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An empirical assessment of the focal species hypothesis

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ABSTRACT

Biodiversity surrogates and indicators are commonly used in conservation management. The focal species approach (FSA) is one method for identifying biodiversity surrogates, and is underpinned by the hypothesis that management aimed at a particular 'focal' species will convey protection to co-occurring species. This concept has been the subject of much debate, in part because the validity of the FSA has not subject to detailed empirical assessment of the extent to which a given focal species actually co-occurs with other species in an assemblage. We address this knowledge gap using large-scale, long-term datasets of temperate woodland birds and selecting focal species associated with threatening processes such as habitat isolation and loss of key vegetation attributes. We quantified co-occurrence patterns among focal species, species in the wider bird assemblage, and species of conservation concern. We found that some, but not all, focal species were associated with high levels of species richness. We also found that one of our selected focal species displayed anti-surrogate properties by having a negative association with the occurrence of other species - a previously undescribed property of nominated focal species. Furthermore, combinations of focal species were not associated with substantially elevated levels of bird species richness compared to levels associated with individual species. Our assessment of the focal species hypothesis provides new insight into the strengths and limitations of focal species approach in conservation management, It also suggests that while there is some merit to the underpinning concept of the focal species approach, there were examples where a nominated focal species performed no better than other species in the assemblage.

Keywords: Biodiversity surrogates, focal species, threatened woodland birds, anti-surrogates, conservation practice.

INTRODUCTION

A critical part of conservation management actions is to assess their effectiveness, although this is often not done, or is done poorly (Muir 2010; Lindenmayer & Gibbons 2012). The use of surrogates and indicators is often important in assessing the effectiveness of management interventions because it is not possible to measure all biodiversity in all environments (Chase & Geupel 2005).

Many kinds of surrogates have been proposed for use in conservation and environmental management (Caro 2010; Grantham et al. 2010). A commonly one is the concept of umbrella species, in which the protection of a large and charismatic species is expected to "convey protection" for many other (typically smaller-bodied) species. This is because umbrella species need large areas to persist and large areas typically support more species (Seddon & Leech 2008; Branton & Richardson 2010). The focal species approach is a related form of surrogacy used around the world (Lambeck 1997; Watson et al. 2001; Beazley & Cardinal 2004; Hess et al. 2006; Ficetola et al. 2007; Nicholson et al. 2013).

The focal species approach (hereafter FSA) was developed by Lambeck (1997). Under the FSA, the known threatening processes in a given landscape are described. The species most sensitive to each threat are then identified. One or more species may be identified for each threat, and are termed the 'focal' species. Lambeck (1997) defined four types of focal species: area-limited, dispersal-limited, resource-limited, and ecological-process-limited. For example, the minimum area required by the most area-limited species is used to define the minimum patch size needed in a given landscape, and the most dispersal-limited species is used to define the optimal configuration of patches with respect to inter-patch distance. The FSA therefore involves the identification of a set of species for the management of key threatening processes and habitat restoration (Lambeck 1997). A key assumption under the FSA is that because the most demanding species are selected,

management interventions aimed at conserving those focal species will confer protection on a large number of less demanding and naturally co-occurring species (Lambeck 1997; USFWS 2012).

The FSA has been controversial and discussions about its validity continue to the present day (e.g. Nicholson et al. 2013). A key criticism has been the validity of the assumption that protection of the most sensitive species to particular threats will lead to the protection of other (less sensitive) species. In particular, focal species may be poor surrogates for the presence of other species that have different habitat requirements, dispersal capabilities, or sensitivities to disturbance (Lindenmayer et al. 2002; Short & Parsons 2004). For example, the effects of environmental change on birds (which are the primary group for which the FSA has been applied) may not be indicative of the responses of other organisms (e.g. mammals, reptiles or plants). Even closely related species in the same guild may respond differently to habitat loss or landscape fragmentation (Collinge 2009). A second reservation has been that, in the absence of detailed population models supported by field data, it can be difficult (if not unrealistic) to identify the species most sensitive to a given threatening process (Lindenmayer et al. 2002). Variation in the spatial and temporal scales of threatening processes, and the lack of transferability of focal species from one landscape to another, are other challenges faced in selecting focal species for specific threats.

One of the unique characteristics of the FSA is that it is based on the *a priori* hypothesis that nominated focal species with particular traits (dispersal limitation, area sensitivity etc.) will be broadly representative of other members of their taxon. This hypothesis lends itself to being explicitly tested, but we argue that it has not been adequately assessed to date. That is, a key knowledge gap in debates about the FSA has been a lack of empirical assessment of the extent to which a given focal species actually co-occurs with other species in an assemblage. Here we address this knowledge gap by reporting the results

of a novel empirical assessment of the hypothesis underpinning the FSA. We focus on Australian temperate eucalypt woodland birds – the same ecosystem and taxonomic group for which the FSA was first developed (Lambeck 1997), and which supports many endangered vegetation communities (Department of the Environment 2013) and an array of bird species of conservation concern (Montague-Drake et al. 2009; Ford 2011). We use a decade-long dataset gathered from a large number of temperate woodland sites to answer four questions:

1. Is the occurrence of nominated focal species associated with high levels of bird species richness? We expected that when a nominated focal species occurs in a site, then many other species should co-occur because they are by definition less resource-, habitat- or dispersal-limited than the focal species. Hence, the occurrence of particular focal species should be positively associated with high levels of bird species richness.
2. Is the occurrence of nominated focal species associated with increased occurrence of birds of conservation concern (*sensu* Montague-Drake et al. 2009)? An effective focal species should be one that co-occurs with many species of conservation concern. Therefore, we sought to determine whether particular focal species were positively associated with high levels of richness of birds of conservation concern.
3. Which species of birds typically co-occur with a nominated focal species? We identified bird species co-occurring with a given focal species. Specifically, we quantified the change in the occurrence of particular species given the occurrence of a given focal species.
4. Is the occurrence of combinations of nominated focal species associated with high levels of bird species richness? It has been suggested that a suite of focal species should be used as a surrogate to guide management actions (Lambeck 1997;

Nicholson et al. 2013). Therefore, we sought to determine if the occurrence of pairs or triplets of focal species led to greater relative gains in species richness than other sets of focal species.

The FSA is one of a suite of approaches under the rubric of biodiversity surrogates and indicators (Caro 2010) – indeed there is a massive and rapidly expanding literature encompassing more than 7995 articles on this topic (Westgate et al. unpublished data). Hence, this paper and the empirical approaches we used in assessing the hypothesis that underpins the FSA is an important contribution to better understanding the effectiveness of biodiversity surrogates for conservation and land management.

METHODS

Study area

Our study comprised 134 temperate woodland remnants located on 45 farms on the South-west Slopes of New South Wales, south-eastern Australia. Our sites and farms were located in an area spanning the towns of Junee (0552952E 6140128N) in the north, Albury (0494981E 6008873N) in the south (a distance of 150 km), and Gundagai (600532E 6119073N) and Howlong (467090E 6017897N) in the east and west respectively (a distance of 120 km). The 134 remnant sites encompassed a range of structural conditions – old growth (70 sites), natural seedling regrowth (35 sites) and coppice (i.e. multi-stemmed) regrowth woodland (29 sites). The regrowth sites were identified based on a high stem count (particularly of small eucalypts), but also had a limited number of large (>50 cm DBH) remnant trees (thus indicating that the site was regrowth as opposed to a vegetation community typified by small stems). The regrowth sites were of varying ages relating to past, and sometimes multiple, disturbances, such as clearing and fire. The regrowth was generally dense across the site, indicating that it had been largely cleared in the past. No sites had native vegetation plantings present. The predominant form of native vegetation was

temperate eucalypt woodland (*sensu* Lindenmayer et al. 2010) dominated by White Box *Eucalyptus albens*, Grey Box *E. microcarpa*, or other eucalypt tree species such as Yellow Box *E. melliodora*, Blakely's Red Gum *E. blakelyi*, Red Stringybark *E. macrorhyncha* and Red Ironbark *E. sideroxylon*. Our permanent field sites have been subject to a range of grazing regimes, including grazing exclusion, 'crash grazing' and set-stocking. Our134 field sites covered the range of environmental conditions that occur in temperate eucalypt woodlands in our study region and hence the work was representative of the conditions in the broader ecosystem.

Focal species selection

Based on the recommendations of Lambeck (1997) on the application of the FSA, we used the following process to identify a candidate set of focal species for this investigation. First, we examined the results of other studies of woodland birds within (or near to) our study region (e.g. Watson et al. 2001; Freudenberger et al. 2004; Montague-Drake et al. 2009). Second, we documented the factors shown to have a significant influence on the occurrence of woodland birds in those studies, including patch size, patch isolation and the availability of resources. Third, guided by results from previous studies, together with recommendations of focal species status from earlier investigations (e.g. Watson et al. 2001; Freudenberger et al. 2004), we selected a set of focal species based on sensitivity to key threatening processes. We list these species in Table 1. Most of the selected species are among the subset of approximately 20 species in the temperate woodland bird assemblage considered to be of conservation concern (reviewed by Montague-Drake et al. 2009) (Appendix S1).

Bird survey protocols

Our study region supports more than 155 bird species (Appendix S1), of which over half are woodland dependent, including more than 20 species of conservation concern. Approximately 35% of the bird species are migratory, part-migratory, dispersive or nomadic.

The bird assemblage contains a range of native "generalist" species that occur in heavily cleared paddocks and cultivated areas (e.g. the Brown Songlark). Only four species are exotic, of which two have declined significantly over the past decade (Lindenmayer & Cunningham 2011).

We completed surveys of birds on all 134 sites in the spring of 2002, 2004, 2006, 2008, 2009 and 2011 and the winter of 2004, 2007, 2008 and 2011. Our surveys entailed repeated 5 minute point interval counts at each of the 0 m, 100 m and 200 m points along a permanent transect at each site. In each survey year, all sites were surveyed by two different observers on different days. We completed counts between 5.30–9.30 am and did not undertake surveys on days of poor weather (rain, high wind, fog or heavy cloud cover).

We recorded all birds seen or heard in discrete distance classes at each of the three permanent markers at each site. For this study, we considered a bird to be present at a site if it was recorded by at least one observer on at least one marker at a radius of not greater than 50 m. We aggregated our data across all years. Thus, for the purposes of this investigation, we conducted 60 individual point counts at each of 134 sites.

Statistical methods

To answer Questions 1 and 4, we calculated the mean species richness given the occurrence of one or more focal species, and compared that to the mean over all sites, whether or not focal species co-occurred. For Question 1, we tested the association between species richness and individual focal species by fitting a negative binomial regression of richness on occurrence of that species. This is similar to Poisson regression, but allows a more general relationship between mean and variance: the variance of the negative binomial can be expressed as $m + (m^2/a)$, where m is the mean and a is the aggregation (or dispersion) parameter (infinite aggregation corresponds to the Poisson distribution). We estimated a separate value of a for each model rather than trying to impose a common value, using the

generalised linear model facilities of the GenStat statistical system (VSN International, 2013).

For Question 1, we also investigated the relationship between potential focal species and species richness by examining the average percentage occurrence of a species at sites with different levels of species richness. For spring and winter separately, we averaged species richness over years at each site and used these averages to categorize the sites into quintiles: i.e., into five classes of species richness, with approximately equal number of sites in each class. We then calculated the average percentage occurrence of each species over the sites in each quintile. This approach allowed us to produce a visual display of how occurrence increased or decreased in association with increasing richness of sites. We used color coding to identify those species with strong surrogate characteristics, through being much more likely to occur at sites with high species richness than at low ones. This approach also enabled us to identify birds with strong "anti-surrogate" behavior, and likely to be associated with low levels of bird species richness. We quantified the gradient for each species as the slope of a logistic regression of occurrence of that species on the averaged site-specific species richness.

To address Questions 2 and 3, we assessed the association between two individual species by calculating an odds ratio: the odds of the first species occurring when the second was present, divided by the odds of the first species occurring regardless of the presence of the second. This is a measure of how effective the second species was as an indicator of occurrence of the first (or as an indicator of absence, if the odds ratio was less than 1). We interpreted an odds ratio greater than 3 or less than ⅓ as indicating an ecologically "substantial" association. In terms of percentages, an odds ratio of 3 corresponds to any of the following changes: from 3.6% occurrence to 10%, 10% to 25%, 25% to 50%, 50% to 75%, or 75% to 90%. Conversely, an odds ratio of ⅓ corresponds to any of those changes reversed,

i.e. 10% to 3.6%, etc. An odds ratio of 3, derived from two independent binomial samples, is statistically significantly different from 1 at the 5% level as long as there are 30 or more observations in each sample. We have many more observations in our dataset, so there was no doubt of statistical significance of any of the reported associations at this level.

Detection/occupancy analyses

Detection/occupancy analysis (*sensu* Mackenzie et al. 2006) is now widely regarded as a standard statistical approach for use in interrogating ecological datasets. However, we have elected not to include detectability in our analysis for three key reasons. (1) Detailed statistical analyses by Welsh et al. (2013) suggests that the current statistical methods for detection/occupancy do not improve model fit and in some cases can make the outcomes worse. (2) Our data were observations of presence/absence at three points at each site, with the survey repeated by a different observer on a different day. We therefore do not have sufficient data to carry out a detection/occupancy analysis without amalgamating observations across seasons or years, which we do not think is appropriate (even if such analysis were robust) because of marked inter-season and year-to-year differences in probabilities of occupancy and detection for many bird species. (3) Based on the survey protocols summarised above, we accounted for known sources of variation in our surveys in the most appropriate and feasible manner by: (i) using a very large number of sites and surveying multiple points per site (local spatial heterogeneity), (ii) surveying on multiple days (temporal heterogeneity) and (iii) using multiple observers (observer heterogeneity) (see Cunningham et al. 1999).

RESULTS

We completed 1331 point counts at 134 sites between 2002 and 2011 and detected 156 species of birds. Average species richness was 13.4 species per site in spring and 9.8 species

per site in winter, respectively. The distribution of values was well represented as negative binomial with an aggregation parameter of ~14 for spring and ~17 for winter.

1. Is the occurrence of nominated focal species associated with high levels of bird species richness?

The occurrence of each nominated focal species (except the Superb Parrot) was associated with significantly higher species richness ($p < 0.02$ for all species, calculated by analysis of deviance of the fitted model), ranging from 3–6 additional species in spring and 1–4 in winter, excluding the focal species itself (Fig. 1). The Superb Parrot was associated with significantly lower species richness in spring ($p = 0.05$), although there was no reduction for winter.

Many other bird species had greater levels of associated species richness than any of the nominated focal species (Fig. 1), but all of them were rare (occurred < 5% of the time). Restricting attention to species recorded 10% or more of the time, we still found 10 species in spring, and four in winter, associated with levels of richness greater than those found for the most common focal species (Brown Treecreeper).

We found a wide range of gradients of increasing occurrence, and also some species for which occurrence decreased with increasing richness. We show in Table 2 only the proposed focal species and those species for which the average increase or decrease in odds was at least 25%, and the average percentage occurrence was at least 2%, in at least one season. All increases or decreases in Table 2 were significantly different from zero ($p < 0.004$). A complete list of results is given in Appendix S6.

Four of the specified focal species exhibited a strong positive gradient in occurrence from species-poor to species-rich sites; the Superb Parrot exhibited a negative gradient in spring. However, all of them were less common than three other species (White-plumed Honeyeater, Willie Wagtail, Grey Shrike-thrush), which also had strong positive gradients.

By contrast, the Noisy Miner displayed anti-surrogate behaviour in both seasons, occurring at over 95% of species-poor sites, dropping to about 30% at species-rich sites in spring and 45% in winter. Sixteen of the 21 species of conservation concern (Appendix S1) had strong positive gradients (average increase in odds of >25%) when the species occurred at least 2% of the time on average.

2. Is the occurrence of nominated focal species associated with increased occurrence of birds of conservation concern?

The occurrence of a nominated focal species (other than the Superb Parrot) was associated with an increased level of occurrence of species of conservation concern in both spring and winter, and these increases were substantial (odds ratio > 3) for 45% of the pairs of species (Table 3). However, in several cases, the occurrence of a nominated focal species was associated with the **absence** of species of conservation concern. For instance, in spring, the occurrence of the Hooded Robin was associated with the absence of the Grey-crowned Babbler, the Scarlet Robin and the Speckled Warbler. In winter, occurrence of the Eastern Yellow Robin was associated with the absence of eight species. However, all of these absences were for pairs of species in which at least one was rare (< 5% occurrence; see Table 3).

3. Which species of birds typically co-occur with a nominated focal species?

Using the same criterion employed in the above analyses (i.e. an odds ratio > 3.0), we found that the Grey Shrike-thrush, the White-plumed Honeyeater and Willie Wagtail were substantially more likely to be observed with each of the focal species (except the Superb Parrot), both in winter and spring, except with the Mistletoebird in winter (Appendix S2). We also found that the Crested Shrike-thrush, Jacky Winter and Restless Flycatcher had strong associations with all of the focal species, except the Superb Parrot. In addition, one of the focal species itself (the Brown Treecreeper) was substantially more likely to be observed with

three of the other focal species. We also identified the Noisy Miner, Pied Butcherbird and Grey Butcherbird as species that were substantially **less** likely to be observed with each of the focal species (Appendix S3).

4. Is the occurrence of combinations of nominated focal species associated with high levels of bird species richness?

Combinations of focal species were not generally associated with higher species richness than an individual focal species (Appendix S4). For sites where either of a pair of focal species was present, the best combination in spring was the Eastern Yellow Robin or Hooded Robin, with an additional 4.4 additional species on average, though there were only 451 sites (5.7%) where one or other of them occurred. The best combination in winter was the Superb Parrot or Hooded Robin, but they were associated with only 2.1 additional species on average, and there were only 17 sites (3.2%) where one or other of them occurred.

When we excluded rare combinations of focal species (< 5% occurrence), no pairs of focal species were associated with more than 1 additional species. For sites where both of a pair of focal species was present, we found that all combinations were rare (< 5% occurrence; Appendix S5). The best combination, ignoring very rare combinations (< 1% occurrence), in spring was the Brown Treecreeper and Eastern Yellow Robin with 4.9 additional species; in winter, the best result was the Brown Treecreeper and Hooded Robin, which together were associated with 5.1 additional species (Appendices 4 and 5). For sets of three alternative focal species, the best combination was 2.9 additional species in spring with Eastern Yellow Robin, Hooded Robin or Mistletoebird. The best for winter was 1.2 additional species with the occurrence of the Eastern Yellow Robin, Hooded Robin or Superb Parrot.

DISCUSSION

Biodiversity surrogates require rigorous assessment to test their underlying assumptions (Lindenmayer & Fischer 2003; Caro 2010; Grantham et al. 2010). We assembled a large

dataset to assess empirically the hypothesis underpinning the FSA, i.e. that a pre-specified focal species will co-occur with many other (less sensitive) species in an assemblage. We assessed a considerable body of earlier work to identify species thought to be most sensitive to threatening processes which limit the size of remaining habitat patches, isolate habitat patches, and reduce resource availability. We quantified the total number of species and the richness of species of conservation concern associated with nominated focal species. Our study was motivated by addressing a series of four questions. We discuss each of these questions in the remainder of this paper, and conclude with some commentary on key issues that arise from our investigation**.**

Is the occurrence of nominated focal species associated with high levels of bird species richness and high levels of richness of bird species of conservation concern?

The occurrence of a nominated focal species was typically associated with high levels of species richness and focal species were most often recorded on species-rich sites. Focal species also were often associated with high richness of species of conservation concern. Because almost all of our pre-specified focal species were typically associated with species-rich sites (Table 2) and a higher level of occurrence of species of conservation concern in both spring and winter (Table 3), our analyses suggest these nominated focal species **do** have some value as surrogates for bird species richness. Our approach to assessing the occurrence of particular species across a gradient of species-poor to species-rich sites is a useful general method for assessing the validity of particular pre-specified taxa as focal species.

An important issue for some of our nominated focal species was that they were comparatively rare, even on species-rich sites, although others were reasonably common (e.g. Brown Treecreeper and Superb Parrot). We suggest that rarity can limit the value of particular taxa as focal species. This is because one of the keys to the FSA is that species are responsive (to the ‘threatening process’ or habitat attribute being conserved) and also

measurable, which means that effective focal species must be recorded relatively frequently (without being ubiquitous). For example, we found that the Eastern Yellow Robin was more likely to occur on species-rich sites, but was still uncommon: it was recorded on only 11% of species-rich sites in spring and 6% in winter (Table 2). This species on its own, therefore, is a poor indicator of species-richness: its occurrence may be indicative of richness, but its absence is not indicative of an absence of species-richness. It is possible that it could be a useful indicator in conjunction with other species, but our results for Question 4 do not support that either. Notwithstanding the above findings, our analyses also revealed that several bird species that were not focal species had higher or similar numbers of other bird species associated with them compared to the nominated focal species (e.g. Willie Wagtail and Grey Shrike-thrush; see Fig. 1). These birds are common, not of conservation concern, and are unlikely to be robust indicators of key threatening processes that were readily apparent from the literature or our previous extensive field studies in the target ecosystem (see Table 1). Hence, the reasons why many other species typically co-occur with them remain unclear. Nevertheless, our approach to empirically assessing the FSA might be useful for identifying the surrogacy potential of additional (previously not identified) species to co-occur with large numbers of other species. We therefore suggest that the selection of focal species requires an objective analysis of co-occurrence of all species in an assemblage, and subsequent *a posteriori* selection of focal species based on knowledge of occurrence and high associated richness, as well as links to any threatening processes specific to a landscape.

What are the relationships between the occurrence of combinations of focal species and bird species richness, or the richness of bird species of conservation concern?

Our study indicated that some birds of conservation concern were associated with some of the nominated focal species. However, we also found species of conservation concern that did **not** co-occur with any focal species, raising questions about the representativeness of focal

species in our study landscape. Most advocates of the FSA recommend the use of a **set** of species to manage landscapes (Lambeck 1997; USFWS 2012). This makes intuitive sense as a key step in selecting particular focal species includes selecting species that are the most dispersal-limited, most area-limited, most resource-limited (Lambeck 1997) – as we have done in this study (see Table 1). However, sets of focal species did not substantially elevate associated levels of bird species richness and richness of species of conservation concern beyond those levels associated with a single nominated focal species. These results are likely to be related to a lack of complementarity due to differences in habitat and other requirements. Hence, conditions suitable for a particular focal species and the other taxa associated with it may not be suitable for other focal species (and associated species).

"Anti-surrogacy" patterns

We recorded two inter-related kinds of negative surrogacy patterns: **(1)** those in which a particular species of conservation concern was **negatively** associated with the occurrence of a given focal species, and **(2)** those in which a given nominated focal species typically occurred on sites with low species richness.

Our analyses revealed strong evidence of negative effects where the occurrence of a nominated focal species was associated with the **absence** of a given species of conservation concern – a kind of "anti-surrogate" relationship. An example was the Superb Parrot. The occurrence of this bird was actually lower in the presence of nearly all of the other nominated focal species, and in over half the combinations, other taxa of conservation concern were not observed with this focal species. Moreover, the Superb Parrot was most often recorded on species-poor sites (Table 2), a result further underscoring its "anti-surrogate" characteristics.

Although the Superb Parrot is a bird of conservation concern, it is typically associated with extensively modified croplands as its primary food source and large old trees for nesting (Manning et al. 2012). This is in marked contrast with the many species dependent on

remnant patches of woodland in our study area (see Montague-Drake et al. 2009). This may explain both why it was typically not associated with other nominated focal species and why it was found primarily on species-poor sites (Table 2).

Negative surrogacy implies that although the occurrence of some focal species may be associated with many other species (including species of conservation concern), there will nevertheless be other focal species that might be associated with low levels of co-occurrence of other species. This implies a need for caution in the application of the FSA because management actions targeted for a given species may well not benefit many other species (including species of conservation concern). This could lead to management failures in which efforts to conserve particular species through the use of the FSA may not achieve the intended conservation goal. Our results suggests that while the FSA has value for conservation practice, there is also a need to ensure that management actions: (1) are sufficiently flexible to capture taxa of conservation concern that might not occur in species-rich sites (akin to the complementarity principles in reserve selection algorithms [see Margules & Pressey 2000]), and (2) create a range of habitat conditions in a landscape to ensure that suitable habitat for a particular species that is not associated with a given focal species nevertheless still occurs in parts of that landscape.

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SUPPORTING INFORMATION

Complete list of observed bird species recorded in surveys conducted between 2002 and 2011 (Appendix S1), Species with substantially high odds ratios of being observed with each individual focal species (Appendix S2), Species with substantially low odds ratios of being

observed with each individual focal species (Appendix S3), Percentage occurrence and average species richness at sites with either of two focal species present, by season (Appendix S4), Percentage occurrence and average species richness at sites with both of two focal species present, by season (Appendix S5), Average percentage occurrence of all species across sites with different levels of species richness (Appendix S6), and References cited in Table 1 (Appendix S7) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table 1. Nominated focal species and the underlying basis for their selection.

Key ecological processes	Species	Reference/s*
Patch-isolation limitation - dispersal	Brown Treecreeper	Cooper & Walters 2002; Montague-Drake et al. 2009
Patch-isolation limitation	Eastern Yellow Robin	Freudenberger 2001; Watson et al. 2001; Freudenberger & Brooker 2004
Patch-isolation limitation	Hooded Robin**	Watson et al. 2001
Patch-area limitation	Eastern Yellow Robin	Freudenberger 2001, Freudenberger & Brooker 2004; Montague-Drake et al. 2009
Patch-area limitation	Hooded Robin	Watson et al. 2001
Patch-area limitation	Brown Treecreeper	Barrett (1995) in Cooper & Walters 2002; Walters et al. 1999
Resource limitation (logs)	Brown Treecreeper	Noske 1979; Maron & Lill 2005; Montague-Drake et al. 2009
Resource limitation (hollow-bearing trees)	Brown Treecreeper	Cooper et al. 2002
Resource limitation (hollow-bearing trees)	Superb Parrot	Manning et al. 2012
Resource limitation (mistletoe)	Mistletoebird	Watson 2011; Watson & Herring 2012; Ikin et al. 2014
Resource limitation (mistletoe)	Hooded Robin	Montague-Drake et al. 2009; Watson 2011

* References cited are available online at Supporting Information Appendix S7.

** Watson et al. (2001) also suggested that the Hooded Robin was a focal species for resource limitation, but did not specify which particular resources in temperate eucalypt woodlands were limiting for this species.

Table 2. Average percentage occurrence of selected species across sites with different levels of species richness, defined as quintiles of average richness over years, by season. Hue indicates focal or anti-surrogate behaviour: red-brown if occurrence increases with species richness, blue if it decreases (this dichotomy is also indicated by the sign of "%inc", when viewed in black and white). Intensity indicates occurrence, ranging from darkest for > 50%, through > 25%, > 10%, to lightest for <3.6%. Quintiles for spring are: (1) < 9.9 species, (2) < 12.0, (3) < 14.0, (4) < 16.9, (5) > 16.9; and for winter: (1) < 7.5, (2) < 9.0, (3) < 10.5, (4) < 11.9, (5) > 11.9). Columns labelled "%inc" quantify the trends as the average percentage increase in odds of occurrence of a species corresponding to an increase of one species in the site-specific species richness. Nominated focal species are highlighted in yellow.

Species	Spring						Winter					
Richness quintile:	1	2	3	4	5	%inc	1	2	3	4	5	%inc
Black-chinned Honeyeater	0	1	1	7	12	24	0	2	2	4	10	65
Brown Treecreeper	1	9	20	48	68	51	0	10	18	39	56	69
Buff-rumped Thornbill	0	1	3	5	9	24	2	2	2	3	15	30
Common Bronzewing	2	11	9	16	22	15	1	4	7	15	18	32
Crested Shrike-tit	0	2	6	22	37	35	1	5	1	15	17	38
Diamond Firetail	0	0	4	6	15	28	0	2	0	12	9	50
Dusky Woodswallow	1	3	13	31	41	33	0	1	1	3	6	51
Eastern Yellow Robin	0	0	0	2	11	48	0	2	0	2	6	39
Flame Robin	0	0	0	0	0	—	0	2	14	20	23	37
Fuscous Honeyeater	0	1	1	4	11	36	0	1	0	10	14	68
Golden Whistler	0	0	0	1	3	32	1	4	3	4	16	33
Grey Butcherbird	31	13	7	7	3	-22	16	6	8	3	1	-29
Grey Fantail	0	2	2	4	11	26	1	6	10	10	17	20
Grey Shrike-thrush	4	15	25	47	80	52	2	15	10	44	61	65

Hooded Robin	0	1	3	2	13	32	0	2	0	3	6	51
Jacky Winter	1	5	7	16	33	31	0	7	5	13	30	55
Little Friarbird	1	3	16	23	35	28	0	2	1	4	6	44
Mistletoebird	0	4	5	8	20	22	0	4	5	6	14	34
Noisy Miner	97	86	69	50	32	-27	96	73	70	47	45	-29
Olive-backed Oriole	0	1	1	3	7	35	0	0	0	2	2	57
Peaceful Dove	1	3	9	14	32	34	0	2	3	9	14	37
Red Wattlebird	2	8	19	29	39	26	8	17	19	34	44	32
Restless Flycatcher	0	1	6	16	31	40	1	3	5	15	23	44
Rufous Whistler	1	10	9	18	32	25	0	2	4	2	6	16
Sacred Kingfisher	1	4	5	13	32	29	0	0	0	0	0	—
Scarlet Robin	0	0	0	0	1	—	0	2	1	2	11	51
Silvereye	0	0	0	3	2	26	0	2	0	4	6	32
Superb Fairy-wren	1	3	14	16	32	28	1	6	10	22	31	43
Superb Parrot		18	5	12	5	-13	1	2	1	0	0	—
Varied Sittella	0	0	0	0	4	37	0	1	0	0	2	35
Western Gerygone	0	1	5	1	9	21	0	0	1	1	2	30
White-browed Babbler	1	1	3	4	11	20	0	3	1	6	9	42
White-naped Honeyeater	1	1	1	0	4	20	0	2	3	9	16	57
White-plumed Honeyeater	11	38	61	83	93	64	28	50	73	82	91	65
White-throated Treecreeper	1	1	1	9	13	29	0	1	0	2	10	65
Willie Wagtail	9	43	74	84	92	66	21	33	61	64	81	49
Yellow-faced Honeyeater	0	1	1	1	4	26	0	1	1	9	12	54

Table 3. Odds ratio of occurrence of each species of conservation concern in the presence of each focal species (shown in italic) compared to the average occurrence ignoring occurrence of the focal species.

Focal species:		**BTC**	**EYR**	**HR**	**M**	**SPR**
Conservation species	**%**					
	SPRING					
Black-chinned Honeyeater	4.4	2.7	3.8	5.9	2.5	0.8
Brown Treecreeper	29.4	–	9.6	8.8	3.3	0.2
Crested Shrike-tit	13.5	3.5	4.3	4.8	2.2	0.4
Diamond Firetail	5.0	3.1	6.3	8.9	2.1	0
Dusky Woodswallow	17.9	4.1	2.5	6.1	2.0	0.3
Flame Robin	0	–	–	–	–	–
Grey-crowned Babbler	4.2	0.3	1.2	0	1.2	0.6
Hooded Robin	3.5	2.8	4.8	–	4.9	0.3
Jacky Winter	12.3	3.4	7.1	6.2	3.1	0.1
Painted Honeyeater	0.4	1.1	0	20.3	9.3	0
Red-capped Robin	1.8	1.7	0	6.7	1.0	0.5
Restless Flycatcher	10.8	3.1	15.3	6.2	3.1	0.5
Rufous Whistler	14.1	1.9	11.3	1.7	3.1	0.8
Scarlet Robin	0.1	3.4	0	0	0	0
Southern Whiteface	1.5	2.9	3.4	7.8	7.4	0
Speckled Warbler	1.3	2.4	8.7	0	2.8	0
Superb Parrot	13.8	0.3	0	0.2	0.6	–
Swift Parrot	0	–	–	–	–	–
Varied Sittella	0.8	3.5	6.9	4.9	9.6	0
White-browed Babbler	3.8	3.1	4.5	5.5	3.4	0

White-browed Woodswallow	18.0	2.6	1.1	3.4	1.7	0.7
WINTER						
Black-chinned Honeyeater	3.7	3.7	0	4.7	0.8	0
Brown Treecreeper	25.2	–	7.9	6.7	4.3	1.0
Crested Shrike-tit	8.0	2.9	4.3	13.4	2.1	0
Diamond Firetail	4.9	4.2	4.4	8.7	3.6	0
Dusky Woodswallow	2.1	2.2	0	8.7	4.9	0
Flame Robin	11.8	2.5	2.8	3.3	2.1	0
Grey-crowned Babbler	2.4	0.9	0	0	1.3	0
Hooded Robin	2.4	2.9	8.9	–	5.7	0
Jacky Winter	11.4	2.9	6.5	3.5	2.2	0
Painted Honeyeater	0	–	–	–	–	–
Red-capped Robin	0.9	0	0	0	3.4	0
Restless Flycatcher	9.7	3.0	5.3	1.7	1.3	0
Rufous Whistler	2.8	1.1	3.5	0	0	0
Scarlet Robin	3.2	1.9	11.4	9.2	3.2	0
Southern Whiteface	1.7	2.7	0	4.9	1.9	0
Speckled Warbler	0.7	2.0	0	0	8.9	0
Superb Parrot	0.7	1.0	0	0	0	–
Swift Parrot	0.2	0	0	0	0	0
Varied Sittella	0.6	2.7	17.8	32.3	5.7	0
White-browed Babbler	4.1	2.9	5.2	1.9	3.3	0
White-browed Woodswallow	0	–	–	–	–	–

Figure legends

Fig. 1. Average species richness given the occurrence of individual species plotted against percentage occurrence of that species, by season, using a log scale on both axes. Proposed focal species are shown in red and in capitals, and species with associated richness less than 3 or 1.5 species more than average are excluded, in spring or winter, respectively. Codes for particular species are given in Appendix S1. The y-axis is "jittered"; i.e., a small random number is added to reduce over-writing of species with the same mean species richness. Note that several bird species in the assemblage had higher associated species richness than the nominated focal species.