red).

(d) Spatial map for 'Nectarivores' showing mean values. The color scale ranges from -6.02 (light blue) to 0.95 (dark purple).

(e) Spatial map for 'Insectivores' showing mean values. The color scale ranges from -3.34 (yellow) to 0.32 (dark red).

242

243 **Figure 3:** (a) Fixed effect estimates of the association between environmental, biotic and climatic effects and woodland bird abundance. Factorial effects are relative to the
 244 following levels: Blossom = absent; Water distance = 0 (i.e. water present); Land use: National park/Nature reserve; Breeding season = 2016/17. Points denote the posterior
 245 means and the error bars denote the 95% credibility intervals for the effects. Only significant fixed effects or effects with significant factor levels (where estimates \pm 95%
 246 credibility intervals do not overlap zero) from the top models, based on lowest DIC, are shown. See figure S8 for the full model summary;; (b-e): Spatial fields for the SPDE
 247 random effect of response variables of total (b), small resident (c), nectarivorous (d) and insectivorous (e) woodland bird abundance based on bird monitoring point locations
 248 (Figure 1).



250

251 **Figure 4:** Fixed effect estimates of the interaction between breeding season \times live mistletoe
 252 abundance on woodland bird abundance. Points denote the posterior means and the error bars denote
 253 the 95% credibility intervals for the effects. Estimates are derived from the same model as shown in
 254 Figures 3 and S8.

255 DISCUSSION

256 Using a spatially-extensive dataset spanning a five-year period before, during and after a major
 257 drought, we show that the association between mistletoes and woodland birds strengthens during
 258 severe drought, and therefore that mistletoes may play a key role in moderating the negative impacts
 259 of below-average rainfall and above-average temperatures on vertebrate abundance. Paradoxically, we
 260 found substantial drought-associated mistletoe dieback in parts of south-eastern Australia. Given the
 261 increased frequency and severity of drought and heatwave events predicted under impending climate
 262 change¹⁹, our results suggest mistletoes are at risk from large-scale die-off over coming decades.
 263 Mistletoe die-off could have cascading impacts on community composition⁴, with the greatest effects
 264 on resident and insectivorous species that are least able to avoid drought and heatwave effects via
 265 dispersal or dietary plasticity. We highlight the need for further research and long-term, spatially-
 266 extensive monitoring to better understand the dynamics and drivers of mistletoe mortality, and to
 267 inform conservation actions to maintain their keystone role in functioning ecosystems globally.

268 Land-use was a key predictor of live mistletoe abundance, with relatively lower abundances occurring
269 in peri-urban areas such as street trees and recreational parks and reserves. We also found a strong
270 positive relationship between mistletoe abundance and mistletoebird presence- a mistletoe specialist
271 and the primary disperser of mistletoe seeds¹⁵. Mistletoebirds are scarce in suburban areas, although
272 further work is needed to disentangle cause and effect in the relationship between mistletoebirds and
273 mistletoe abundance.

274 We also found effects of tree species composition on mistletoe abundance. Many mistletoe species are
275 specialists on a small range of host tree genera³⁹, with specialisation at the genus or family level
276 associated with increased susceptibility to drought¹⁰. In terms of our study species, needle-leaf
277 mistletoes are specialists on she-oaks, which fringe riparian zones throughout south-eastern Australia.
278 Box mistletoe tends to parasitise box-gum-ironbark tree species that predominate in more western
279 woodlands within the study range³⁹, while long-flowered mistletoe depends primarily on hosts in the
280 Myrtaceae spotted gum-ironbark forests in the north and east of the study range.

281 There was widespread and often high rates of mistletoe mortality throughout the study range, with
282 needle-leaf mistletoe approaching 100% mortality in some core regent honeyeater breeding areas.
283 Riparian corridors are critical drought refugia for many bird species²⁸ and in heavily-cleared valleys⁴⁸,
284 needle-leaf mistletoe nectar and fruit have become a primary breeding resource for multiple bird
285 species⁴⁹. Mass needle-leaf mistletoe mortality rapidly renders large stretches of core breeding habitat
286 unviable for an entire assemblage of threatened species⁵⁰.

287 Mistletoe mortality was particularly high at lower latitudes towards the north of the study range,
288 where drought effects were most pronounced. These spatial patterns support evidence from the INLA
289 models that identified climatic predictors of mistletoe die-off. There were negative associations
290 between dead mistletoe abundance and both maximum summer temperature and summer rainfall in
291 the peak drought years of 2018 and 2019. Previous work describing drought-induced mortality in
292 mistletoes documented marked differences between species, with 4% mortality in grey mistletoe
293 *Amyema quandang* parasitising Acacias, but 31% for harlequin mistletoe *Lysiana exocarpi*
294 epiparasitic on the grey mistletoe. This difference is instructive—although both species were

295 subjected to the same temperature regime, the epiparasitic species would have experienced more than
296 double the water deficit given losses in the intermediate host⁶. Woodlands in the north of our study
297 range were particularly badly affected by drought impacts, with hilltops and riparian corridors
298 suffering widespread *Eucalyptus* and *Casuarina* mortality, respectively²⁵. The results of our models
299 reflected these trends, detecting a negative association between overall tree health and dead mistletoe
300 abundance (Figure 3a). The effect was small, however, suggesting that drought-induced die-off of
301 host tree species only partly explains observed patterns of mistletoe mortality, and that mistletoes are
302 unlikely to be a key driver of host-tree mortality during drought^{5,10}.

303 Mistletoe mortality showed high positive spatial autocorrelation at the local scale of 0-6 km. Since
304 rainfall and temperature data showed consistent annual differences throughout the study range,
305 additional factors other than climate effects may be driving small-scale spatial structure in mistletoe
306 die-off. High proportions of dead mistletoe could be explained by low recruitment due to the local
307 extinction of key seed-dispersing animals such as mistletoebirds due to factors other than mistletoe
308 die-off. Loss of seed dispersers may be stochastic in fragmented habitats⁵¹, or due to the impact of
309 despotic competitors such as noisy miners⁴⁴. We found no evidence that mistletoe mortality was
310 linked to mistletoebird absence, nor noisy miner abundance, but our models of live mistletoe
311 abundance and woodland birds suggest that noisy miner presence (and mistletoebird absence) could
312 be barriers to mistletoe recovery in areas they suffer mass mortality.

313 Mortality could also be driven by more nuanced local factors such as topography and geology. Aspect
314 and height also modulate insolation and nutrient concentration; two factors known to affect mistletoe
315 establishment and growth^{1,3}. Regional-scale climatic forcing, coupled with the increasing proportion
316 of remnant vegetation on rocky hillsides and other low productivity landforms diminishes the capacity
317 of trees to host mistletoes to maturity⁵², squeezing mistletoes to those few remaining catchment
318 landforms where moisture and nutrient availability suffice. In addition to fundamental differences in
319 water availability and cation concentrations, different host species exhibit divergent architectures,
320 rates of evapotranspiration and physiological responses to acute heat and water deficit¹⁰, subjecting
321 mistletoes within their canopies to contrasting microclimates that may exacerbate the direct effects of

322 climatic factors. Land management strategies could also cause mistletoe die-offs. Pesticides, livestock
323 effluent, salinity changes and water abstraction may themselves, or through interactions with climate
324 extremes, host vigour or animal associates push mistletoes beyond stress thresholds. Novel pathogenic
325 infections may also kill mistletoes, but there is currently no evidence of pathogen-induced mistletoe
326 die-off.

327 Importantly, none of the factors implicated in mistletoe mortality are region-specific, with many of
328 the suspected drivers related to land-use intensification and climate change. Rather than being
329 peculiar to eastern Australia, regional scale mistletoe mortality may well be occurring in other parts of
330 the World^{5,13}. Although frequently overlooked by forest scientists, ecologists and restoration
331 practitioners, our findings reinforce the emerging view that mistletoes are bioindicators of
332 environmental health, challenging the preconception that these parasites necessarily kill their hosts
333 and devalue wildlife habitats^{3,53}.

334 As a single term, our models did not identify mistletoe abundance as a key predictor of woodland bird
335 abundance. By far the strongest predictor of woodland bird abundance was blossom abundance, which
336 included both Eucalyptus and mistletoe species in the blossom score. Blossom abundance was not
337 only associated with high abundance of nectarivorous species, but also of small residents and
338 insectivores. This suggests that booms in Eucalypt and mistletoe blossom have cascading trophic
339 impacts²⁰ or that, through lagged responses to rainfall⁵⁴, blossom is a bioindicator of broader
340 ecosystem productivity in space and time. Land use, water proximity, vegetation community and
341 noisy miner abundance were the other main factors explaining woodland bird abundance. However,
342 these effects have been researched extensively by others^{44,55-57} but were important to control for in the
343 modelling process rather than areas of interest *per se*.

344 There was a significant positive interaction between mistletoe abundance and breeding season on bird
345 abundance in the peak drought breeding seasons of 2018/19 and 2019/20 (Figure 4b). These results
346 suggest that mistletoes could play a key role in sustaining local bird populations during prolonged dry
347 periods when other resources such as eucalypt blossom, invertebrates and seeds are limited.
348 Associations with surviving mistletoes were strongest during the drought for small residents and

349 insectivores. Many nectarivores are nomadic or migratory and can therefore avoid the worst impacts
350 of temperature and rainfall extremes by undertaking long-distance movements to coastal refugia⁵⁸⁻⁵⁹.
351 However, small residents, many of which are insectivorous, are limited in their ability to avoid
352 drought impacts via dispersal⁴⁶. Exploitation of microhabitat features such as live mistletoes could be
353 the difference between life and death for small residents and insectivores during severe drought^{46,60}.

354 Because we accounted for mistletoe nectar in the blossom scores, the positive interaction between live
355 mistletoe abundance and breeding season during the drought event suggests that the benefits of
356 mistletoes for woodland birds during drought are likely to reach beyond the provision of nectar
357 resources^{45,46}. These may include nesting resources⁹, or invertebrate availability, both within the
358 canopy and on the forest floor. As with other parasitic plants, mistletoe-enriched litter boosts litter-
359 dwelling invertebrate abundance, including those preferentially consumed by insectivorous birds^{46,61}.
360 Our results may also reflect an indirect association between mistletoe and birds during drought, such
361 that other, unexplained factors driving bird abundance may also predict mistletoe abundance. We
362 aimed to control for many of these potential factors, including distance to water, canopy and shrub
363 cover as well as tree species composition. Clearly, more work is needed to identify the mechanisms
364 underpinning the observed patterns.

365 Our study paints a worrying picture that as droughts become more frequent and severe in coming
366 decades, widespread mistletoe die-off is a very real risk. Mistletoe mortality is but one mechanism by
367 which impending climate shifts could have cascading impacts at higher trophic levels. Now is the
368 time to improve monitoring of mistletoe populations, particularly with broad-scale longitudinal data
369 that until now may not have been considered necessary, to better understand the dynamics and drivers
370 of their mortality, address threats through conservation actions and thus minimise the impacts of the
371 decline of mistletoes from ecosystems globally.

372

373 **DATA AVAILABILITY:**

374 All bird and habitat data and associated R code are available via the dryad digital repository. Due to
375 the sensitive nature of the data involving Critically Endangered species we have offset the spatial
376 location data.

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