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# Creating past habitat maps to quantify local extirpation of Australian threatened birds

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Supplementary material for this article is available online

## Abstract

Habitat loss is driving the extirpation of fauna across Earth. Many species are now absent from vast areas where they once occurred in inhabited continents, yet we do not have a good understanding of the extent to which different species have been locally extirpated, nor the degree to which range contractions and habitat loss has contributed to this local extirpation. Here, for the first time, we use a combination of scientific literature, historical sources, spatial data, and expert elicitation to map the past extent of potential habitats, and changes thereto, of 72 of Australia's most imperiled terrestrial birds. By comparing the area of potential habitat within the past and current ranges of these taxa, we quantify the extent over which each of Australia's threatened terrestrial birds have likely been extirpated and assess the amount and configuration of potential habitat that remains. Our results show that since 1750 (before European colonization), at least one extant taxon of threatened bird has disappeared from over 530 million hectares (69%) of Australia, through both range contractions and loss of potentially suitable habitat (noting these are not mutually exclusive phenomena). Ten taxa (14%) have likely been extirpated from >99% of their past potential habitat. For 56 taxa (78%), remaining habitat within their current potential habitats has become fragmented. This research paints a sobering picture of the extent of local extirpation of threatened birds from much of Australia over a 250 years time period. By mapping and quantifying this loss, these findings will help refine scientific understanding about the impact of habitat removal and other pervasive threats that are driving this observed extirpation.

## 1. Introduction

Earth is currently facing a species extinction crisis as humans progressively destroy, degrade, and fragment the planet's natural landscapes (Butchart *et al* 2010, Venter *et al* 2016, Sanderson *et al* 2002, Boakes *et al* 2010). Approximately 60% of the terrestrial world is now under moderate or intense human pressure (Williams *et al* 2020), resulting in the alteration of major macroecological patterns and the widespread extirpations of species (Pacifici *et al* 2020). Extirpation—or the local extinction—of species is a direct result of many anthropogenic pressures. These include habitat degradation and fragmentation (Watson *et al* 2018), invasion of non-native or overabundant native species (Ford *et al* 2001), and changes to the ecological processes and functions that support species persistence (e.g. fire regimes and water flows) (Lintermans *et al* 2020, McLauchlan *et al* 2020). The outright removal of natural habitats, and their conversion to intensive human land uses, is perhaps the most easily observable of these pressures (Szabo *et al* 2011, Ceballos *et al* 2020).

Local extirpation impacts all taxonomic groups, including birds (Radford *et al* 2005, Szabo *et al* 2012, Ceballos *et al* 2020). Across Australia, local and regional extirpations of previously widespread birds have been observed in the Mount Lofty Ranges (Szabo *et al* 2011); Victoria (Robinson 1991); the Western Australian wheatbelt (Saunders and Ingram 1995); New England Tableland (Barrett *et al* 1994); the tropical northern savannas (Franklin 1999); and the greater Sydney region (Keast 1995). At the continental scale, more than 16% (134 of 828) of native Australian birds are now listed as threatened by the Commonwealth Government under the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act; Australian Government 2018a), with many species and subspecies (hereafter, 'taxa') at heightened risk of extinction in the next 20 years (Garnett 2019).

While there have been previous continental-scale studies of recent (2000–2017) anthropogenic clearing of threatened species habitat (Ward *et al* 2019), change of mean habitat patch size (Tulloch *et al* 2016), and the extent of loss of potential habitat for entire bird assemblages (Simmonds *et al* 2019b), there has been no quantification of all local extirpations for Australia's threatened bird taxa. This failure to place contemporary losses in their full historical context is commonplace (Whittaker *et al* 2005) and problematic because it prevents full understanding of how much taxa have contracted, and how much of original habitat remains for these birds (both within current ranges, but also across their past ranges). This presents a problem because, for example, many species conservation plans require a target threshold (e.g. 10%–40%) to be conserved by protecting remnant habitat and/or restoring degraded sites (Andren 1994, Maron *et al* 2012, Simmonds *et al* 2019a). Although this threshold should relate to the fraction of the species' original range and habitat availability, often a species' current range is used as a default. For species whose range and area of occupancy have contracted severely, there is a risk that decision-makers and planners will opt for unacceptably low baselines for protection and restoration, with potentially sub-optimal conservation outcomes (Smith *et al* 2010, Soga and Gaston 2018). This is commonly known as the shifting baseline syndrome (Soga and Gaston 2018). That is, we incrementally perceive and accept lower environmental values as the norm over time, as these losses accrue. Shifting baseline syndrome is increasingly recognized as one of the critical challenges to addressing a wide range of global biodiversity problems (Soga and Gaston 2018).

Understanding patterns of extirpation can help guide recovery of threatened taxa. An understanding of the extent of 'dark diversity' (i.e. individual species up to entire assemblages that have been locally extirpated from where they once occurred) and the extent to which this may have been driven by vegetation loss can help guide decisions about which suite of actions (e.g. habitat protection, threat management, and/or restoration) should be prioritized for which taxa, where (Lewis *et al* 2017). By examining and mapping extirpation, decision-makers can be better equipped to set targets, and implement protection, management, and restoration to recover assemblages. For example, if <1% of a species' potential habitat remains, both protection and restoration is essential, but if a threatened species retains most of its remaining habitat intact then it is likely that the species needs better management of other threatening processes in that remaining habitat.

What constitutes 'habitat' for any given species is a topic of ongoing discussion in ecology and biogeography (Kirk *et al* 2018). This contention is amplified by challenges of spatial resolution (both of data, and our understanding of niche-specificity of species) and changes through time (e.g. habitat degradation and its effect on species occupancy). As such, broad-scale analyses and comparisons often rely upon broad 'habitat' classifications based on spatial vegetation datasets (Cunningham *et al* 2014, Ochoa-Quintero *et al* 2015, Tulloch *et al* 2016, Reside *et al* 2019, Simmonds *et al* 2019b). Key to such an approach is that specific terms are clearly defined and distinguished, and that interpretation of the results is appropriate, given the assumptions made. In our analysis, we focus on terrestrial (i.e. not wading, sea or wetland) birds, and define their 'range' as the space over which the taxon occurs, of which some proportion contains vegetation that provides resources (e.g. food, shelter, breeding) to support populations and viable metapopulations. We refer to this suitable vegetation within the species' range as 'potential habitat', although for various reasons it may not be constantly occupied. Through anthropogenic actions like the outright removal of vegetation that was potential habitat, species can be extirpated from areas. This loss of potential habitat amount for the species may (or may not) result in a species' range contracting. However, range contractions can also be driven by other factors such as invasive species, inappropriate fire regimes, or disease, either in isolation from or in synergy with removal of vegetation—thus, some 'past potential habitat' may remain outside of a species' currently described range.

In this study, we estimated local extirpation of Australia's avifauna across two centuries. To do this, we produced maps of 'past potential habitat' and 'current potential habitat' for 72 Australian threatened birds (the subset of nationally-listed threatened birds with terrestrial habitat associations). By producing high resolution continental maps of past potential habitat and current potential habitat, we were able to estimate the area from which each taxon has likely been locally extirpated (see figure 1 for conceptualization of extirpation, which is a function of loss of potential habitat and range contractions). We also compared extirpation among taxa with different distributions (wide-ranging/range-restricted),

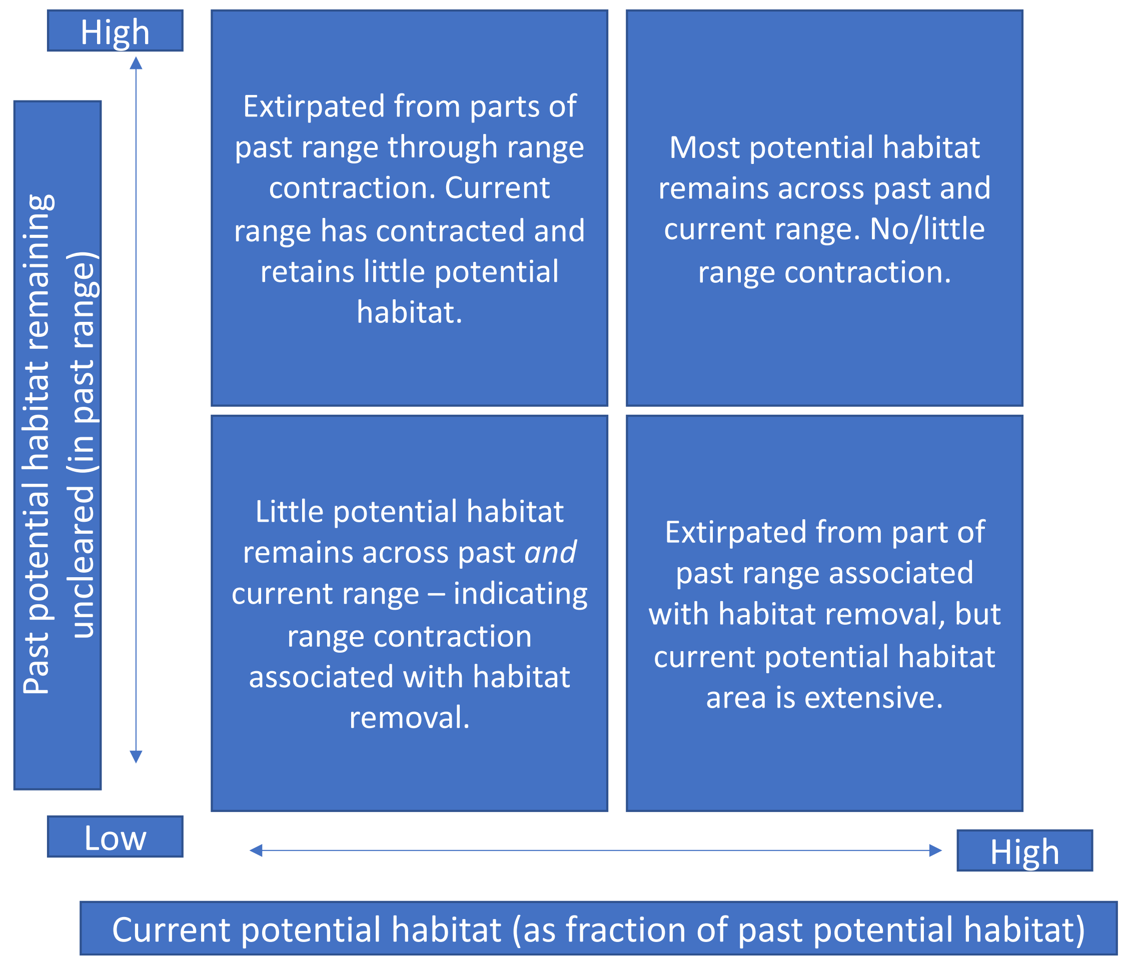


**Figure 1.** Conceptual depiction showing the different circumstances leading to the extirpation of birds from their past potential habitat. This is a function of both outright removal of potential habitat, and range contractions (which will at least in part, be a reflection of the removal of potential habitat).

threat statuses, and broad life-history traits (ground-dwelling/non-ground dwelling) to provide insights into taxa-specific traits that might lead to higher vulnerability of extirpation. For example, ground-nesting birds may be more vulnerable to extirpation due to Australia's invasive predators (Isaksson *et al* 2007). Our research goals were to provide a taxon-specific evaluation of likely extirpation, based on loss of potentially suitable habitat and range contractions for Australia's threatened terrestrial birds. Specifically, we examined the following questions: (a) how much potential habitat did threatened birds have immediately prior to European transformation of Australia; (b) how much potential habitat has been removed for each taxon (c) how has the range of each taxon changed; (d) combining the results from questions b and c, to what extent have taxa likely been extirpated from places where they were once likely to occur? We further explored how the configuration of current potential habitat compared to that of past potential habitat for each taxon. These data can help inform better assessment of a taxon's threat status (as current assessments are often blind to the degree of historical range loss) and guide future decision-making, such as identifying those areas that could be important for area-based protection or for specific management of pervasive threats within remaining habitat.

## 2. Methods

### 2.1. Study area and time period

Our study area is the mega-biodiverse continent of Australia. The scope of analysis is two snapshots, 1750 and 2009 (driven by the availability of continental vegetation maps, which we translated to potential habitat maps—see below), and we consider all Australian native terrestrial bird species and subspecies that were listed at January 2020 as either vulnerable, endangered, or critically endangered under the EPBC Act (hereon 'taxa').

### 2.2. Past potential range maps

To identify past ranges we collated published information on the historical distribution/occurrence of each taxon and searched for other documented records of locations from which each taxon was previously recorded. To do this, we used a combination of information on former distributions in the action plan for Australian birds, editions 1992, 2000, and 2010 (Garnett 1992, Garnett and Crowley 2000, Garnett *et al* 2010), Commonwealth Government recovery plans (Commonwealth of Australia 2021), and bird field guides (Cayley 1931, Simpson and Day 2010; figure S1 available online at stacks.iop.org/ERL/17/024032/mmedia). Each resource contained text describing past sightings and distributions. We extracted every recorded point location at which these sources noted each taxon had been sighted since European colonization (figure S1). These locations were then place-marked using Google Earth Engine and exported as keyhole markup language files that created past sighting maps.

To create past potential range maps, each past sighting map was then intersected with the Interim Biogeographic Regionalisation for Australia (IBRA) subregion map (Commonwealth of Australia 2018a) under the assumption that if a taxon was historically seen in a particular subregion, then (pre-1750) occurrences of vegetation types representative of potential habitat in that subregion represented past potential habitat for that taxon. We chose the 419 IBRA subregions (median size = 966 500 ha) as they are fine in resolution, mostly homogenous, geographically distinct areas based on common climate, geology, landform, native vegetation, and species (Commonwealth of Australia 2018a).

### 2.3. Past potential habitat maps

We identified past potential habitat by extracting spatial data on taxon-specific feeding habitat types from within each taxon's past potential range (as mapped using approach described above). The feeding habitat types were identified by following Garnett *et al* (2015), which is the most comprehensive and up-to-date dataset on the ecological traits of Australian birds (see supplementary information 1 and 2). This dataset assigns all Australian birds to their feeding habitat types based upon the 'major vegetation groups' mapped under the Australian Government's National Vegetation Information System (NVIS 5.1) (Commonwealth of Australia 2018b). The NVIS dataset comprises a high-resolution, continental-scale map of the indicative 1750 extent of Australian native vegetation communities. It depicts Australia's native vegetation communities classified into 30 major vegetation groups at 100 m × 100 m resolution, estimated for 1750 and with a comparable estimated 'current' (circa 2009) dataset. We clipped the major vegetation groups identified as feeding habitat for each taxon (Garnett *et al* 2015) by that taxon's past range. By clipping these past ranges to the pre-European (pre-1750) NVIS dataset, we were able to estimate potentially suitable habitat within the past range of each threatened bird in Australia (i.e. 'past potential habitat'). Using ArcGIS (version 10.4), we merged past potential habitats with the taxon's 'current potential habitat' (i.e. potential habitat with the current range of the species) (see figure 2), under the assumption that if a taxon occurs in a particular location in the present day, it occurred there in 1750. We recognize that there have likely been climate-change induced range shifts (Vanderwal *et al* 2013), and that some taxa could potentially now occur in places they did not occur in 1750.

As a final step of mapping past potential habitat, we drew on knowledge from nine Australian bird experts to review and refine these outputs. The expert elicitation process was done using an online modified Delphi approach (Northcote *et al* 2008). In the first round of communication, experts were asked to iteratively check and, if necessary, modify past potential habitat maps for threatened birds in Australia. If experts disagreed with the maps, they were invited to illustrate where corrections were necessary and why. For example, the maps captured coastal islands within eastern star finch (*Neochmia ruficauda ruficauda*) past potential habitat as they were included within the demarcation of both the subregions and suitable major vegetation groups; however, as there is no evidence this taxon ever used these areas, coastal islands were removed. These corrections were compiled and used to modify the maps, then re-sent to experts, who illustrated any final corrections. After the second round, consensus was achieved. Each past potential habitat map has various strengths and weaknesses depending upon data availability, the ability of the vegetation data to reflect a taxon's habitat preferences, and our knowledge of the natural history and ecology of each taxon. See supplementary information 3 for details.

### 2.4. Current ranges and current potential habitat

To identify current ranges, we used the 'known to occur' and 'likely to occur' categories from the Species of National Environmental Significance species distribution models (SDMs), owned and stored by the Australian Government, at a resolution of 100 m × 100 m. The SDMs were derived from the modeling software, Maxent, using an extensive database of species observation records and national-scale environment data. 'Known to occur' are areas of identified suitable or preferred habitat, while 'likely to occur' are areas of suitable or preferred habitat, within ecologically sensible distances from known locations (but excluding 'known to occur' locations) (Commonwealth Government 2016). Using both 'known to occur' and 'likely to occur' areas, we then extracted areas of potential feeding habitat for each taxon (based on Garnett *et al* 2015) using the high resolution, continental-scale NVIS map containing the current extent of Australian native vegetation (described above) to create 'current potential habitat' maps for each taxon. Current potential habitat maps were

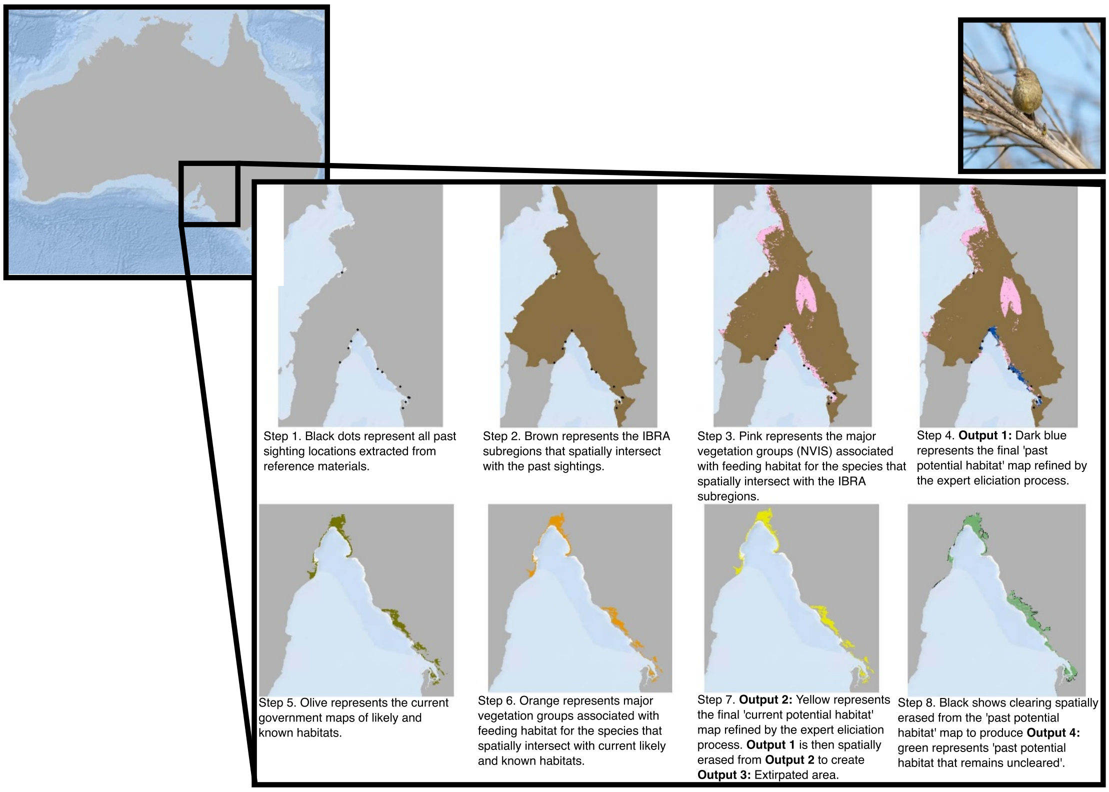


**Figure 2.** Graphical representation of the mapping process to obtain the past potential habitat maps, current potential habitat maps, extirpated area, and past potential habitat that remains uncleared for slender-billed thornbill (*Acanthiza iredalei rosinae*; photo credit: Sam Gordon). In all maps, dark gray represents terrestrial Australia and light blue represents ocean. Reproduced with permission from Sam Gordon (2016). CC BY-NC-SA 2.0.

further vetted within the expert elicitation process (as described above).

### 2.5. Extirpation, habitat loss, and fragmentation

We calculated the area (hectares) of past potential habitat prior to European colonization (pre-1750) and current potential habitat for threatened bird taxa within Australia, to estimate the total area from which each taxon has been locally extirpated as well as the percentage of habitat remaining for each taxon (compared to their respective past potential habitat extents; figure 2). To calculate the amount of suitable vegetation remaining within past potential habitats, we removed any pixels that were mapped as 'cleared' in the current (∼2009) NVIS map from each taxon's past potential habitat. This allowed us to calculate past potential habitat that remains uncleared as percentage of past potential habitat. To investigate the level of fragmentation of each taxon's current potential habitat, we calculated three metrics for both past and current potential habitats: number of patches (Trani and Giles 1999), mean patch size (the mean patch size of each taxon) (Dunn *et al* 1991), and patch density (or the number of patches within the habitat divided by total habitat area (Ripple *et al* 1991, University of Massachusetts 2015)). For each metric, we determined the percentage change for each taxon from 1750 to current.

### 2.6. Comparisons of threat status and ecological traits

To identify whether particular types of taxa were more likely to have experienced greater change in habitat extent, we used listed threatened taxon as the unit of analysis to examine various response variables. We considered the relationship between threat classification (i.e. vulnerable, endangered, and critically endangered); range size (wide-ranging versus range-restricted taxa); and ground-dwelling versus non-ground dwelling and the percentage of extirpation, mean patch size, number of patches, and patch density (calculated as follows):

$$E^i = \frac{P^i - C^i}{P^i} \times 100, \tag{1}$$

where 'percentage of extirpation', $E^i$, is the percentage reduction in potential habitat for taxon $i$, calculated from $P^i$ which is the extent of past potential habitat for taxon $i$ and $C^i$ is the extent of current potential habitat of taxon $i$:

$$S^i = \frac{R^i - T^i}{T^i} \times 100, \tag{2}$$

where $S^i$ is the proportional decrease in mean patch size, $R^i$ is mean patch size in current potential habitat, and $T^i$ is mean patch size in past potential habitat:

$$N^i = \frac{F^i - L^i}{L^i} \times 100, \quad (3)$$

where $N^i$ is proportional increase in patch number, $F^i$ is number of patches in current potential habitat, and $L^i$ is the number of patches in past potential habitat:

$$D^i = \frac{\frac{F^i}{C^i} - \frac{L^i}{P^i}}{\frac{L^i}{P^i}} \times 100, \quad (4)$$

where $D^i$ is proportional increase in patch density, $F^i$ is number of patches in current potential habitat, $C^i$ is the extent of 'current potential habitat', $L^i$ is the number of patches in past potential habitat, and $P^i$ is the extent of past potential habitat.

Levene's test was used to check the homogeneity of variances (Levene 1960). When variances were equal, we used multivariate analysis of variance test, and Welch one-way test (Welch 1951) when variances were unequal (R version 1.2.5033). The Shapiro–Wilk test was used to check the assumption that residuals were normally distributed; when this assumption was violated we used Kruskal–Wallis rank sum test (Kruskal and Wallis 1952, Shapiro and Wilk 1965). To identify multicollinearity among response variables, we also computed Pearson correlation coefficient between percentage of extirpation, proportional decrease in mean patch size, proportional increase in patch number, and proportional increase in patch density.

## 3. Results

We estimated that since 1750, at least one taxon (but many more taxa in large parts of the nation where multiple taxa overlap) have potentially disappeared from over 530 million hectares (69%) of Australia, yet only ~100 million hectares of habitat for threatened taxa has been cleared (figure 3). This indicates that extirpations for over 430 million hectares are associated with threatening processes other than outright vegetation removal.

Stated simply, two thirds of Australia now has a depauperate bird fauna, noting this analysis only deals with a small fraction of the nation's avifauna. Approximately 78% of threatened terrestrial birds in Australia ($n$ = 56) have likely been extirpated from >50% of their past potential habitat. Ten taxa have likely been extirpated from >99% of their past potential habitat, including four (now) critically endangered birds, Tiwi Islands hooded robin (*Melanodryas cucullata melvillensis*), King Island scrubtit (*Acanthornis magna greeniana*), helmeted honeyeater (*Lichenostomus* melanops cassidix), and western ground parrot (*Pezoporus flaviventris*) (table 1 and supplementary information 4).

There was variation when patterns of extirpation and suitable vegetation availability were considered for all threatened taxa (as depicted in figure 1), and this has ramifications for how best to conserve them. Many taxa were found to have relatively small areas of current potential habitat, but large areas of past potential habitat remaining. We found that for 49% of taxa ($n$ = 35/72), >50% of past potential habitat remained uncleared, but the current potential habitat represents less than half of the extent that they previously may have utilized (figure 4). This means other threatening process have substantially reduced their distribution resulting in extirpations as a function of not only vegetation removal (e.g. potential habitat loss), but also range contractions. Some striking examples of this are golden-shouldered parrot, Tiwi Island hooded robin, and Grey Range thick-billed grasswren (*Amytornis modestus obscurior*). Taxa for which large amounts of vegetation representative of potential habitat remains beyond their current range have potential for recovery if this habitat is retained (i.e. not cleared), and management of other pervasive threats is undertaken. Red goshawk (*E. radiatus*) is another example, with ~91% of past potential habitat remaining uncleared, but given the substantial northwards range contraction of this bird driven by a variety of pervasive threats that do not include habitat loss alone, only 73% of the current potential habitat (as a fraction of its past potential habitat) remains available to this taxon. For other taxa, such as princess parrot (*Polytelis alexandrae*), which have not experienced much severe vegetation removal (e.g., potential habitat loss) nor range contractions, most of their current potential habitat (and indeed, past potential habitat) in still *in-situ*. Regent honeyeater (*Anthochaera phrygia*) has only 42% of its past potential habitat remaining uncleared and this drops to only 14% of current potential habitat (compared to past potential habitat) when accounting for the range contraction this bird has experienced. Interestingly, no taxa had high remaining current potential habitat but past potential habitat for which the remaining amount is low.

There was a statistically significant difference in the percentage of extirpation among EPBC Act threat categories (figure 5(a)), with critically endangered taxa having been extirpated from a greater percentage of their past potential habitat (mean = 89.2%) than endangered taxa (mean = 80.0%) or vulnerable (mean = 58.4%; d.f. = 8, $p$ = <0.0003). The same was true of ground-dwelling taxa (mean = 80.1%) compared to non-ground-dwelling taxa (mean = 65.1%, d.f. = 6, $p$ = 0.01; figure 5(b)). We found no statistically significant difference in the percentage of extirpation between wide-ranging and range-restricted taxa, nor in the proportional decrease in mean patch size, proportional increase in patch density, or proportional increase in number of patches among threat classifications, wide-ranging and range-restricted taxa, or ground-dwelling and non-ground dwelling.

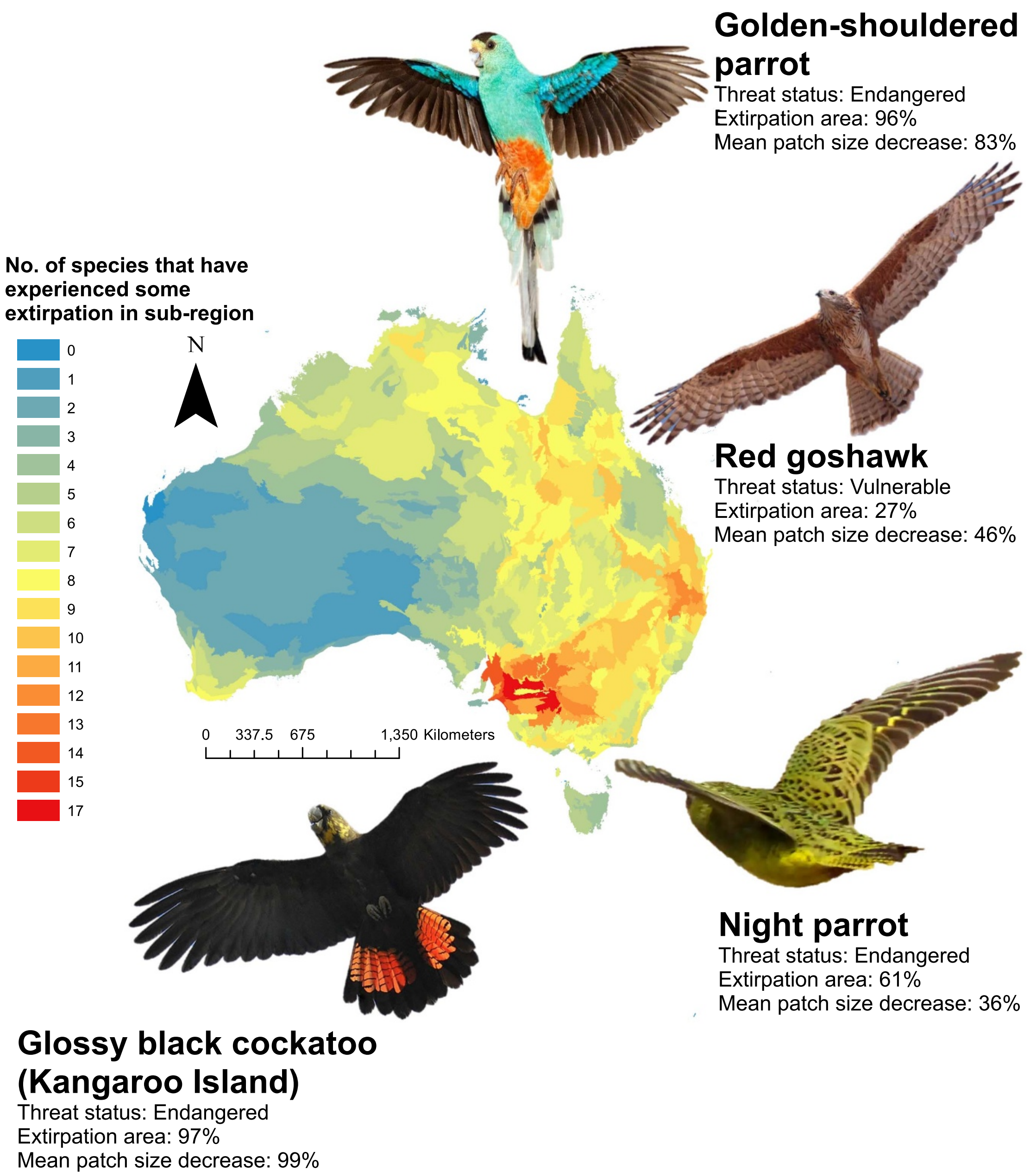


**Figure 3.** Number of threatened taxa that have experienced some extirpation per IBRA sub-region. Subregions range from high numbers of extirpated taxa (17 = dark red) to no taxon extirpation (0 = darkest blue). Birds around the figure are illustrative of those that have experienced high percentage of extirpation (that is, a substantial decrease in current potential habitat compared to past potential habitat). Clockwise starting top left: golden-shouldered parrot (*Psephotus chrysopterygius*, photo credit: Jan Wegener). Reproduced with permission from Jan Wegener. Red goshawk (*Erythrotriorchis radiatus*, photo credit: James Watson), night parrot (*Pezoporus occidentalis*, photo credit: Bruce Greatwich). Reproduced with permission from Bruce Greatwich. Kangaroo Island glossy black-cockatoo (*Calyptorhynchus lathami halmaturinus*, photo credit: Maureen Goninan). This glossy black cockatoo (*Calyptorhynchus lathami*).jpg image has been obtained by the author(s) from the Wikimedia website where it was made available by Sam67fr under a CC BY-SA 3.0 licence. It is included within this article on that basis. It is attributed to Didier B (Sam67fr).

We found that 83% ($n = 60$) of taxa have experienced a combination of extirpation, a decrease in mean patch size, and an increase in patch density. This includes taxa such as buff-breasted button-quail (*Turnix olivii*) and eastern star finch (*N. ruficauda ruficauda*), neither of which have been definitively recorded in recent years. There were significant weak positive correlations between percentage of extirpation and proportional decrease in mean patch size ($r = 0.26$, d.f. = 70, $p = 0.02$), and percentage of extirpation and change in patch density ($r = 0.28$, d.f. = 70, $p = 0.01$), as assessed by Pearson's correlation. Some taxa experienced increased fragmentation of existing habitat, with 49% of taxa ($n = 35$) having experienced an increase in the mean number of patches, 78% of taxa ($n = 56$) having experienced an increase in patch density, and 82% of taxa ($n = 59$) having experienced a decrease in mean patch size.

**Table 1.** The ten taxa that have been locally extirpated from >99% of their past potential habitat.

| Scientific name, common name, and threat status | Past potential habitat (Ha) | Current potential habitat (Ha) | Past potential habitat that remains uncleared as percentage of past potential habitat | Percentage of extirpation (past potential habitat minus current potential habitat divided by past potential habitat) |
|---|---|---|---|---|
| Hooded robin (Tiwi Islands) (*Melanodryas cucullata melvillensis*) critically endangered | 600 000 | 0 | (580 000/600 000) × 100 = 97% | 100% |
| Star finch (eastern) (*N. ruficauda ruficauda*) endangered | 64 000 000 | 0 | (44 000 000/64 000 000) × 100 = 69% | 100% |
| Scrubtit (King Island) (*A. magna greeniana*) critically endangered | 110 000 | 136 | (39 000/110 000) × 100 = 35% | 99% |
| Noisy scrub-bird (*Atrichornis clamosus*) endangered | 2400 000 | 30 000 | (1800 000/2400 000) × 100 = 75% | 99% |
| Helmeted honeyeater (*L. melanops cassidix*) critically endangered | 290 000 | 587 | (100 000/290 000) × 100 = 34% | 99% |
| Western ground parrot (*P. flaviventris*) critically endangered | 480 000 | 2400 | (300 000/480 000) × 100 = 62% | 99% |
| Forty-spotted pardalote (*Pardalotus quadragintus*) endangered | 2700 000 | 21 000 | (1800 000/2700 000) × 100 = 67% | 99% |
| Red-lored whistler (*Pachycephala rufogularis*) vulnerable | 13 000 000 | 170 000 | (8300 000/13 000 000) × 100 = 64% | 99% |
| Eastern bristlebird (*Dasyornis brachypterus*) endangered | 5400 000 | 73 000 | (4000 000/5400 000) × 100 = 74% | 99% |
| Western bristlebird (*Dasyornis longirostris*) endangered | 1000 000 | 7700 | (730 000/1000 000) × 100 = 73% | 99% |

## 4. Discussion

### 4.1. Extirpation of Australia's threatened avifauna

By developing taxon-specific past potential habitat maps, we were able to provide the first approximation of the extent of likely extirpation of Australia's threatened terrestrial birds. We estimate that, since European colonization, anthropogenic extirpation has occurred over 530 million hectares of continental Australia, with approximately 81% of taxa having likely been extirpated from more than half of their past potential habitat. These threatened taxa have lost approximately 100 million hectares of habitat over just 250 years, and many now live in highly fragmented landscapes. Our approach of taking an historical perspective on extirpation, considering both habitat loss and range contractions, provides insight into why Australia now ranks fourth-highest in contemporary global fauna extinction (IUCN 2018).

Our analysis builds on previous studies of local and regional extirpations in Australia. Many areas, including Mount Lofty Ranges (Szabo *et al* 2011); Victoria (Robinson 1991); New England Tableland (Barrett *et al* 1994); the tropical north (Franklin 1999); and the greater Sydney region (Keast 1995) that have high levels of documented extirpation for numerous birds (not just those that are threatened) are also areas that stand out as areas of high extirpation within our analysis. These areas are typically characterized as having lost high proportions of natural land cover, as well as having high human population density, both of which are drivers of species range contractions (Pacifici *et al* 2020).

Since European colonization, Australia has lost ~44% of its native forest and woodlands (Metcalfe and Bui 2017). Unsurprisingly, 135 birds (terrestrial and others) have now been formally listed as threatened with extinction, with an additional 22 listed as extinct under the EPBC Act—by taxonomic group, birds are second only to mammals, which currently have 39 listed extinctions (Commonwealth of Australia 2021). Iconic birds that have been driven to extinction include paradise parrot (*Psephotellus pulcherrimus)* and western rufous bristlebird (*Dasyornis* broadbenti litoralis), both caused predominantly by habitat degradation

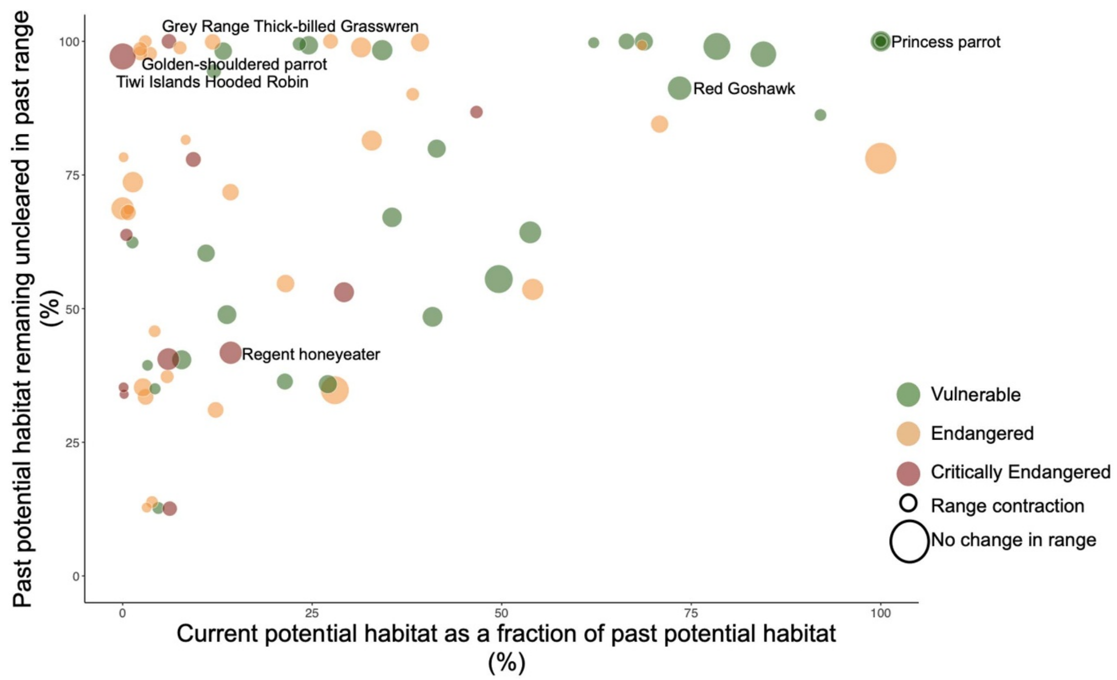


**Figure 4.** Current potential habitat as a fraction of past potential habitat (*x*-axis) varies enormously among the 72 taxon examined, as does the percentage of past potential habitat that remains uncleared across each taxon's respective past range (*y*-axis). Taxon are color-coded by EPBC threat status including vulnerable (green), endangered (yellow), and critically endangered (red), and bubble size reflects the percentage of range contraction for each taxon. Plotted taxa points directly relate to both the conceptual circumstances leading to the extirpation in figure 1.

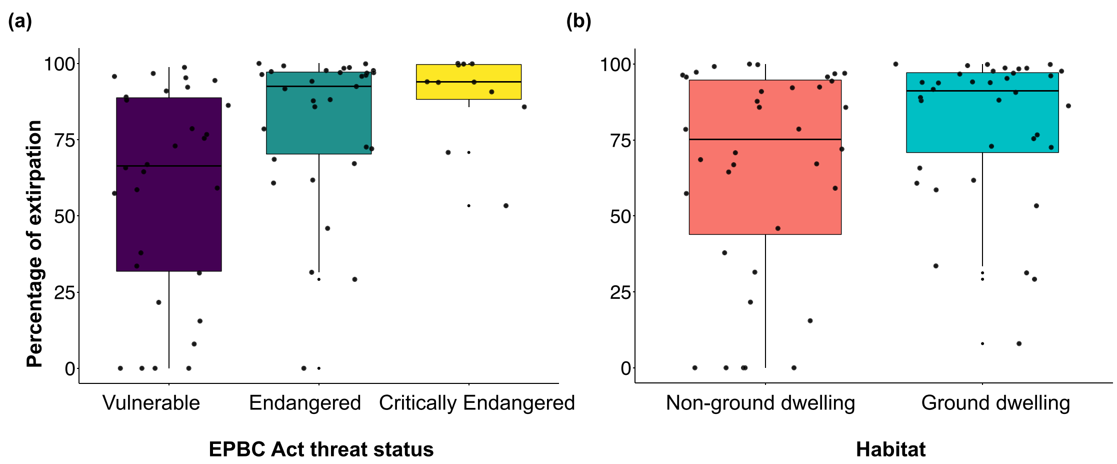


**Figure 5.** Percentage of extirpation (e.g. likely extirpation area as a percentage of past potential habitat) since pre-European colonization by (a) EPBC Act threat status and (b) major habitat association. Boxes indicate the interquartile range, whiskers indicate the minimum and maximum, and lines within each box represent the median value in each dataset.

(Commonwealth of Australia 2000a, 2000b). Other taxa may soon be, or have already been, lost, including Tiwi Islands hooded robin and eastern star finch, which are thought not to have been seen in the past 27 and 25 years, respectively, and are now considered possibly extinct by experts. Despite the precarious state of the nation's avifauna—a reflection of the broader malaise affecting Australia's biodiversity—many threatened species continue to lose habitat at rapid rates from anthropogenic land clearing (Ward *et al* 2019). Since the introduction of the EPBC Act in 1999, threatened species have lost ~7.7 million hectares of potential habitat (Ward *et al* 2019). This recent loss, on top of two centuries of loss and fragmentation of habitat, further inhibits our ability to recover these birds.

Compounding the fact that these birds have been extirpated from large areas, often driven by vast amounts of vegetation removal (outright loss of potential habitat), most taxa now live in highly fragmented landscapes, potentially making it more difficult to migrate, disperse, find resources at different times of the year, and change their distribution in response to a changing climate (Opdam

1991, Schloss *et al* 2012, Pickett and Cadenasso 2018, Tucker *et al* 2018, Ward *et al* 2020). Ground-dwelling taxa, such as King Island scrubtit and western whipbird (*Psophodes nigrogularis leucogaster*) that have experienced both high extirpation and high levels of fragmentation, are now particularly susceptible to extinction and must be prioritized for conservation actions such as restoration, management of invasive predators, implementation of ecologically appropriate fire regimes, and strict area-based protection.

### 4.2. Actions to reverse decline

Protected areas are only one tool in the conservation toolbox, and while they remain critical for biodiversity conservation (United Nations Environment Program 2010), they do not always halt threats (Jones *et al* 2018, Kearney *et al* 2020). Therefore, decision-makers must consider options beyond strict protected areas (Maxwell *et al* 2020, Ward *et al* 2020) when expanding area-based protection. This is especially important when considering Australia's threatened avifauna, many of which occur over vast ranges, and for which much of their remaining habitat is in human-dominated (e.g. agricultural) landscapes. Our maps of current potential habitat, and past potential habitat can inform and guide both government and non-government organizations to broad areas that may be of interest for land acquisition, management of other threats (i.e. invasive species, habitat homogenization, and altered fire regimes), protection, targeted research, and/or restoration.

The conservation of the last remaining habitats, especially those that are intact, is critical for safeguarding biodiversity from extinction (Mokany *et al* 2020), but large-scale restoration will also play a vital role in reversing the trend of decline to prevent further losses for many Australian birds (Strassburg *et al* 2020). This is especially applicable to the heavily transformed south-east and south-west of Australia. While some landscapes will recover naturally over time, invasive species management, fire management, and active replanting will also be necessary for converted and degraded landscapes with no seedbank, to transition back into functioning ecosystems (Maggini *et al* 2013, IPBES 2018). Some taxa for which restoration might be particularly important include regent honeyeater, Mt Lofty Ranges southern emu-wren (*Stipiturus malachurus intermedius*) and white-throated grasswren (*Amytornis woodwardi*), which have been extirpated from more than 30% of their past potential habitat, and for which severe fragmentation characterizes their few remnants of potential habitat.

We acknowledge that some taxa may not be present in some areas of current potential habitat that we quantify and analyze here, given the variety of threats that imperil many of these birds in remaining native vegetation. These include climate change, degradation, invasive species, disease, overabundant native species, and inappropriate fire management (Kearney *et al* 2018), all of which can also drive extirpation. Nonetheless, this quantification (and mapping) of places from which threatened birds have been likely extirpated provides an important framing for further exploration of spatio-temporal patterns, drivers of change, and solutions to recover Australia's avifauna. Such solutions could, with time, allow birds to 'recolonize' sites from which they have been long absent. Moreover, activities like translocations to once occupied, and now actively managed and restored sites are being undertaken for numerous threatened mammals in Australia; the same could conceivably be done for some of the nation's threatened birds. However, noting the risks (e.g. wasted resources, loss of birds with already dwindling numbers), for translocation to be a viable option, we need to have a much deeper understanding of the threats to individual taxa, and how they can be effectively managed at the site and landscape scale.

### 4.3. Caveats and future research

This approach builds upon the method of Simmonds *et al* (2019a) to create continental-scale, taxon-specific potential habitat maps (past and current) for now-threatened terrestrial birds in Australia. We recognize that mapped vegetation of the types preferred by a taxon does not necessarily equate to its occupied habitat, but we have used the best ecological knowledge to link each taxon to a subset of natural ecosystems which they are known to associate, as well as expert elicitation to refine each habitat map (Simmonds *et al* 2019b, Garnett *et al* 2015; see supplementary information 1 and 2). We believe we have employed a robust means of delineating historical ranges of Australian birds given limited data (using accepted 1750 vegetation maps, bird observations, and expert opinions) and that meaningful comparisons can be made, on a continental scale, between this information and current vegetation and bird occurrence maps (see supplementary information 4 for strengths and weaknesses of each potential habitat map).

We believe that our technique of coupling multiple sources of information including remotely sensed data, past records, ecological data, geographically-distinct subregions, and expert elicitation, provides a robust approximation of past potential habitats for Australian threatened birds. Subregions were chosen due to their unique ability to represent localized and homogenous geomorphological units of common climate, geology, landform, native vegetation, and species information. These units may have overestimated the extent of past potential habitat due to taxon-specific requirements of vegetation within these units, but we believe we have addressed this limitation through our expert elicitation process and by utilizing the most comprehensive and up-to-date dataset on the ecological traits of Australian birds (Martin *et al* 2012, Garnett *et al* 2015). These are only clues to a lost world, and we recommend further work examining past taxa habitats to refine and further substantiate these results.

We recognize that land management practices by Indigenous Australians, have, over millennia and to this day, had a considerable influence on patterns of the continent's biota (Bliege Bird *et al* 2008). While we have some indication of the pre-European fauna occurrence (and abundance) (Miller *et al* 2005, 2007, Kaars *et al* 2017), we require a better understanding of how species have responded to environmental and management changes through time, which will strengthen our ability to recover species. In this regard, the findings we present should be considered incomplete—a preliminary exploration of how patterns in Australia's avifauna have changed with the rapid and extraordinary transformation of the continent's land cover post-European colonization (Woinarski *et al* 2019).

This research paints a sobering picture of the local extirpation of Australian threatened birds from much of Australia over a 250 years time period. By mapping and quantifying this loss, these findings can help decision-makers to make more informed decisions about where and how to recover these birds. Clearly, a holistic strategy is needed—Australia is vast and dynamic, and the drivers of extirpation and the ways they interact vary in different parts of the continent. In this regard, our findings reinforce the notion that a 'one size fits all' approach is not an appropriate response to recovering these birds. Some taxa have vast tracts of potential habitat remaining, while others are restricted to a tiny fraction of what they previously had. Our results illuminate the specific nature of the loss each bird has experienced, which can help point to more nuanced, and spatially explicit taxon-specific response.

## Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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## References

Andren H 1994 Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review *Oikos* **71** 355–66

Barrett G, Ford H and Recher H 1994 Conservation of woodland birds in a fragmented rural landscape *Pac. Conserv. Biol.* **1** 245

Bliege Bird R, Bird D W, Codding B F, Parker C H and Jones J H 2008 The 'fire stick farming' hypothesis: Australian aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics *Proc. Natl Acad. Sci. USA* **105** 14796–801

Boakes E H, Mace G M, McGowan P J K and Fuller R A 2010 Extreme contagion in global habitat clearance *Biol. Sci.* **277** 1081–5

Brooks T M, Pimm S L and Oyugi J O 1999 Time lag between deforestation and bird extinction in tropical forest fragments *Conserv. Biol.* **13** 1140–50

Butchart S H M *et al* 2010 Global biodiversity: indicators of recent declines *Science* **328** 1164

Cayley N 1931 What bird is that? (Sydney: Angus and Robertson)

Ceballos G, Ehrlich P R and Raven P H 2020 Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction *Proc. Natl Acad. Sci. USA* **117** 13596–602 (www.ncbi.nlm.nih.gov/pubmed/32482862)

Commonwealth Government 2016 Species of national environmental significance (available at: www.environment.gov.au/science/erin/databases-maps/snes) (Accessed 23 April 2018)

Commonwealth of Australia 2000a *Dasyornis broadbenti litoralis*—rufous bristlebird (western), south-western rufous bristlebird (available at: www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=25972) (Accessed 5 February 2021)

Commonwealth of Australia 2000b *Psephotus pulcherrimus*—paradise parrot (available at: www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=723) (Accessed 5 February 2021)

Commonwealth of Australia 2018a Interim Biogeographic Regionalisation for Australia (IBRA), version 7 (subregions) (available at: https://data.gov.au/dataset/ds-nsw-188ae132-d7b4-4a1a-8785-21786bcbe0bf/details) (Accessed 10 February 2020)

Commonwealth of Australia 2018b National Vegetation Information System (NVIS) Bioregional Assessments Programme (available at: www.environment.gov.au/land/native-vegetation/national-vegetation-information-system) (Accessed 10 June 2018)

Commonwealth of Australia 2021 EPBC act list of threatened species (available at: www.environment.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=fauna) (Accessed 28 March 2018)

Cunningham R B, Lindenmayer D B, Crane M, Michael D R, Barton P S, Gibbons P, Okada S, Ikin K and Stein J A R 2014 The law of diminishing returns: woodland birds respond to native vegetation cover at multiple spatial scales and over time *Divers. Distrib.* **20** 59–71

Dunn C, Sharpe D M, Guntenspergen G R, Stearns F and Yang Z 1991 Methods for analyzing temporal changes in landscape pattern *Quantitative Methods in Landscape Ecology* ed M Turner and R Gardner (Berlin: Springer) pp 173–98

Ford H A, Barrett G W, Saunders D A and Recher H F 2001 Why have birds in the woodlands of southern Australia declined? *Biol. Conserv.* **97** 71–88

Franklin D C 1999 Evidence of disarray amongst granivorous bird assemblages in the savannas of northern Australia, a region of sparse human settlement *Biol. Conserv.* **90** 53–68

Garnett S T *et al* 2015 Biological, ecological, conservation and legal information for all species and subspecies of Australian bird *Sci. Data* **2** 150061

Garnett S 1992 *The Action Plan for Action Plan for Australian Birds* (Canberra: Australian National Parks and Wildlife Service)

Garnett S 2019 Birds red hot list: the Australian birds most at risk of extinction (Melbourne) (available at: www.nespthreatenedspecies.edu.au/media/e4xicyyb/red-hot-list-birds-findings-factsheet.pdf)

Garnett S and Crowley G 2000 *The Action Plan for Action Plan for Australian Birds* Environment Australia (Canberra: Environment Australia)

Garnett S, Szabo J K and Dutson G 2010 *The Action Plan for Australian Birds* (Collingwood: CSIRO Publishing)

IPBES 2018 Global assessment report on biodiversity and ecosystem services of the intergovernmental science- policy platform on biodiversity and ecosystem services (Bonn, Germany)

Isaksson D, Wallander J and Larsson M 2007 Managing predation on ground-nesting birds: the effectiveness of nest exclosures *Biol. Conserv.* **136** 136–42

IUCN 2018 Red list category summary country totals (animals) (available at: www.iucnredlist.org/resources/summary-statistics)

Jones K R, Venter O, Fuller R A, Allan J R, Maxwell S L, Negret P J and Watson J E M 2018 One-third of global protected land is under intense human pressure *Science* **360** 788–91

Kearney S G, Adams V M, Fuller R A, Possingham H P and Watson J E M 2020 Estimating the benefit of well-managed protected areas for threatened species conservation *Oryx* **54** 276–84

Kearney S *et al* 2018 The threats to Australia's imperilled species and implications for a national conservation response *Pac. Conserv. Biol.* **25** 231–44

Keast A 1995 Habitat loss and species loss: the birds of Sydney 50 years ago and now *Aust. Zool.* **30** 3–25

Kirk D A, Park A C, Smith A C, Howes B J, Prouse B K, Kyssa N G, Fairhurst E N and Prior K A 2018 Our use, misuse, and abandonment of a concept: whither habitat? *Ecol. Evol.* **8** 4197–208

Kruskal W and Wallis W 1952 Use of ranks in one-criterion variance analysis *J. Am. Stat. Assoc.* **47** 583–621

Levene H 1960 Robust tests for equality of variance *Contributions to Probability and Statistics* ed I Olkin (Palo Alto, CA: Stanford University) pp 278–92

Lewis R J *et al* 2017 Applying the dark diversity concept to nature conservation *Conserv. Biol.* **31** 40–47

Lintermans M *et al* 2020 Big trouble for little fish: identifying Australian freshwater fishes in imminent risk of extinction *Pac. Conserv. Biol.* **26** 365–77

Maggini R, Kujala H, Taylor M, Lee J, Possingham H, Wintle B and Fuller R 2013 Protecting and restoring habitat to help Australia's threatened species adapt to climate change (NCCARF, Gold Coast)

Maron M, Bowen M, Fuller R A, Smith G C, Eyre T J, Mathieson M, Watson J E M and McAlpine C A 2012 Spurious thresholds in the relationship between species richness and vegetation cover *Glob. Ecol. Biogeogr.* **21** 682–92

Martin T G, Burgman M A, Fidler F, Kuhnert P M, Low-Choy S, Mcbride M and Mengersen K 2012 Eliciting expert knowledge in conservation science *Conserv. Biol.* **26** 29–38

Maxwell S L *et al* 2020 Area-based conservation in the twenty-first century *Nature* **586** 217–27

McLauchlan K K *et al* 2020 Fire as a fundamental ecological process: research advances and frontiers *J. Ecol.* **108** 2047–69

Metcalfe D and Bui E 2017 *Australia State of the Environment 2016: Land* (Canberra)

Miller G H, Fogel M L, Magee J W, Gagan M K, Clarke S J and Johnson B J 2005 Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction *Science* **309** 287–90

Miller G H, Magee J W, Fogel M L and Gagan M K 2007 Detecting human impacts on the flora, fauna, and summer monsoon of Pleistocene Australia *Clim. Past* **3** 463–73

Mokany K, Ferrier S, Harwood T D, Ware C, di Marco M, Grantham H S, Venter O, Hoskins A J and Watson J E M 2020 Reconciling global priorities for conserving biodiversity habitat *Proc. Natl Acad. Sci. USA* **117** 9906–11

Northcote J, Lee D, Chok S and Wegner A 2008 An email-based delphi approach to tourism program evaluation: involving stakeholders in research design *Current Issues in Tourism* **11** 269–79

Ochoa-Quintero J M, Gardner T A, Rosa I, de Barros Ferraz S F and Sutherland W J 2015 Thresholds of species loss in Amazonian deforestation frontier landscapes *Conserv. Biol.* **29** 440–51

Opdam P 1991 Metapopulation theory and habitat fragmentation: a review of Holarctic breeding bird studies *Landsc. Ecol.* **5** 93–106

Pacifici M, Rondinini C, Rhodes J R, Burbidge A A, Cristiano A, Watson J E M, Woinarski J C Z and di Marco M 2020 Global correlates of range contractions and expansions in terrestrial mammals *Nat. Commun.* **11** 1–9

Pickett S and Cadenasso M 2018 Landscape ecology: spatial heterogeneity in ecological systems. American association for the advancement of science landscape ecology: spatial heterogeneity in ecological systems *Science* **269** 331–4

Radford J Q, Bennett A F and Cheers G J 2005 Landscape-level thresholds of habitat cover for woodland-dependent birds *Biol. Conserv.* **124** 317–37

Reside A E, Cosgrove A J, Pointon R, Trezise J, Watson J E M and Maron M 2019 How to send a finch extinct *Environ. Sci. Policy* **94** 163–73

Ripple W J, Bradshaw G A and Spies T A 1991 Measuring forest landscape patterns in the cascade range of Oregon, USA *Biol. Conserv.* **57** 73–88

Robinson D 1991 Threatened birds in Victoria: their distributions, ecology and future *Vict. Nat.* **108** 67–77

Sanderson E W, Jaiteh M, Levy M A, Redford K H, Wannebo A V and Woolmer G 2002 The human footprint and the last of the wild *BioScience* **52** 891–904

Saunders D A, Denis A, Ingram J A and John A 1995 *Birds of Southwestern Australia: An Atlas of Changes in the Distribution and Abundance of the Wheatbelt Avifauna* (Chipping Norton, NSW: Surrey Beatty in association with Western Australian Laboratory CSIRO Division of Wildlife and Ecology)

Schloss C A, Nuñez T A and Lawler J J 2012 Dispersal will limit ability of mammals to track climate change in the Western Hemisphere *Proc. Natl Acad. Sci. USA* **109** 8606–11

Shapiro S and Wilk M 1965 An analysis of variance test for normality (complete samples) *Biometrika* **52** 591–611

Simmonds J S, van Rensburg B J, Tulloch A I T and Maron M 2019a Landscape-specific thresholds in the relationship between species richness and natural land cover *J. Appl. Ecol.* **56** 1019–29

Simmonds J S, Watson J E M, Salazar A and Maron M 2019b A composite measure of habitat loss for entire assemblages of species *Conserv. Biol.* **33** 1438–47

Simpson K and Day N 2010 *Field Guide to the Birds of Australia* 8th edn (Camberwell: Penguin)

Smith R J, di Minin E, Linke S, Segan D B and Possingham H P 2010 An approach for ensuring minimum protected area size in systematic conservation planning *Biol. Conserv.* **143** 2525–31

Soga M and Gaston K J 2018 Shifting baseline syndrome: causes, consequences, and implications *Front. Ecol. Environ.* **16** 222–30

Strassburg B B N *et al* 2020 Global priority areas for ecosystem restoration *Nature* **586** 724–9

Szabo J K, Vesk P A, Baxter P W J and Possingham H P 2011 Paying the extinction debt: woodland birds in the Mount Lofty Ranges, South Australia *Emu* **111** 59–70

Szabo J, Khwaja N, Garnett S and Butchart S 2012 Global patterns and drivers of avian extinctions at the species and subspecies level *PLoS One* **7** e47080

Trani M K and Giles R H 1999 An analysis of deforestation: metrics used to describe pattern change *For. Ecol. Manage.* **114** 459–70

Tucker M A *et al* 2018 Moving in the anthropocene: global reductions in terrestrial mammalian movements *Science* **359** 466–9

Tulloch A I T, Barnes M D, Ringma J, Fuller R A, Watson J E M and Mori A 2016 Understanding the importance of small patches of habitat for conservation *Indian Pediatr.* **53** 418–29

United Nations Environment Program 2010 Secretariat of the convention on biological diversity. Page COP 10 decision X/2: strategic plan for biodiversity 2011–2020 (Taylor & Francis Group)

University of Massachusetts 2015 Patch density (available at: www.umass.edu/landeco/research/fragstats/documents/Metrics/Area-Density-Edge Metrics/Metrics/C6-PD.htm#:∼:text=Patch density has the same,among landscapes of varying size) (Accessed 1 March 2020)

van der Kaars S, Miller G H, Turney C S M, Cook E J, Nürnberg D, Schönfeld J, Kershaw A P and Lehman S J 2017 Humans rather than climate the primary cause of Pleistocene megafaunal extinction in Australia *Nat. Commun.* **8** 14142

Vanderwal J, Murphy H T, Kutt A S, Perkins G C, Bateman B L, Perry J J and Reside A E 2013 Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change *Nat. Clim. Change* **3** 239–43

Venter O *et al* 2016 Global terrestrial human footprint maps for 1993 and 2009 *Sci. Data* **3** 160067

Ward M, Saura S, Williams B, Ramírez-Delgado J P, Arafeh-Dalmau N, Allan J R, Venter O, Dubois G and Watson J E M 2020 Just ten percent of the global terrestrial protected area network is structurally connected via intact land *Nat. Commun.* **11** 1–10

Ward M, Simmonds J S, Reside A E, Watson J E M, Rhodes J R, Possingham H P, Trezise J, Fletcher R, File L and Taylor M 2019 Lots of loss with little scrutiny: the attrition of habitat critical for threatened species in Australia *Conserv. Sci. Pract.* **1** e117

Watson J E M *et al* 2018 The exceptional value of intact forest ecosystems *Nat. Ecol. Evol.* **2** 599–610

Welch B 1951 On the comparison of several mean values: an alternative approach *Biometrika* **38** 330–6

Whittaker R J, Araújo M B, Jepson P, Ladle R J, Watson J E M and Willis K J 2005 Conservation biogeography: assessment and prospect *Divers. Distrib.* **11** 3–23

Williams B A *et al* 2020 Change in terrestrial human footprint drives continued loss of intact ecosystems *One Earth* **3** 371–82

Woinarski J C Z, Braby M F, Burbidge A A, Coates D, Garnett S T, Fensham R J, Legge S M, McKenzie N L, Silcock J L and Murphy B P 2019 Reading the black book: the number, timing, distribution and causes of listed extinctions in Australia *Biol. Conserv.* **239** 108261