Conservation Biology

Contributed Paper

An Empirical Assessment of the Focal Species Hypothesis

D.B. LINDENMAYER,* P.W. LANE, M.J. WESTGATE, M. CRANE, D. MICHAEL, S. OKADA, AND P.S. BARTON

Fenner School of Environment and Society, ARC Centre of Excellence for Environmental Decisions; and National Environmental Research Program, The Australian National University, Canberra, ACT, 0200, Australia

Abstract: *Biodiversity surrogates and indicators are commonly used in conservation management. The focal species approach (FSA) is one method for identifying biodiversity surrogates, and it is underpinned by the hypothesis that management aimed at a particular focal species will confer protection on co-occurring species. This concept has been the subject of much debate, in part because the validity of the FSA has not been subject to detailed empirical assessment of the extent to which a given focal species actually co-occurs with other species in an assemblage. To address this knowledge gap, we used large-scale, long-term data sets of temperate woodland birds to select 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. Some, but not all, focal species were associated with high levels of species richness. One of our selected focal species was negatively associated with the occurrence of other species (i.e., it was an antisurrogate)—a previously undescribed property of nominated focal species. Furthermore, combinations of focal species were not associated with substantially elevated levels of bird species richness, relative to levels associated with individual species. Our results suggest that although there is some merit to the underpinning concept of the FSA, there is also a need to ensure that actions are sufficiently flexible because management tightly focused on a given focal species may not benefit some other species, including species of conservation concern, such of which might not occur in species-rich assemblages.*

Keywords: Biodiversity surrogates, threatened woodland birds, anti surrogates, conservation practice

Una Evaluación Empírica de la Hipótesis de Especie Focal

Resumen: *Los sustitutos de la biodiversidad y los indicadores se usan comúnmente en el manejo de la conservación. La estrategia de especie focal (FSA, en inglés) es un método para identificar a los sustitutos de la biodiversidad y está respaldado por la hipótesis de que el manejo de una especie focal particular llevará a la protección de especies co-ocurrentes. Este concepto ha sido sujeto de mucho debate, en parte porque la validez de la FSA no se ha sometido a una evaluación empírica detallada de la extensión a la cual una especie focal dada realmente co-ocurra con otras especies en un ensamblado. Para dirigirnos a este vacío de conocimiento, usamos series de datos de largo plazo y a gran escala de aves de bosque templado para elegir una especie focal asociada con procesos de amenaza como el aislamiento de hábitat y la pérdida de atributos vegetales clave. Cuantificamos los patrones de co-ocurrencia entre especies focales, especies en el ensamblado de aves más amplio y especies de importancia de conservación. Algunas, pero no todas, de las especies focales estuvieron asociadas con niveles altos de riqueza de especies. Una de nuestras especies focales seleccionadas estuvo asociada negativamente con la ocurrencia de otra especie (es decir, era un anti-sustituto) – una propiedad de las especies focales nominadas no descrita previamente. Además, las combinaciones de especies focales no estuvieron asociadas con niveles elevados de riqueza de especies de aves, en relación con los niveles asociados con especies individuales. Nuestros resultados sugieren que mientras exista alguna cualidad que respalde el concepto de estrategia de especie focal, también hay una necesidad de asegurar que las acciones son suficientemente flexibles porque el manejo plenamente enfocado en una especie focal dada puede no*

*email david.lindenmayer@anu.edu.au
Paper submitted August 1, 2013; revised manuscript accepted February 26, 2014.

Conservation Biology, Volume 28, No. 6, 1594–1603

DOI: 10.1111/cobi.12330

beneficiar a otras especies, incluidas las de importancia de conservación, de las cuales pueden no ocurrir en ensamblados con riqueza de especies.

Palabras Clave: Anti-sustitutos, aves de bosque amenazadas, práctica de la conservación, sustitutos de la biodiversidad

Introduction

The use of surrogates and indicators is often important in assessments of 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 common one is the umbrella species for 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 (FSA) is a related form of surrogacy and is used around the world (e.g., Lambeck 1997; Watson et al. 2001; Nicholson et al. 2013).

The FSA was developed by Lambeck (1997). Under the FSA, 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. These are the focal species. Lambeck (1997) defined 4 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 interpatch 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 (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 to 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. We addressed this knowledge gap by reporting the results of a novel empirical assessment of the hypothesis underpinning the FSA. We focused 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 used a decade-long data set gathered from a large number of temperate woodland sites to answer the following questions. First, 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, 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.

Second, 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 co-occur 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.

Third, 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.

Fourth, 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 (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); there is a large and rapidly expanding literature encompassing more than 7995 articles on this topic (M.J.W. et al., unpublished data). Hence, this paper and the empirical approaches we used to assess the hypothesis that underpins the FSA are important contributions to understanding the effectiveness of biodiversity surrogates for conservation and land management.

Methods

Study Area

Our study sites were composed of 134 temperate woodland remnants on 45 farms on the South West Slopes of New South Wales in southeastern Australia. The sites and farms were in areas outside 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. The 134 remnant sites encompassed a range of structural conditions—old growth (70 sites), natural seedling regrowth (that regenerated from seeds shed by scattered paddock trees) (35 sites), and coppice (i.e., multi-stemmed) regrowth woodland (29 sites). The regrowth sites had high stem counts (particularly of small eucalypts) and a limited number of large (>50 cm diameter at breast hight [DBH]) remnant trees (which indicated 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 the original vegetation on the site had been virtually completely cleared in the past. Native vegetation was not planted in any regrowth sites. The predominant form of native vegetation on regrowth sites was temperate eucalypt woodland (sensu Lindenmayer et al. 2010) dominated by white box (*Eucalyptus albens*), grey box (*E. microcarpa*), yellow box (*E. melliodora*), Blakely's red gum (*E. blakelyi*), red stringybark (*E. macrorhyncha*), or red ironbark (*E. sideroxylon*). Our permanent field sites have been subject to a range of grazing regimes, including grazing exclusion, crash grazing (i.e., intensive grazing for a very limited period), and set stocking (i.e., prolonged, high-intensity grazing). Our 134 field sites covered the range of environmental conditions that occur in temperate eucalypt woodlands in our study region; 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) our study region (e.g., Watson et al. 2001; Freudenberger and Brooker 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 and recommendations of focal species status from earlier investigations (e.g., Watson et al. 2001; Freudenberger and Brooker 2004), we selected a set of focal species based on sensitivity to key threatening processes (Table 1). Most of the selected species are among the subset of approximately 20 species in the temperate woodland bird assemblage considered of conservation concern (reviewed by Montague-Drake et al. 2009) (Supporting Information).

Bird Survey Protocols

Our study region supports more than 155 bird species (Supporting Information), of which over half are woodland dependent, including more than 20 species of conservation concern. Approximately 35% of the bird species are migratory, partially migratory, dispersive, or nomadic. The bird assemblage contains many native generalist species that occur in heavily cleared paddocks and cultivated areas (e.g., the Brown Songlark [*Megalurus cruralis*]). Only 4 species are non-native, of which 2 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 in the winter of 2004, 2007, 2008, and 2011. Our surveys entailed repeated 5-min point interval counts at each of the 0, 100, and 200 m points along a permanent transect at each site. In each survey year, all sites were surveyed

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

Limitation	*Species*	*Reference*[a]
Patch isolation	Brown Treecreeper	Cooper & Walters 2002; Montague-Drake et al. 2009
	Eastern Yellow Robin	Freudenberger 2001; Watson et al. 2001; Freudenberger & Brooker 2004
	Hooded Robin[b]	Watson et al. 2001
Patch area	Eastern Yellow Robin	Freudenberger 2001; Freudenberger & Brooker 2004; Montague-Drake et al. 2009
	Hooded Robin	Watson et al. 2001
	Brown Treecreeper	Barrett (1995) in Cooper & Walters 2002; Walters et al. 1999
Resource (logs)	Brown Treecreeper	Noske 1979; Maron & Lill 2005; Montague-Drake et al. 2009
Resources (hollow-bearing trees)	Brown Treecreeper	Cooper et al. 2002
	Superb Parrot	Manning et al. 2012
Resource (mistletoe)	Mistletoebird	Watson 2011; Watson & Herring 2012; Ikin et al. 2014
	Hooded Robin	Montague-Drake et al. 2009; Watson 2011

[a] *References cited are available in the Supporting Information.*
[b] *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.*

by 2 different observers on different days. We completed counts from 0530 to 0930 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 3 permanent markers at each site. For this study, we considered a bird present at a site if it was recorded by at least one observer on at least one marker at a radius of not >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 Analyses

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. 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 used the generalized linear model facilities of the GenStat statistical system (VSN International 2013) to estimate a separate value of a for each model rather than trying to impose a common value overall value of a.

We also investigated the relationship between potential focal species and species richness by examining the average percent 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 5 classes of species richness, with approximately equal number of sites in each class). We then calculated the average percent 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 identified those species with strong surrogate characteristics as those much more likely to occur at sites with high species richness than at sites with low species richness. This approach also allowed us to identify birds as strong antisurrogates (i.e., those likely to be associated with low levels of bird species richness). We quantified the gradient of surrogacy suitability for each species as the slope of a logistic regression of occurrence of that species on the averaged site-specific species richness.

We assessed the association between 2 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 <1). We interpreted an odds ratio >3.00 or <0.33 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 0.33 corresponds to any of those changes reversed (i.e., 10% to 3.6%, etc.). An odds ratio of 3, derived from 2 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. There were many more observations in our data set, so there was no doubt of statistical significance of any of the reported associations at this level.

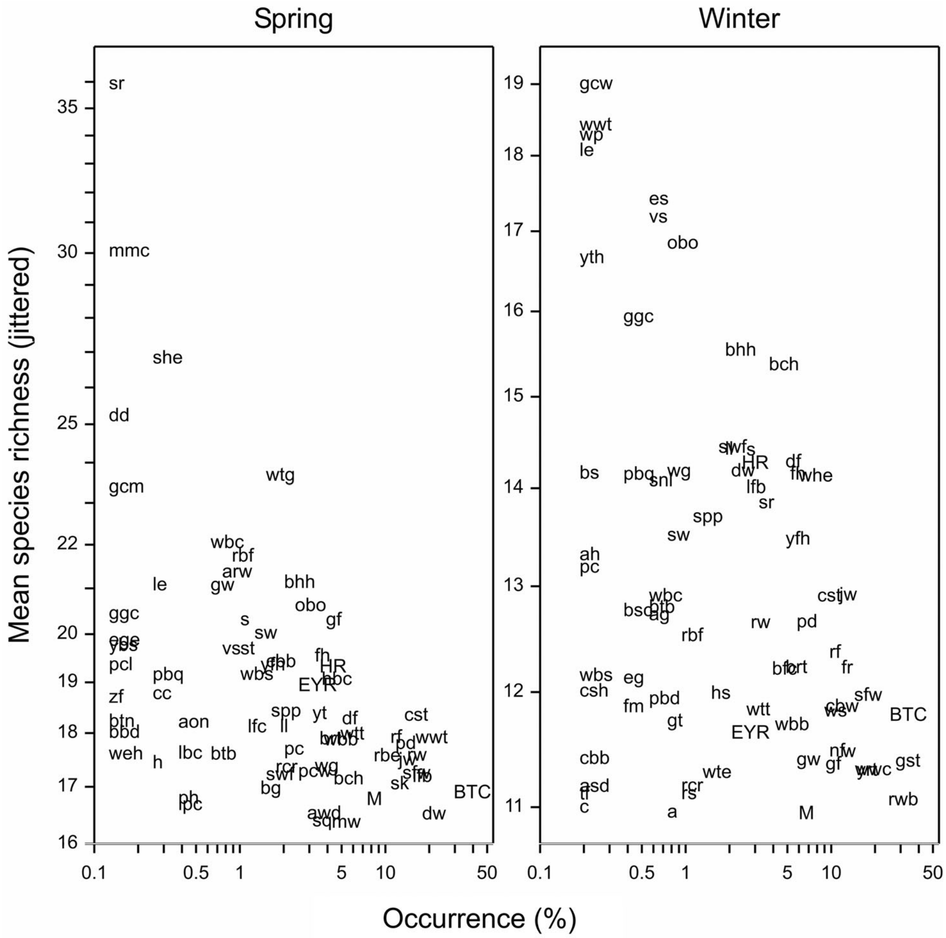

Figure 1. Average species richness given the occurrence of individual species plotted against percent occurrence of that species, by season. Both axes are on a log scale. Abbreviations of focal species are in capital letters. Species with associated richness of <3 in spring and species with associated richness 1.5 more than average in winter are excluded. Codes for particular species are given in Supporting Information. Jittered means a small random number is added to reduce over-writing of species with the same mean species richness. Several bird species in the assemblage had higher associated species richness than the nominated focal species.

Detection and Occupancy Analyses

Detection–occupancy analysis (sensu MacKenzie et al. 2006) is now widely regarded as a standard statistical approach for use with ecological data sets. However, we did not include detectability in our analysis for 3 key reasons. First, detailed statistical analyses by Welsh et al. (2013) suggest that the current statistical methods for detection occupancy do not improve model fit and in some cases can make the outcomes worse. Second, our data were presence–absence data obtained from 3 points at each site, with the survey repeated by a different observer on a different day. We therefore did not have sufficient data to carry out a detection–occupancy analysis without amalgamating observations across seasons or years, which was not appropriate (even if such analysis were robust) because of marked interseason and year-to-year differences in probabilities of occupancy and detection for many bird species. Third, based on our survey protocols, we accounted for known sources of variation in our surveys in the most appropriate and feasible manner by using a very large number of sites and surveying multiple points per site (local spatial heterogeneity), surveying on multiple days (temporal heterogeneity), and using multiple observers (observer heterogeneity) (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/site in spring and 9.8 species/site in winter. The distribution of values was well represented as negative binomial with an aggregation parameter of approximately 14 for spring and approximately 17 for winter.

Co-Occurrence of Focal Species with High Bird Species Richness

The occurrence of each nominated focal species (except the Superb Parrot [*Polytelis swainsonii*]) was associated with significantly higher species richness ($p < 0.02$ for all focal species); the number of additional co-occurring species ranged from 3 to 6 species in spring and 1 to 4 additional species 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 higher levels of associated species richness than any of the nominated focal species (Fig. 1), but all of them were rare (occurred <5% of the

Species	Spring[a] Richness quintile 1	2	3	4	5	% change[c]	Winter[b] Richness quintile 1	2	3	4	5	% change[c]
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	28	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

[a] Quintiles for spring are: 1, < 9.9 species; 2, < 12.0; 3, < 14.0; 4, < 16.9; 5, > 16.9.
[b] Quintiles for winter are: 1, < 7.5 species; 2, < 9.0; 3, < 10.5; 4, < 11.9; 5, > 11.9.
[c] The average percentage increase in odds of occurrence of a species corresponding to an increase of one species in the site-specific species richness.

Figure 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 behavior: red-brown if occurrence increases with species richness, blue if it decreases (this dichotomy is also indicated by the sign of "% change" when viewed in black and white). Intensity indicates occurrence, ranging from darkest for >50% through >25% and >10% to lightest for <3.6%. Nominated focal species are highlighted in yellow.

time). Restricting attention to species recorded 10% or more of the time, 10 species in spring and 4 species in winter were associated with levels of richness greater than those found for the most common focal species (Brown Treecreeper [*Climacteris picumnus*]).

Gradients of increasing occurrence ranged widely and, for some species, occurrence decreased with increasing richness (Fig. 2). 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 are shown in Fig. 2. All increases or decreases in Fig. 2 were significantly different from zero ($p < 0.004$). A complete list of results is in Supporting Information.

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 3 other species (White-plumed Honeyeater [*Lichenostomus penicillatus*], Willie Wagtail [*Rhipidura leucophrys*], Grey Shrike-Thrush [*Colluricincla harmonica*]), which also had strong

Table 2. Odds ratio of occurrence of each species of conservation concern in the presence of each focal species compared with the average occurrence ignoring occurrence of the focal species itself.

	Spring						*Winter*					
Focal species	*%*	*BTC*	*EYR*	*HR*	*M*	*SPR*	*%*	*BTC*	*EYR*	*HR*	*M*	*SPR*
Brown Treecreeper	29.4	–	9.6	8.8	3.3	0.2	25.2	–	7.9	6.7	4.3	1.0
Hooded Robin	3.5	2.8	4.8	–	4.9	0.3	2.4	2.9	8.9	–	5.7	0
Superb Parrot	13.8	0.3	0	0.2	0.6	–	0.7	1.0	0	0	0	–
Other species of conservation concern												
Black-chinned Honeyeater	4.4	2.7	3.8	5.9	2.5	0.8	3.7	3.7	0	4.7	0.8	0
Crested Shrike-tit	13.5	3.5	4.3	4.8	2.2	0.4	8.0	2.9	4.3	13.4	2.1	0
Diamond Firetail	5.0	3.1	6.3	8.9	2.1	0	4.9	4.2	4.4	8.7	3.6	0
Dusky Woodswallow	17.9	4.1	2.5	6.1	2.0	0.3	2.1	2.2	0	8.7	4.9	0
Flame Robin	0	–	–	–	–	–	11.8	2.5	2.8	3.3	2.1	0
Grey-crowned Babbler	4.2	0.3	1.2	0	1.2	0.6	2.4	0.9	0	0	1.3	0
Jacky Winter	12.3	3.4	7.1	6.2	3.1	0.1	11.4	2.9	6.5	3.5	2.2	0
Painted Honeyeater	0.4	1.1	0	20.3	9.3	0	0	–	–	–	–	–
Red-capped Robin	1.8	1.7	0	6.7	1.0	0.5	0.9	0	0	0	3.4	0
Restless Flycatcher	10.8	3.1	15.3	6.2	3.1	0.5	9.7	3.0	5.3	1.7	1.3	0
Rufous Whistler	14.1	1.9	11.3	1.7	3.1	0.8	2.8	1.1	3.5	0	0	0
Scarlet Robin	0.1	3.4	0	0	0	0	3.2	1.9	11.4	9.2	3.2	0
Southern Whiteface	1.5	2.9	3.4	7.8	7.4	0	1.7	2.7	0	4.9	1.9	0
Speckled Warbler	1.3	2.4	8.7	0	2.8	0	0.7	2.0	0	0	8.9	0
Swift Parrot	0	–	–	–	–	–	0.2	0	0	0	0	0
Varied Sittella	0.8	3.5	6.9	4.9	9.6	0	0.6	2.7	17.8	32.3	5.7	0
White-browed Babbler	3.8	3.1	4.5	5.5	3.4	0	4.1	2.9	5.2	1.9	3.3	0
White-browed Woodswallow	18.0	2.6	1.1	3.4	1.7	0.7	0	–	–	–	–	–

Abbreviations: BTC, Brown Treecreeper; EYR, Eastern Yellow Robin; HR, Hooded Robin; M, Mistletoebird; SPR, Superb Parrot.

positive gradients. By contrast, the Noisy Miner (*Manorina melanocephala*) was an antisurrogate in both seasons, occurring at over 95% of species-poor sites, dropping to about 30% at species-rich sites in spring and to 45% in winter. Sixteen of the 21 species of conservation concern (Supporting Information) had strong positive gradients (average increase in odds of >25%) when the species occurred at least 2% of the time on average.

Occurrence of Focal Species with 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 2). 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 (*Melanodryas cucullata*) was associated with the absence of the Grey-crowned Babbler (*Pomatostomus temporalis*), the Scarlet Robin (*Petroica boodang*), and the Speckled Warbler (*Chthonicola sagittata*). In winter, occurrence of the Eastern Yellow Robin (*Eopsaltria australis*) was associated with the absence of 8 species. However, all of these absences were for pairs of species in which at least one was rare (<5% occurrence; see Table 2).

Co-Occurrence of Birds with a Focal Species

With an odds ratio >3.0, 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) in winter and spring, except with the Mistletoebird (*Dicaeum hirundinaceum*) in winter (Supporting Information). The Jacky Winter (*Microeca fascinans*) and Restless Flycatcher (*Myiagra inquieta*) had strong associations with all the focal species except the Superb Parrot. In addition, one of the focal species itself (Brown Treecreeper) was substantially more likely to be observed with 3 of the other focal species. We also identified the Noisy Miner, Pied Butcherbird (*Cracticus nigrogularis*), and Grey Butcherbird (*Cracticus torquatus*) as species that were substantially less likely to be observed with each of the focal species (Supporting Information).

Occurrence of Combinations of Focal Species with High Bird Species Richness

Combinations of focal species were not generally associated with higher species richness than an individual focal species (Supporting Information). 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 the other 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 the other occurred.

When we excluded rare combinations of focal species (<5% occurrence), no pairs of focal species were associated with more than one additional species. For sites where both of a pair of focal species were present, all combinations were rare (<5% occurrence; Supporting Information). 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 (Supporting Information). For sets of 3 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

Focal Species Occurrence and High Bird Species Richness

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 prespecified focal species were typically associated with species-rich sites (Fig. 2) and a higher level of occurrence of species of conservation concern in both spring and winter (Table 2), our results suggest these nominated focal species have 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 prespecified 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 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 measurable, which means that effective focal species must be recorded relatively frequently (without being ubiquitous). For example, 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 (Fig. 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, in regards to the question of whether occurrence of combinations of nominated focal species is associated with high levels of bird species richness, do not support that either. Notwithstanding the above findings, our results also revealed that several bird species that were not focal species had higher or similar numbers of other bird species associated with them than 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 many other species typically co-occur with them remain unclear. Nevertheless, our empirical approach to assessment of the FSA may be useful for identifying the surrogacy potential of additional (previously not identified) species that 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 subsequently a posteriori selection of focal species based on knowledge of occurrence and high associated richness, as well as links to threatening processes specific to a landscape.

Relationships between Occurrence of Combinations of Focal Species and Bird Species Richness

Some birds of conservation concern were associated with some of the nominated focal species. However, some species of conservation concern 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 because a key step in selecting particular focal species is selecting species that are the most dispersal limited, most area limited, and 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).

Antisurrogacy Patterns

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

We found strong evidence of negative effects where occurrence of a nominated focal species was associated with the absence of a given species of conservation concern—a kind of antisurrogate relationship. An example was the Superb Parrot. The occurrence of this bird was lower in the presence of nearly all the other nominated focal species and lower in over half the combinations of sets of focal species; other taxa of conservation concern were not observed with this focal species. Moreover, the Superb Parrot was most often recorded on species-poor sites (Fig. 2), a result further underscoring its antisurrogate characteristics.

Although the Superb Parrot is a bird of conservation concern, it is typically associated with extensively modified croplands because crop seeds are its primary food source. It requires large old trees for nesting, although these can be scattered paddock trees in otherwise cropped areas (Manning et al. 2012). These habitat requirements are in marked contrast with the many species dependent on remnant patches of woodland in our study area (see Montague-Drake et al. 2009) and may explain why the species was typically not associated with other nominated focal species and why it was found primarily on species-poor sites (Fig. 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 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 suggest that although the FSA has value for conservation, there is also a need to ensure that actions 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 create a range of habitat conditions in a landscape to ensure that habitat for a particular species that is not associated with a given focal species nevertheless still occurs in parts of that landscape.

Acknowledgments

This project was supported by an Australian Research Council Laureate Fellowship. We thank the editor, G. Guepel, and several anonymous referees for robust but insightful comments that improved earlier versions of the manuscript.

Supporting Information

Lists of observed bird species recorded in surveys conducted from 2002 to 2011 (Appendix S1), species with substantially high odds ratios of being observed with each individual focal species (Appendix S2), and species with substantially low odds ratios of being observed with each individual focal species (Appendix S3); percent occurrence and average species richness at sites with either of 2 focal species present (Appendix S4); percent occurrence and average species richness at sites with both of 2 focal species present (Appendix S5); and average percent occurrence of all species across sites with different levels of species richness (Appendix S6) 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.

Literature Cited

Branton, M., and J. S. Richardson. 2010. Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. Conservation Biology **25:**9–20.

Caro, T. 2010. Conservation by proxy. Indicator, umbrella, keystone, flagship, and other surrogate species. Island Press, Washington, D.C.

Chase, M. K., and G. R. Geupel. 2005. The use of avian focal species for conservation planning in California. Pages 130–142 in C. J. Ralph and T. D. Rich, editors. Bird conservation implementation and integration in the Americas: Proceedings of the Third International Partners in Flight Conference. [USDA Forest Service Gen. Tech. Report PSW GTR-191, Albany, California.]

Collinge, S. K. 2009. Ecology of fragmented landscapes. The Johns Hopkins University Press, Baltimore.

Cooper, C. B., and J. R. Walters. 2002. Independent effects of woodland loss and fragmentation on Brown Treecreeper distribution. Biological Conservation **105:**1–10.

Cooper, C. B., J. R. Walters, and J. Priddy. 2002. Landscape patterns and dispersal success: simulated population dynamics in the Brown Treecreeper. Ecological Applications **12:**1576–1587.

Cunningham, R. B., D. B. Lindenmayer, H. A. Nix, and B. D. Lindenmayer. 1999. Quantifying observer heterogeneity in bird counts. Australian Journal of Ecology **24:**270–277.

Department of the Environment. 2013. Threatened ecological communities. Available from http://www.environment.gov.au/topics/biodiversity/threatened-species-ecological-communities/threatened-ecological-communities (accessed November 2013).

Ford, H. A. 2011. The causes of decline of birds of eucalypt woodlands: advances in our knowledge over the last 10 years. Emu **111:**1–9.

Freudenberger, D. 2001. Bush for birds: biodiversity enhancement guidelines for the Saltshaker Project, Boorowa, NSW. CSIRO Wildlife and Ecology/Greening Australia, A.C.T. and SE NSW Inc., Canberra.

Freudenberger, D., and L. Brooker. 2004. Development of the focal species approach for biodiversity conservation in the temperate agricultural zones of Australia. Biodiversity and Conservation **13:**253–274.

Grantham, H. S., R. L. Pressey, J. A. Wells, and J. A. Beattie. 2010. Effectiveness of biodiversity surrogates for conservation planning: different measures of effectiveness generate a kaleidoscope of variation. PLoS One **5:**DOI: 10.1371/journal.pone.0011430.

Ikin, K., P. S. Barton, I. Stirnemann, J. R. Stein, D. Michael, M. Crane, S. Okada, and D. B. Lindenmayer. 2014. Multi-scale associations between vegetation cover and woodland bird communities across a large agricultural region. PLoS One **9:**e97029.

Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology **11:**849–856.

Lindenmayer, D. B., and R. B. Cunningham. 2011. Longitudinal patterns in bird reporting rates in a threatened ecosystem: Is change regionally consistent? Biological Conservation **144:**430–440.

Lindenmayer, D. B., A. Manning, P. L. Smith, H. P. Possingham, J. Fischer, I. Oliver, and M. A. McCarthy. 2002. The focal species approach and landscape restoration: a critique. Conservation Biology **16:**338–345.

Lindenmayer, D. B., A. F. Bennett, and R. J. Hobbs. (eds). 2010. Temperate woodland conservation and management. CSIRO Publishing, Melbourne.

MacKenzie, D. I., J. D. Nichols, J. A. Royal, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling. Academic Press, Sydney.

Manning, A. D., P. Gibbons, J. Fischer, D. Oliver, and D. B. Lindenmayer. 2012. Hollow futures? Tree decline, lag effects and hollow-dependent species. Animal Conservation **16:**395–403.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature **405:**243–253.

Maron, M., and Lill, A. 2005. The influence of livestock grazing and weed invasion on habitat use by birds in grassy woodland remnants. Biological Conservation **124:**439–450.

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

Nicholson, E., D. B. Lindenmayer, K. Frank, and H. P. Possingham. 2013. Testing the focal species approach to making conservation decisions for species persistence. Diversity and Distributions **19:**530–540.

Noske, R. 1979. Co-existence of three species of treecreepers in north-eastern New South Wales. Emu **79:**120–128.

Seddon, P. J., and T. Leech. 2008. Conservation short cut, or long and winding road? A critique of umbrella species criteria. Oryx **42:**240–245.

Short, J., and B. Parsons. 2004. A test of the focal species approach in Western Australia. Final Report for Land and Water Australia Project CSE 9: Testing Approaches to Landscape Design in Cropping Lands: Component Three Report (Western Australia). Land and Water Australia and CSIRO Sustainable Ecosystems, Canberra.

USFWS (US Fish and Wildlife Service). 2012. Draft guidance on selecting species for design of landscape-scale conservation. Available from http://www.fws.gov/landscape-conservation/draft-guidance.html (accessed January 2014).

VSNI. 2013. GenStat 16th Edition (computer software). Available from http://www.vsni.co.uk (accessed November 2013).

Walters, J. R., H. A. Ford, and C. B. Cooper. 1999. The ecological basis for sensitivity of brown treecreepers to habitat fragmentation: a preliminary assessment. Biological Conservation **90:**13–20.

Watson, D. M. 2011. Mistletoes of southern Australia. CSIRO Publishing, Melbourne.

Watson, D. M., and M. Herring. 2012. Mistletoe as a keystone resource: an experimental test. Proceedings of the Royal Society B: Biological Sciences **279:**3853–3860.

Watson, J., D. Freudenberger, and D. Paull. 2001. An assessment of the focal species approach for conserving birds in variegated landscapes in southeastern Australia. Conservation Biology **15:**1364–1373.

Welsh, A. H., D. B. Lindenmayer, and C. F. Donnelly. 2013. Fitting and interpreting occupancy models. PLoS One **8:**e52015.