

TESTING HYPOTHESES ASSOCIATED WITH BIRD RESPONSES TO WILDFIRE

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Abstract. Disturbance is a key ecological process influencing the distribution and abundance of many elements of the earth's biota. Predicting the response of biota to disturbance is therefore important, but it nevertheless remains difficult to make accurate forecasts of response. We tested predictions from disturbance-related theories and concepts in 10 vegetation types at Booderee National Park (southeastern Australia) using a retrospective study of bird responses to fire history (over 35 years) on 110 sites and a prospective study following a single wildfire event in 2003 at 59 of these sites. Our data did not support predictions from the intermediate-disturbance hypothesis; observed bird species richness at a site was significantly ($F_{1,99} = 6.30$, $P = 0.014$) negatively related to the number of fires since 1972 and was 8.7% lower (95% CI, 1.8–15.1%) for each additional fire. In contrast to fire history effects, we found that after the 2003 fire, the vast majority of individual species and the bird assemblage per se in most vegetation types recovered within two years. Thus, recovery after a single fire did not reflect long-term effects of multiple fires on overall bird species richness at a site. We postulated that the recovery of bird species richness and bird assemblage composition after the 2003 fire would be fastest in structurally simple vegetation types and slowest in structurally complex vegetation, but observed the opposite. Although observed bird species richness in vertically heterogeneous forest and woodland had returned to prefire levels by 2006, bird species richness in structurally simple vegetation types (e.g., sedgeland) had not. Postfire vegetation regeneration, together with a paucity of early-successional specialists, would explain the speed of recovery of the bird assemblage and why it changed relatively little during our investigation.

Key words: avifauna; biological legacies; bird community; disturbance; fire history; fire severity; sedgeland; southeastern Australia; vegetation management; wildfire event.

INTRODUCTION

Fire is a key ecological process in ecosystems around the world (Agee 1993, Bradstock et al. 2002, Andersen et al. 2003, Burton et al. 2003). However, in many landscapes, the sequence of fires or fire history (sensu Gill 1975) has changed in the past few centuries (Covington 2003, Andersen et al. 2005) as a result of such factors as active fire suppression (Zackrisson 1977, Spies et al. 2004), logging (Thompson et al. 2007), urban encroachment on natural areas (Cary et al. 2003), and possibly climate change (Lenihan et al. 2003, Pittock 2005). Such changes are believed to be having negative impacts on biodiversity (Woinarski and Recher 1997, Schurbon and Fauth 2003, Noss et al. 2006). For example, altered fire history is thought to be threatening biota in Australia: more than 50 species of birds are at risk and only land clearing threatens a greater number of species (Woinarski 1999, Garnett and Crowley 2000).

Given this, a better understanding of the effects of fire on biodiversity is vital to designing management strategies that best manage areas of native vegetation (Richards et al. 1999, Bradstock et al. 2005).

Many authors (e.g., Keith et al. 2002, Parr and Andersen 2006) have highlighted the lack of attempts to monitor and predict the impacts of the sequence of fires on biodiversity. However, this can be complex because, for example, (1) different fires can burn at different severities in the same vegetation type (Smucker et al. 2005, Kotliar et al. 2007), giving rise to considerable local- and landscape-scale patchiness (DeLong and Kessler 2000, Mackey et al. 2002, Turner et al. 2003, Kulakowski and Veblen 2007); (2) fires can burn differently in different vegetation types (Agee 1993, Andersen et al. 2005); and (3) differences in the timing of a fire or series of fires can produce markedly different impacts on biota (Bradstock et al. 2002, Thompson et al. 2007). Therefore, a research and management challenge remains to identify ecologically appropriate and socially acceptable fire management practices for different vegetation types and their associated biota (Gill et al. 1999, Parr and Chown 2003, Spies et al. 2004, Haynes et al. 2006).

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In this paper, we describe a study of bird responses to fire in 10 vegetation types at Booderee National Park within the Jervis Bay Territory in southeastern Australia. We quantified fire effects on birds through a retrospective study of a series of fires over time ("fire history") and a prospective investigation of birds following a single conflagration (a "fire event") in December 2003. We explored fire effects at the population, bird assemblage (community), and species (individual species and all species combined) levels. We tested predictions from theories and concepts directly or indirectly linked with the impacts of natural disturbances on biodiversity.

First, we quantified relationships between fire history and bird species richness and compared our findings with predictions from the intermediate-disturbance hypothesis. Under this hypothesis, species richness is predicted to be highest on sites subject to intermediate values for the number of fires and time since fire rates. This is because they will tend to have a mixture of early-successional and late-successional species (Connell 1978, Shiel and Burslem 2003). Since 1972, the number of fires in any given part of Booderee National Park has varied from none to five and the time since the last fire ranges from four to 35 years. Given this information and based on the intermediate-disturbance hypothesis, we tested the prediction that bird species richness should be highest in areas that have experienced 2–3 past fires and areas where ~12–16 years have elapsed since the last fire.

Second, we examined relationships between vegetation structure, species richness, and bird species recovery after a single major wildfire in 2003. Fire burns differently in different vegetation types (Agee 1993, Whelan 1995) and the impacts of fire on bird biota may be mediated through temporal recovery patterns of vegetation structure and composition. The vertical vegetation structure hypothesis (MacArthur and MacArthur 1961, Recher 1969) predicts that bird diversity will be highest in vertically complex vegetation types such as forest and woodland and lowest in structurally simple environments (e.g., sedge-land). However, the recovery of vegetation structure may take longer in structurally complex vegetation than where vertical vegetation structure is simple. We tested the prediction that the recovery of bird species richness and bird assemblage composition after the 2003 fire would be fastest in structurally simple vegetation types and slowest in structurally complex vegetation characterized by high levels of vertical heterogeneity (*sensu* Brokaw and Lent 1999).

Third, we examined relationships between biological legacies and bird persistence and recovery following the 2003 fire. Biological legacies are defined by Franklin et al. (2000) as: "...organisms, organically-derived structures, and organically-produced patterns that survive from the pre-disturbance system." They can influence the

type and pace of recovery of biota after disturbance (Foster et al. 1998, Turner et al. 2003). The more of the pre-disturbance stand structure that persists after fire, the faster plant and animal populations should return to prefire levels (Franklin et al. 2000, Whelan et al. 2002). We tested the prediction that more species of birds would persist and/or recover fastest on sites with high levels of biological legacies remaining after the 2003 fire.

Fourth, we quantified relationships between bird response to the 2003 fire and bird life history attributes. Several studies have identified predictable relationships between disturbance and animal life history attributes or functional groups (e.g., Hansen and Urban 1992, Loyn 1993). These include investigations of fire (e.g., Raphael et al. 1987, Imbeau et al. 1999, Saab et al. 2007). We sought to determine if there were subsets of species from the bird assemblage that responded in a similar way to the 2003 fire and that had sets of life history attributes in common. Finally, we examined the effects of the 2003 fire at Booderee National Park on a number of individual species.

Our overarching aim in completing this study was to improve understanding of biodiversity responses to both fire history and a single fire event. Such new knowledge is important, given that several recent studies have predicted that fire size, fire frequency, and/or fire severity will increase in the near future as a consequence of climate change (Cary 2002, Lenihan et al. 2003, Pittock 2005, Westerling et al. 2006). An understanding of the response of biodiversity to individual fire events and sequences of fires will be crucial to better inform appropriately targeted management practices for bird communities in a wide range of ecosystems where fire is an important ecological process. For example, managers will seek knowledge on which species, vegetation types, and fire patterns to monitor. There is considerable precedent for targeted management of fire and bird communities in many coastal ecosystems in eastern Australia, particularly those that support threatened plant and animal species and that are close to human infrastructure that requires protection from wildfire (Woinarski 1999, Garnett and Crowley 2000). In the particular case of Booderee National Park, a detailed fire management plan has been in place for almost 10 years (Department of Environment and Water Resources 2007).

METHODS

Study area

We conducted this study at Booderee National Park, a ~7500-ha area co-managed by the Wreck Bay Aboriginal Community and Parks Australia (a section of the Australian Federal Government's Department of the Environment and Water Resources). Booderee National Park is located 200 km south of Sydney and 20 km south of the city of Nowra on the southern coast of New South Wales, southeastern Australia (approx-

mate midpoint is 35°10' S latitude, 150°40' E longitude). The area has a temperate maritime climate with an average rainfall of 1150 mm per annum spread relatively evenly over the year. Average minimum and maximum air temperatures are 18–24°C for January (summer) and 9.5–15°C for July (winter) (Bureau of Meteorology 2007).

We targeted Booderee National Park for study because it has some important features. First, it supports an extremely diverse bird assemblage (Braithwaite et al. 1995), including important populations of a number of high-profile taxa of conservation concern. For example, Booderee National Park supports the largest known remaining population of the Eastern Bristlebird (*Dasyornis brachypterus*), a species believed to be sensitive to the impacts of wildfires (Baker 1997, 2000). A second reason why we targeted Booderee National Park for this investigation was that it supports extraordinary patchiness and heterogeneity in vegetation types, ranging from dry heathland to warm temperate rain forest, which are markedly different in floristics and structure (Ingwersen 1977, Mills 1995, Williams 1995, Taws 1998). For this study, we recognized 10 broad categories of native vegetation cover in Booderee National Park (Appendix A).

A third factor influencing our selection of Booderee National Park as a study area was that fire is a not-uncommon form of disturbance across the full range of vegetation types at Booderee National Park (Whelan 1995, Whelan et al. 2002), with the exception of warm temperate rain forest (Gill et al. 1999). Fire severity may be variable, ranging from low-severity surface fires to high-severity stand-replacing events such as those that occur approximately every 8–20 years in heathland (Recher et al. 1975).

Some aspects of fire history dating back several decades have been reasonably well documented and carefully mapped at Booderee National Park (Ingwersen 1977, Taws 1998); the number of fires recorded for any given area in the park varies from zero to five. Ignition for these fires varies from unknown to lightning strike to deliberate human ignition. The severity of past fires at Booderee National Park has not been quantified, but anecdotal information from long-term ranger staff in the region indicates there was considerable spatial variation in the severity of each fire as well as marked variation in severity between individual fires.

Unlike some areas of temperate and boreal North America, which support early-successional specialist bird taxa (e.g., Murphy and Lehnhausen 1998, Hutto 2006), there are few unique bird assemblages closely associated with recently burned habitats in any of the vegetation types at Booderee National Park or similar places elsewhere in coastal eastern Australia. A possible exception is the Ground Parrot (*Pezoporus wallicus*), which can quickly colonize burned heathland and sedgeland; however, it may then occupy these areas for many years (Keith et al. 2002).

Survey design and permanent site establishment

Important spatial data on vegetation cover, fire history, and other variables have been captured in a Geographic Information System (GIS) that has been developed for Booderee National Park (ArcView, ESRI, Redlands, California, USA). Using these spatial data, we established a protocol for site selection at the commencement of this project by identifying important stratifying variables. The three stratifying variables that we selected were: (1) vegetation, classified into 10 vegetation types (see Appendix A); (2) fire history, classified into four classes of time since the last fire (0–10 years, 11–20 years, 21–30 years, and >30 years); and (3) future burning, assigned to two classes (areas designated for prescribed burning between 2002 and 2006 under the management plan for Booderee National Park and those to remain unburned). We manipulated the GIS to overlay vegetation and fire history maps to form “homogeneous” polygons characterized by each of the three classifying factors. We mapped these polygons and then calculated the area of each polygon. We created a list of all polygons and constructed a table of counts (classified by vegetation, fire history, future fire, and polygon area [ha]). We selected a stratified random sample of polygons for study after excluding polygons that contained places sacred to the local Wreck Bay Aboriginal Community and polygons measuring <1.5 ha in size, which were too small to contain a valid (100 m long) straight-line survey site. The selection process that we employed ensured that: (1) the full range of vegetation type by fire history and by future burning classes was represented; (2) there was replication of each class with a focus on replication of the most common classes; (3) there was a good geographic “spread” of selected polygons throughout the national park to avoid potential problems with geographic bias (see Fig. 1); and (4) the number of samples was generally proportional to the total area occupied by each class. As a result, the rarest combinations were represented only twice (for example, woodland that had not been burned for more than 30 years), whereas the most common combination (woodland last burned between 11 and 20 years previously) was represented nine times. We were acutely aware that this approach risked missing the detection of the fire responses of rarer species.

Using the GIS, we produced a set of geo-location points and hard-copy maps of selected polygons to ensure that each polygon could be precisely located on the ground. We then established one 100 m long permanent straight-line site within each selected polygon. Our choice of site length was influenced by the substantial heterogeneity in vegetation cover at Booderee National Park, where abrupt changes in vegetation type often occur over a short distance.

We permanently established a total of 110 field sites, each consisting of star picket markers set at 0-, 20-, 40-, 60-, 80-, and 100-m points. We estimated and recorded

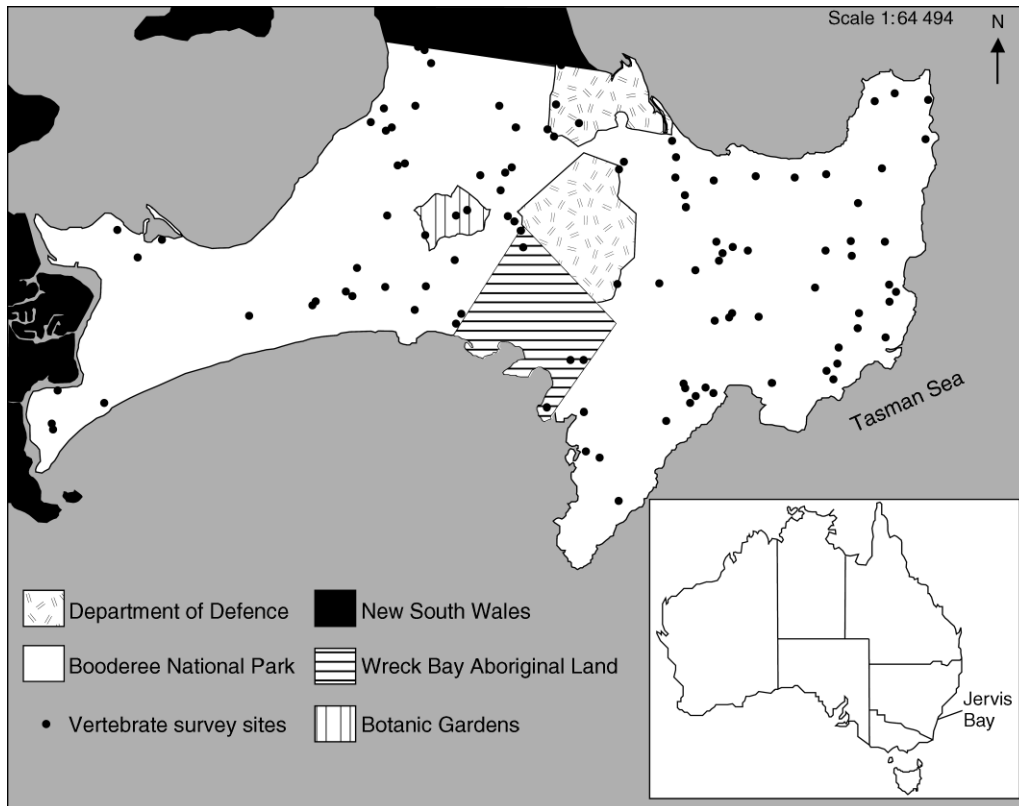


FIG. 1. The general location of Booderee National Park in the Jervis Bay Territory and the location of field survey sites (circles) in Booderee National Park, Australia.

the coordinates of the first and last point at each site using a global positioning system.

2003 wildfire

Following establishment of all 110 sites in our study and the completion of bird counts in September 2003 (see below), a wildfire in late December 2003 burned ~50% of Booderee National Park. The fire was lit by an arsonist and started at a location that was the approximate midpoint of Booderee National Park; 59 sites were burned at varying levels of severity (see below and Appendix A). We repaired the infrastructure on all our damaged sites and recommenced surveys of all burned and unburned sites in early 2004. However, the prescribed burning program planned for Booderee National Park was modified and the objectives of the study that we report here were altered to focus on the impacts of fire history dating back to 1972 and the effects of the 2003 fire on birds.

Bird counting protocols

We completed two visits of 5 minutes each at the 20-m and 80-m permanent points placed along the 110 sites, for a total of 440 point-interval counts (*sensu* Pyke and Recher 1983) annually. We recorded all birds seen or heard within a polygon and assigned observations to

different distance classes from a point: 0–25 m, 25–50 m, 50–100 m, and >100 m. The survey protocol that we used was specifically designed to quantify site occupancy and for our statistical analyses, we did not assume that individual counts at the two points on the same site were independent. Each site was surveyed on a different day by a different observer to reduce day effects on detection and to overcome potential observer heterogeneity problems (Cunningham et al. 1999, Field et al. 2002). We completed surveys in late September each year, which is the breeding season for the majority of species and when summer migrants have arrived.

Vegetation data and other covariates

In addition to the stratifying (design) variables just outlined, we measured a number of covariates (see Appendix B) and used them as potential explanatory variables in statistical modeling. For example, using past fire-mapping data, we calculated the number of fires in the past 35 years and the time elapsed since the last fire at each site. These data were used in modeling bird response to fire history.

We established vegetation plots measuring 20 × 20 m in size at the 20–40 m and 60–80 m points at each site to gather covariates for use for modeling of the response of birds to the fire in 2003 (see Appendix B). We measured

site-based and other covariates in 2004 (immediately after the December 2003 fire) and again in late 2005 (immediately after the 2005 bird counts).

We recognized five categories of fire severity for the 2003 fire. We based this classification on two criteria. The first was the direct effects on vegetation cover: 0, no fire; 1, understory burned; 2, midstory burned but not killed; 3, midstory killed; 4, midstory killed and overstory burned. The second was based on the extent of damage to metal tags attached to the top of each of seven star pickets established at 20-m intervals along our 100 m long sites (zero damage = no fire; damage class 5 = a melted marker tag). For areas characterized by a mix of fire severities, we chose the one that was dominant.

We used aerial photography coupled with ground-based surveys to gather landscape-context data in 200 m and 500 m radius concentric circles around each of our 110 field sites (Appendix B). These data included an estimate of the amount (ha) of burned vegetation in each vegetation type in these areas around each of the 110 sites. Finally, we gathered a range of measures of floristic composition and vegetation structure at each of the 110 survey sites (see Appendix B).

Bird life history attributes

Several studies have shown that avian responses to disturbance can be linked with life history attributes (e.g., Hansen and Urban 1992, Woinarski 1999, Brawn et al. 2001). Given this, we collated data from the literature on life history and other attributes for each bird species. We summarized data on body mass, group type (solitary, pairs, or flock), social system (monogamous, polygamous, and so on), type of nest (cavity, cup, mud bowl, and so on), nest placement (horizontal fork, ground, and so on), nesting height, number of eggs laid in a clutch, broods per year, movement behavior (resident vs. migrant, latitudinal or altitudinal migrant), and foraging guild.

Statistical analysis

We omitted one site located in the Booderee Botanic Gardens from the statistical analysis because the site is highly modified and supports a number of plant taxa that are not locally endemic.

To test species richness responses, in the first stage of statistical analysis, we explored relationships between fire history and observed bird species richness at a site. For each combination of year and site, we calculated the total number of species that were observed. We fitted quasi-Poisson generalized linear models (McCullagh and Nelder 1989) with a log-link function to observed species richness and we used deviance ratio tests to assess the statistical significance of the contributions of site attributes such as the number of past fires and the time since fire, as well as the effect of the fire itself.

We investigated the response of the bird assemblage to the 2003 fire in the second phase of our analysis. We used correspondence analysis (Greenacre 1984, Digby

and Kempton 1987) to explore our data sets and identify which bird life history attributes were linked significantly with bird responses.

In the third phase of data analyses, we quantified the responses of individual species to the 2003 fire by plotting longitudinal (temporal) profiles based on bird observation frequencies. We then examined whether detection frequencies for individual species differed significantly between sites that were burned in 2003 and those that were not.

Finally, we constructed statistical models of the factors influencing the detection of a subset of three species recorded between 2003 and 2006. Each species was relatively common and represented one of three broad types of longitudinal response curves that we identified (Appendix D). We used generalized linear models (GLM) (McCullagh and Nelder 1989) assuming a quasi-binomial distribution and a logit-link function, to model the probability of observation and hence determine the significance and nature of individual species' responses to temporal effects, vegetation type, vegetation structure, fire, and other effects. The number of variables was always an order of magnitude less than the number of sites. We assessed models using a modified version of the Schwarz information criterion (Schwarz 1978), $(\text{deviance}/f) + p \log_e n$, where deviance is the residual deviance and f is the scale parameter estimated from fitting the GLM, p is the number of parameters estimated, and n is the number of observations. After a model had been selected it was refitted as generalized linear mixed model (GLMM) (McCulloch and Searle 2001) to allow for the spatial site to site component of variance. We tested the statistical significance of effects using the method of Kenward and Roger (1997). We discarded terms that were found to be nonsignificant at this stage.

RESULTS

Observed species richness and fire history

We recorded 104 bird species from 39 families over the four years of repeated field surveys; Appendix C lists their common and scientific names. Prior to the 2003 fire, we recorded 71 species across our 110 survey sites. The observed species richness detected on an individual site varied from one to 24 species.

To quantify relationships between observed bird species richness and fire history, we first examined observed species richness-vegetation type interrelationships. We found that observed bird species richness varied significantly ($F_{9,99} = 5.1$, $P < 0.001$) among vegetation types (Table 1). We found that *Casuarina* woodland had the highest observed species richness (19.8 ± 2.8 species, mean \pm SE) and it was substantially higher than other kinds of vegetation such eucalypt forest (14.2 ± 1.2 species) and eucalypt woodland (12.4 ± 1.0 species) (Table 1). The most structurally simple vegetation type (sedgeland) was characterized by mod-

erate levels of observed species richness (12.1 ± 1.7) (Table 1).

We found that observed species richness at a site in 2003 was significantly ($F_{1,99} = 6.30$, $P = 0.014$) negatively related to the number of fires since 1972; sites that had been burned more frequently had the fewest species. We found that species richness per site was 8.7% lower (95% confidence interval, 1.8–15.1%) for each additional fire. The relationship between the number of fires and observed species richness was similar across vegetation types, although some kinds of vegetation rarely burned over the past 35 years (Fig. 2).

We explored our pre-2003 observed bird species richness data for relationships with other potential explanatory variables but none was identified. For example, we found no significant relationship between observed species richness and time since fire.

Observed species richness relationships after the 2003 wildfire

After the 2003 fire, we found that the only significant covariate effects for observed species richness, apart from vegetation type, came from: (1) fire severity, which had a significant negative effect on observed species richness ($F_{4,106} = 7.70$, $P < 0.001$; see Fig. 3), and (2) the percentage of unburned vegetation within 500 m of a site, which had a significant positive effect on observed species richness ($F_{1,82} = 5.72$, $P = 0.019$).

Pre- and post-2003 observed bird species richness in burned and unburned areas

Our pre-2003 fire data for observed species richness in the 10 vegetation types provided the basis for subsequent comparisons between both (1) burned and unburned areas and (2) pre-2003 fire and post-2003 fire levels of observed species richness for each vegetation type. We observed similar numbers of species across all sites combined in the years after the fire: 76 species in 2004, 63 in 2005, and 69 in 2006. However, we identified significant (see Table 2) differences in observed species richness between burned and unburned sites for some vegetation types. In 2004, these were dry shrubland, wet shrubland, sedgeland, wet heathland, and woodland. In 2005 and 2006, the difference between burned and unburned sites was significant only for sedgeland.

We found that wet heathland and wet shrubland sites had not returned to prefire levels by 2006. However, the differences in observed species richness between burned and unburned wet heathland and wet shrubland sites were statistically significant only for 2004. For the sedgeland sites, we note that there was a significant difference between burned and unburned sites for sedgeland in 2003 prior to the fire, indicating that these two groups of sites already differed from each other. Overall in 2003, 25 species were observed on the five unburned sites compared with 30 on the burned sites. The corresponding figures were 16 and 31 species in 2004, 12 and 24 species in 2005, and 14 and 25 species in

TABLE 1. Fitted values for bird species richness prior to a major wildfire in 2003 from a quasi-Poisson generalized linear model with vegetation type as the only predictor.

Vegetation type	Species richness for a single site	SE
<i>Casuarina</i> woodland	19.8	2.78
Rain forest	15.1	1.92
Low shrubland	14.8	2.20
Wet shrubland	14.5	2.67
Forest	14.3	1.21
Woodland	12.4	1.03
Sedgeland	12.1	1.71
Dry shrubland	9.3	1.42
Wet heathland	8.4	1.53
Dry heathland	7.8	0.87

2006. We could not explain the reduction in observed species richness in terms of the loss of particular individual species, with the absence of different species on different sites in different years. As an example, the Yellow-faced Honeyeater was observed on burned sites in 2004 and 2006 but not in 2005.

Our data do not provide any convincing evidence that the immediate effects of fire persisted beyond the year after the fire. In the case of sedgeland, the differences observed in 2005 and 2006 were similar to those observed prior to the fire.

Bird assemblage responses

We explored patterns of response of the bird assemblage by analyzing data gathered for birds that were recorded on a reasonably common basis. Our criterion for selection was detection on 20 or more occasions (~1%) out of a maximum possible 1760 detections (110 sites \times 2 plots per site \times 2 observers/site/year \times 4 years), and this resulted in the inclusion of 36 species in the bird assemblage. When we applied correspondence analysis (Greenacre 1984) to the matrix of bird detection counts for each year separately, we found that the first component was strongly related to vegetation type; in particular, it was consistently related to the complexity of the vegetation, especially as measured by the number of vegetation layers.

The scores for the first component for the species in different years were highly correlated (greater than 0.7 for all pairs of years), but for the second component only the scores for 2003 and 2006 were highly correlated ($r = 0.79$). This suggested that on the one hand there was considerable stability in community structure, and that on the other hand, reductions following the fire in 2003 had largely disappeared by 2006. Scores for sites in different years had quite low correlations. This indicated that there was not a strong association between bird assemblages and particular sites.

The first component of correspondence analysis for all combinations of sites and years had the same interpretation as the first component for individual years, whereas the second component represented a gradient from species which appeared to prefer unburned sites to

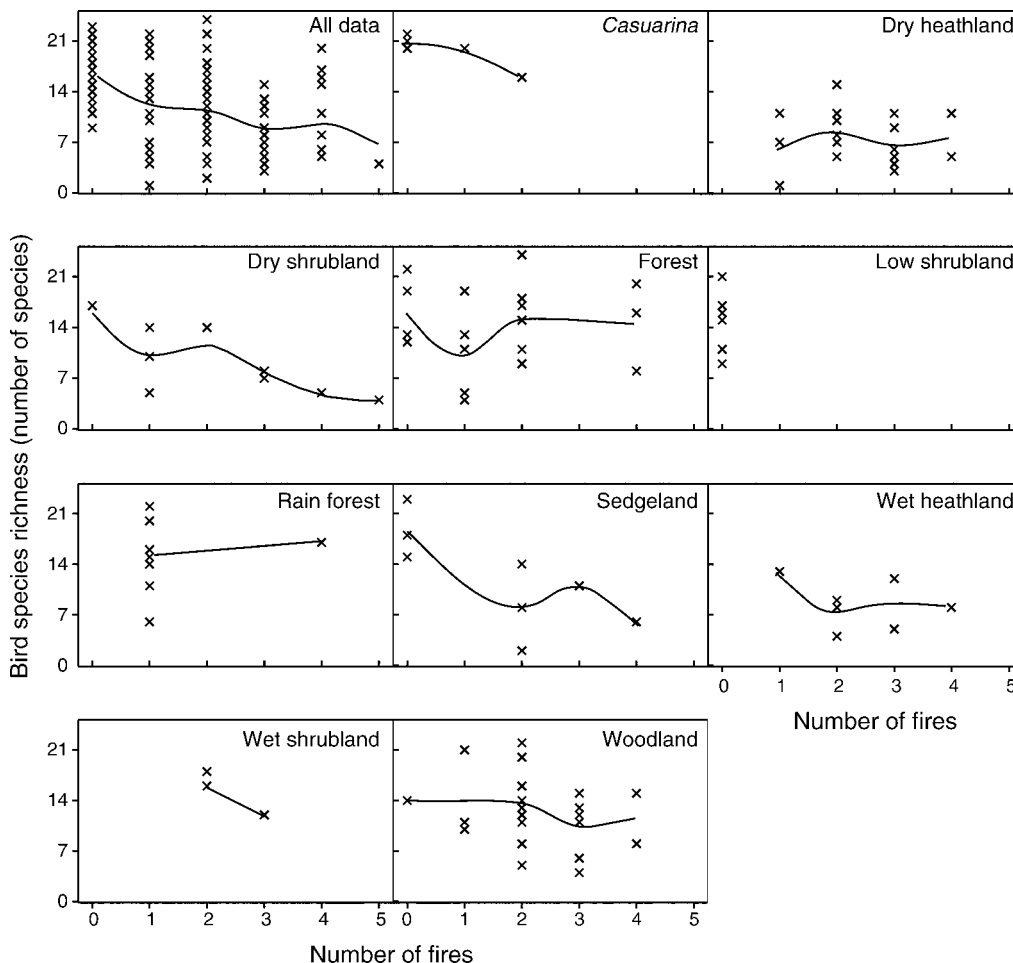


FIG. 2. Relationship of bird species richness in 2003 with the number of fires for different vegetation types. The solid line reflects a fitted relationship to the data. Crosses correspond to individual sites.

those which appeared to tolerate medium-severity burning (Fig. 4).

In an additional set of analyses of the bird species assemblage, we sought to determine if there were relationships between bird life history attributes and bird responses as derived from correspondence analysis. We found significant relationships between the first dimension scores and maximum nest height ($F_{1,34} = 16.5$, $P < 0.001$) and type of nest ($F_{4,31} = 5.5$, $P = 0.002$). There was a clear distinction between dome nests with a low score and bowl, hollow, and suspended purse nests with a high score. Cup nests had an intermediate score. Some other life history attributes, such as dispersal ratio, exhibited a statistically significant relationship with the first component, dispersal ratio ($F_{1,34} = 7.21$, $P = 0.011$), cube root of body mass ($F_{1,34} = 4.64$, $P = 0.039$), and mean length of wing ($F_{1,34} = 5.30$, $P = 0.28$). We found no significant relationship between the second component of correspondence analysis and any bird life history attributes.

Longitudinal responses of individual bird species after the 2003 wildfire

We plotted longitudinal responses to fire severity (including no burning) for all individual bird species after the 2003 wildfire, except those that were observed on 15 occasions or fewer (Appendix D). We identified four broad types of longitudinal responses. (1) For many species, the response curves in less severely burned areas were very similar to those in unburned areas (e.g., Striated Thornbill and Fan-tailed Cuckoo). Some species exhibited a general trend for an overall increase in detection over time (e.g., Eastern Spinebill and Silveryeye), whereas the opposite was apparent for others (e.g., Rufous Whistler, Noisy Friarbird, and White-browed Scrubwren) (Appendix D). (2) Few species exhibited significant interactions between temporal differences in detection and burn severities (e.g., Shining Bronze-Cuckoo [$F_{8,203} = 3.1$, $P = 0.003$]). In this case, detections in 2006 for burned sites were significantly lower ($F_{1,94} = 32.4$, $P < 0.001$) than on unburned sites.

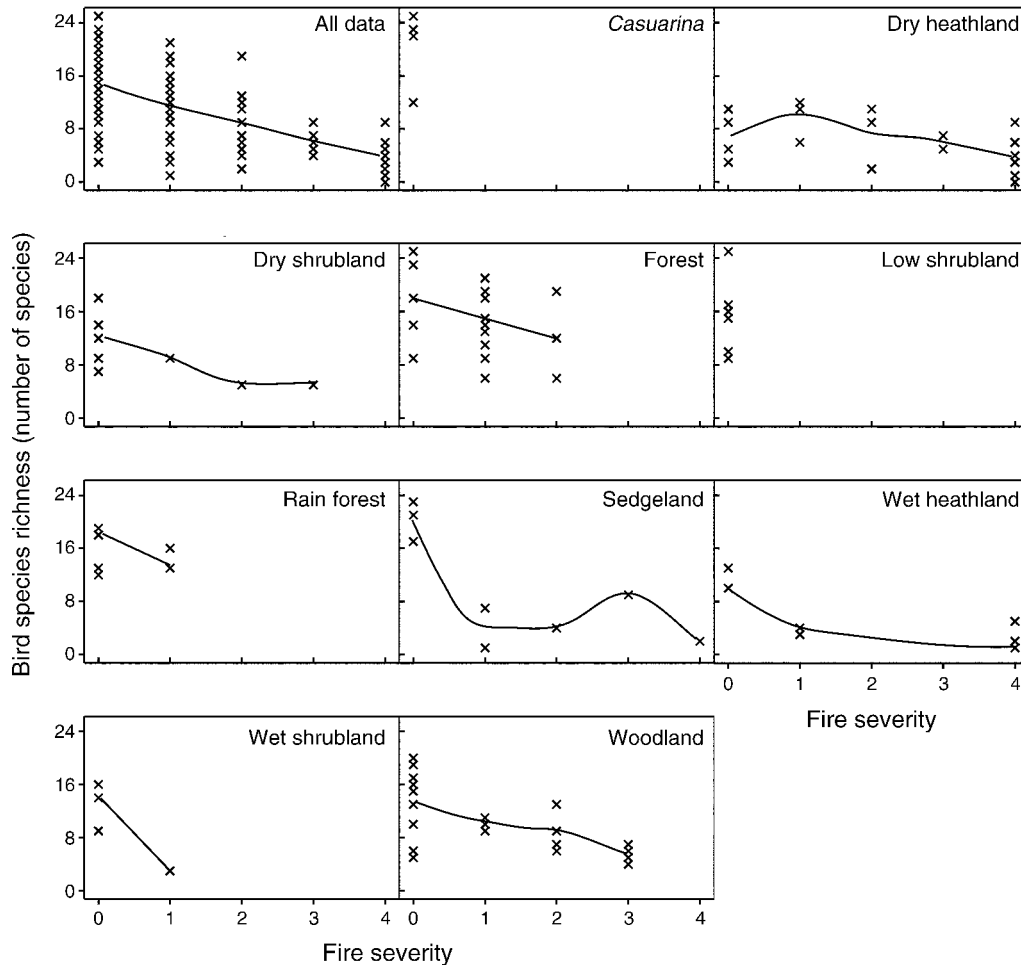


FIG. 3. Bird species richness in 2004 in relation to fire severity for different vegetation types. Fire severity categories (see text) are: 0, no fire; 1, understory burned; 2, midstory burned but not killed; 3, midstory killed; 4, midstory killed and overstory burned. The solid line reflects a fitted relationship to the data. Crosses correspond to individual sites.

They also had not returned to prefire (2003) levels by 2006 (Appendix D). (3) Detections for a number of taxa declined steeply initially after the fire but then returned rapidly to prefire levels, typically by 2005 (e.g., Eastern Yellow Robin, White-throated Treecreeper, and Eastern Bristlebird) (Appendix D). (4) Some species exhibited a spike in postfire detections in unburned sites, mirroring the reduction in burned sites (e.g., Golden Whistler and New Holland Honeyeater). The Australian Raven and Laughing Kookaburra exhibited the opposite response; decreasing detections on the unburned sites but increasing in the burned sites (Appendix D). We based these results on F tests derived from fitting GLMMs to pairs of years.

Individual bird species models

We modeled three species with responses broadly typical of the broad types of longitudinal profiles summarized in Appendix D: the Eastern Whipbird (*Psophodes olivaceus*), the Eastern Yellow Robin (*Eop-*

saltia australis), and the Rufous Whistler (*Pachycephala rufiventris*).

We found that detections of the Eastern Whipbird on burned sites fell on all sites in 2004, but by 2005, detections on the burned sites had returned to 2003 levels only to fall again in 2006. Analysis of data from 2004, 2005, and 2006 indicated that a number of fire-related variables had a significant influence on the detection rate for the Eastern Whipbird. In particular, we found that the species was significantly more likely to be recorded on sites with higher amounts of unburned vegetation in the surrounding 500 m ($F_{1,120} = 35.5$, $P < 0.001$), and sites that were closer to areas of unburned vegetation ($F_{1,185} = 6.9$, $P = 0.010$) (Table 3). The Eastern Whipbird also was more likely to be recorded on sites with lower values of elevation ($F_{1,114} = 4.4$, $P = 0.037$) and higher numbers of understory plant species ($F_{1,271} = 9.1$, $P = 0.003$).

We omitted wet heathland sites from model-fitting for the Eastern Yellow Robin because it was uncommon on

TABLE 2. Temporal changes in bird species richness for five vegetation types following fire in 2003 (after the 2003 survey) compared to unburned sites.

Vegetation type and survey year	Bird species richness			z †	Significance (P) of effect†
	Unburned	Burned	Difference		
Dry shrubland					
2003	9.9	7.6	2.4	-0.86	NS
2004	12.1	6.3	5.8	2.00	0.045
2005	8.8	9.2	-0.4	-0.15	NS
2006	8.0	0.5	-1.6	-0.56	NS
Wet shrubland					
2003	15.3	12.0	3.3	0.54	NS
2004	13.0	3.0	10.0	2.05	0.041
2005	13.6	4.0	9.6	1.92	NS
2006	10.3	7.0	3.3	0.72	NS
Sedgeland					
2003	18.6	8.0	10.6	2.99	0.003
2004	20.3	4.5	15.8	4.74	<0.001
2005	11.3	4.5	6.8	2.70	0.007
2006	12.7	3.7	8.9	3.47	0.001
Wet heathland					
2003	10.5	7.6	2.9	0.92	NS
2004	11.5	3.0	8.5	3.26	0.001
2005	6.0	3.8	2.2	1.03	NS
2006	8.5	4.2	4.3	1.74	NS
Woodland					
2003	11.3	13.1	-1.8	-0.88	NS
2004	13.2	7.9	5.3	2.96	0.003
2005	11.5	12.1	-0.6	-0.29	NS
2006	9.1	9.7	-0.6	-0.33	NS

Notes: These tests are based on estimated effects prior to back-transformation. The effects divided by their estimated standard errors were assumed to be normally distributed. The approximate of F tests of Kenward and Roger (1997) give almost identical results because the effective denominator degrees of freedom were greater than 165 in every case.

† From GLMM fit.

them. We found that observations of the species declined significantly on burned sites between 2003 and 2004, but not on unburned sites. The best model for this species for observations in 2004, 2005, and 2006 included only one explanatory variable, percentage of leaf litter ($F_{1,180} = 14.0$, $P < 0.001$). The fitted model (with mean \pm SE) for probability of observation, p , was

$$\text{Logit}(p) = -2.29(\pm 0.235) + 0.01682(\pm 0.00450)\% \text{Leaf Litter}.$$

The Rufous Whistler exhibited a considerable decline in abundance immediately after the 2003 fire for all sites, burned and unburned. Low abundance persisted on sites with few midstory species but recovered where there were more midstory plant species (Table 4). This interaction was highly significant ($F_{3,305} = 30.7$, $P < 0.001$). There was also a significant reduction in abundance as the number of vegetation types within 500 m increased ($F_{1,89} = 8.0$, $P = 0.006$), the coefficient in the linear predictor being -0.45 ± 0.161 .

DISCUSSION

To quantify bird response to fire, we used both a retrospective study encompassing many sites with well-

known fire history dating back 35 years and a prospective natural experimental approach comprising many burned sites surveyed before and after fire that were contrasted with matched unburned sites. In addition, we reported findings at the population, bird assemblage (community), and species (individual and all species combined) levels. We then related these results to postulates based on widely applied theories and concepts. On the basis of this approach, we identified several unexpected findings. Two in particular were: (1) the rapidity of the recovery of the bird assemblage and most individual taxa after a single (2003) fire, but a significant effect of fire history as reflected by lower observed species richness on sites where there had been a number of fires over the past 35 years; and (2) vegetation type differences in the response of bird species richness that were opposite to those anticipated on the onset of our investigation. We discuss these and other key results in further detail in the remainder of this paper.

Fire and bird species richness

We postulated at the start of this study that, based on the intermediate-disturbance hypothesis (sensu Connell 1978), we would observe the highest levels of observed

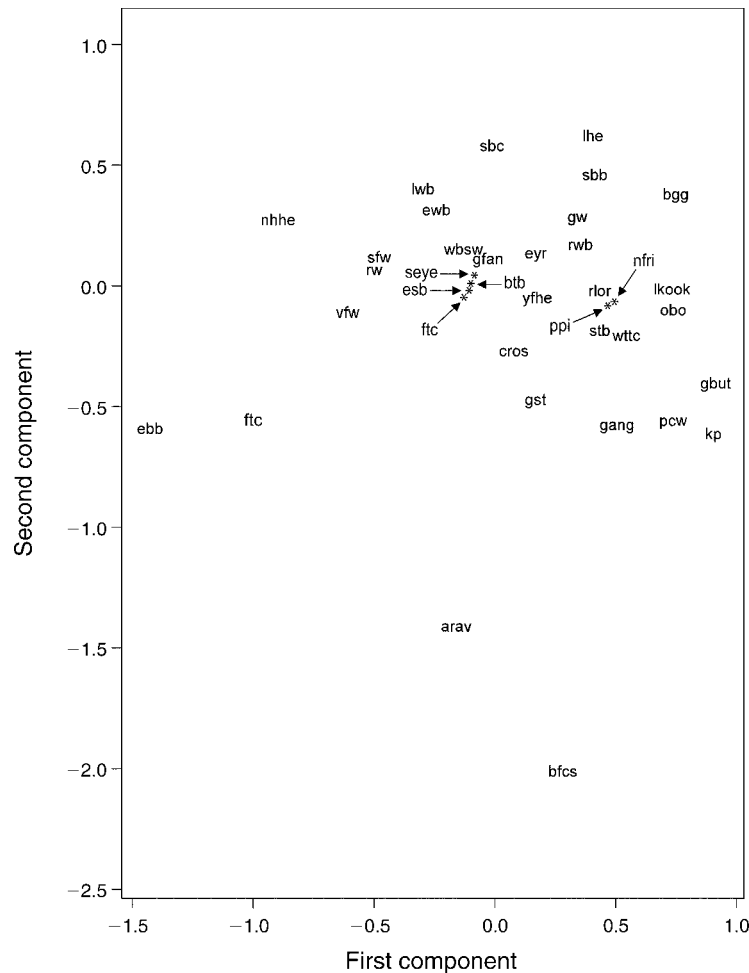


FIG. 4. First two components for species from correspondence analysis of data for all combinations of sites and years. See Appendix C for abbreviation codes for individual bird species. The first component strongly reflected the influence of vegetation type on the bird species assemblage, in particular, a contrast between structurally complex vegetation types such as forest and woodland vs. more simply structured sedgeland and wet heathland. The second component reflected a contrast between bird species that preferred unburned sites and those that tolerated sites subject to medium-severity fire.

species richness at sites subject to intermediate numbers of fires (2–3 fires since 1972) and an intermediate period of time since fire (~12–16 years). We also anticipated that the highest observed species richness might occur on sites burned in 2003 that were subject to intermediate levels of fire severity. A normal bell-shaped curve would be apparent as a result of such relationships (Wilson 1994). We found no substantive evidence to support such patterns for birds in any of the vegetation types studied. Observed species richness declined significantly at a site with an increasing number of fires over the past 35 years, irrespective of vegetation type (Fig. 2). Similarly, we showed that observed species richness declined with increasing fire severity at sites burned in 2003 (Fig. 3), although for the vast majority of vegetation types, the return to prefire levels was rapid and was almost complete by 2005. Hence, the rapidity of return to pre-2003 fire levels prevented any opportunity

for a normal-curve-shaped pattern of observed species richness response to have developed. The findings of our investigation add weight to the work of others that suggest empirical support for the intermediate-disturbance hypothesis is inconsistent (e.g., Collins 1992, Schwilk et al. 1997, Bascompte and Rodriguez 2000, Beckage and Stout 2000, Schurbon and Fauth 2003).

TABLE 3. Coefficients and standard errors for logistic regression model for observations of the Eastern Whipbird (*Psophodes olivaceus*).

Term	Estimated coefficient	Standard error
Constant	-1.11	0.136
Percentage unburned vegetation within 500 m after 2003 fire	0.016	0.00436
Elevation (m)	-0.0082	0.00391
Number of understory species	0.084	0.0280

TABLE 4. Fitted observation rates for the Rufous Whistler (*Pachycephala rufiventris*) for varying numbers of midstory plant species for the four years of survey (linear predictor \pm its standard error in parentheses).

Year	Number of midstory plant species		
	0	3	5
2003	0.22 (1.24 \pm 0.220)	0.19 (-1.47 \pm 0.205)	0.16 (-1.69 \pm 0.340)
2004	0.02 (-4.14 \pm 0.394)	0.03 (-3.49 \pm 0.283)	0.06 (-2.84 \pm 0.409)
2005	0.02 (-3.74 \pm 0.321)	0.10 (-2.16 \pm 0.359)	0.36 (-0.56 \pm 0.704)
2006	0.01 (-4.53 \pm 0.430)	0.07 (-2.62 \pm 0.395)	0.33 (-0.71 \pm 0.819)

Notes: Values were derived from a quasi-Poisson generalized linear mixed model with site as a random effect and year, number of midstory plant species, and number of vegetation types within 500 m as fixed effects. The relationship between the observation rate and the predictors was assumed to be linear on the logistic scale.

Observed bird species richness, vegetation complexity, and postfire response

An additional area of work in this study was the relationship between vegetation type, species richness, and postfire observed species richness. Based on research by MacArthur and MacArthur (1961) and Recher (1969) demonstrating relationships between species richness and the vertical complexity of the vegetation, we postulated that prefire observed bird species richness would be highest in the most vertically complex vegetation types, but after the 2003 wildfire it would take longer in these vegetation types to return to prefire levels. Our prefire data showed broad relationships between vertical complexity and species richness; woodland and forest supported a higher average number of species than structurally more simple vegetation types such as sedgeland, heathland, and shrubland (Table 1). However, the relationship was not particularly strong, as the most structurally simple vegetation type, sedgeland, had intermediate levels of observed species richness (Table 1).

Our postfire data produced a more unexpected result, opposite to that postulated at the beginning of the investigation. That is, although observed bird species richness in structurally complex vegetation types had returned to prefire levels by 2006, it had not in more structurally simple types like sedgeland sites. A possible explanation for our findings for birds is that the speed of bird recovery might be more closely allied with differences in plant recovery mechanisms (Noble and Slatyer 1981, Gill et al. 1999) than with initial (prefire) vegetation complexity. Vegetation response in areas such as woodland and forest has largely been via epicormic resprouting from the trunks and large branches of trees, the vast majority of which survived the 2003 fire and quickly began resprouting. Structurally complex vegetation cover has characterized these vegetation types and this may be a key factor contributing to the rapidity of postfire bird response. Conversely, many plant species in sedgeland have regenerated from seed shed during and immediately after the fire, and the structural recovery of the vegetation has been slower than in other vegetation

types. This highlights the fact that bird species' responses to fire must first be underpinned by a good understanding of the relationships between birds and vegetation type.

Many previous studies of fire and vertebrate responses have contrasted burned and unburned areas and generally have overlooked fire severity in areas that have been burned (but see Smucker et al. 2005, Kotliar et al. 2007) and the patchiness of the vegetation within boundaries of a burned area (Schmiegelow et al. 2006). However, several recent investigations have highlighted the importance of quantifying fire severity in studies of disturbance effects on avifauna. For example, Smucker et al. (2005) and Kotliar et al. (2007) described interspecific differences in response to fire severity. Kotliar et al. (2007) showed that many taxa exhibited positive or neutral responses in density within 1–2 years of fire, even in locations where fire severity was moderate to high. Some of these outcomes are consistent with those of our study, including sites burned at high severity in 2003. We identified significant negative effects of the severity of the 2003 fire on observed species richness, but despite an incomplete postfire bird assemblage in sedgeland, for most other vegetation types observed bird species richness rapidly returned to prefire levels after the 2003 wildfire. We identified similar patterns for many individual species. Thus, in common with the results of Kotliar et al. (2007), we found that many species could tolerate the effects of one moderate-to-severe fire.

Our findings for the rapid response of the bird assemblage following the 2003 fire were in marked contrast to the results of many studies of northern temperate and boreal forest. In some of these northern temperate and boreal ecosystems, particularly those where high-intensity disturbances are stand-replacing events, areas can take prolonged periods to regenerate after perturbation (Burton et al. 2003, Shatford et al. 2007). These areas can be floristically and structurally distinct from mid- and late-successional stands (Franklin et al. 2002, Franklin and Agee 2003, Fraser et al. 2004). They also can support a suite of early-successional species (Hutto 1995, 2006, Brawn et al. 2001,

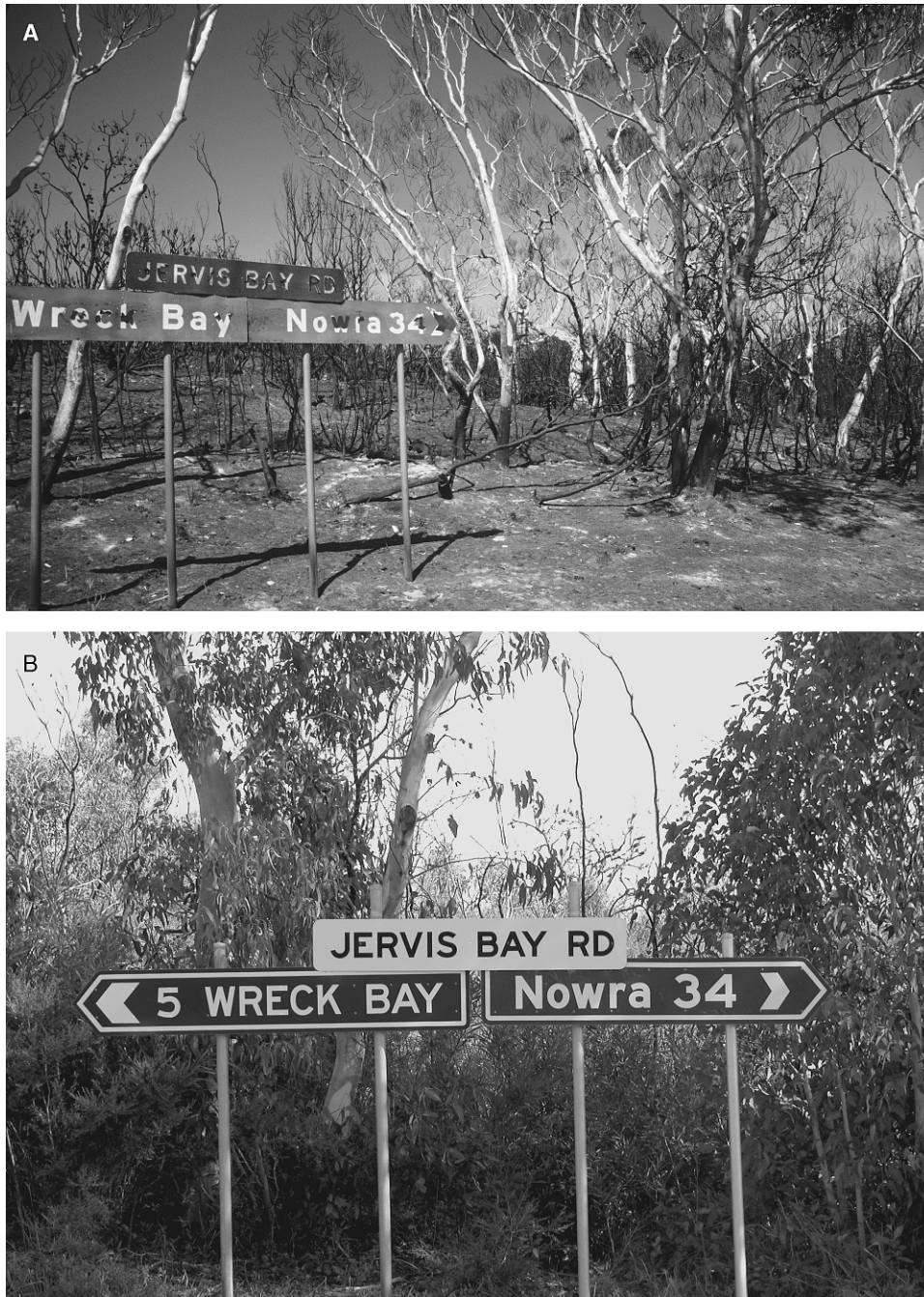


FIG. 5. Location close to the 0 m point of a woodland site in Booderee National Park that was surveyed for birds repeatedly between 2003 and 2006: (A) two days after high-severity fire (category 3) in December 2003 at the site and (B) three years after the 2003 fire (photo credits: D. Lindenmayer and C. MacGregor).

Imbeau et al. 2001, Hoyt and Hannon 2002, Smucker et al. 2005).

By contrast, the majority of vegetation types that we studied generally recovered quickly and this, in part, may explain why they are characterized by few, if any, specialist early-successional birds. A paucity of early-successional specialists also would explain why the

composition of the bird assemblage was little changed over the duration of our investigation. Postfire conditions, particularly high levels of rainfall, appear to have promoted vegetation growth and structural regeneration and, in turn, aided bird species recovery in most vegetation types (Fig. 5). It is notable that our field measurements of the vegetation suggest that vegetation

layers in forest and woodland vegetation types have returned to pre-2003 fire levels, although not in others such as sedgeland, where bird responses have been slower. We also note that the use of the term "recovery" is inappropriate for a number of individual bird species because detection rates for them changed little both before and after the 2003 fire and between burned and unburned areas (Appendix D). This occurred even on those sites subjected to high-severity fire in 2003.

Biological legacies and bird responses

Several studies have highlighted the importance of biological legacies in shaping the post-disturbance responses of plants and animals (Foster et al. 1998, Turner et al. 2003). Our findings further underscore the importance of biological legacies. The amount of unburned vegetation in the area surrounding a site was a significant explanatory variable in logistic regression models for observed species richness in 2004 (immediately following the 2003 wildfire) and also in statistical models developed for a number of individual species (e.g., the Eastern Whipbird; Table 4). In addition, we found the response curves for some species in less severely burned areas were similar to those in unburned areas (Appendix D). These findings suggest that the presence of biological legacies either facilitates the persistence of a given species on a site following a fire (see Whelan et al. 2002) or promotes the return of some species to pre-disturbance levels (Turner et al. 2003, Lindenmayer et al. 2005). We note, however, that species richness and density may be misleading indicators of habitat quality (van Horne 1983) because of factors such as nest predation or habitat patches being inhabited by one sex only (Temple and Cary 1988). Further detailed studies of breeding success and other population parameters (e.g., see Zquette et al. 2000) would be required to establish if these measures are related to the presence of birds at a site. However, our data suggest that at many sites, populations of some species such as the Eastern Bristlebird have been increasing in the past two years (D. B. Lindenmayer, *personal observation*).

Assemblage patterns and life history attributes

We identified interesting patterns for the bird assemblage that contained several findings consistent with our results for observed species richness and for some individual bird taxa. The first component of correspondence analysis (Fig. 4) strongly reflected the influence of vegetation type on the bird species assemblage, in particular, a contrast between structurally complex vegetation types such as forest and woodland vs. more simply structured sedgeland and wet heathland. Notably, scores for the first component for the species in different years were highly correlated (>0.7 for all pairs of years), indicating stability in bird community composition. We were able to link particular life history attributes (nesting height and nest type) to

these outcomes. We expected these life history responses because more species of birds are likely to nest higher in taller forest and woodland vegetation. In addition, structural features such as tree hollows are also more prevalent in these vegetation types (reviewed by Gibbons and Lindenmayer 2002), which would account for the significant relationship that we observed.

We found that the second dimension of correspondence analysis reflected a contrast between birds that preferred unburned sites to those that tolerated sites subject to medium-severity fire. We also found that the impacts on bird community structure of the 2003 fire had largely disappeared by 2006. No life history attributes were associated with the second component of correspondence analysis. A number of studies have highlighted strong relationships between plant life history attributes and sequences of fires (e.g., Noble and Slatyer 1980). However, attempts to identify clear and readily predictable associations between animal responses and fire have not been particularly fruitful in Australia (Whelan et al. 2002). Outcomes are often site specific, and it is possible there may not be a set of "vital attributes" (*sensu* Noble and Slatyer 1980) that determines responses for animals as there has been hypothesized for plants (Whelan et al. 2002, Bradstock et al. 2005). As in the case of work on the rapidity of postfire response, our findings for relationships between life history attributes and animal responses to fire are in marked contrast to those from the temperate and boreal forest ecosystems of the northern hemisphere. In those environments, there are often predictable relationships between postfire habitat, animals, and their life history attributes (e.g., Raphael et al. 1987, Imbeau et al. 1999, Saab et al. 2007). The reasons for such differences are not immediately clear but they may be associated with the rapidity of postfire vegetation recovery. This would, in turn, limit the spatiotemporal availability of suitable habitat for early-successional specialists in the vegetation types that we studied. Another possible reason for differences might be that the findings we have reported are based on a single major study. Additional studies from areas similar to the one in our investigation would be required to strengthen the inference of fire responses we have drawn.

Management implications

Integrating fire management and biodiversity conservation is a challenging task because of the many factors that must be considered, particularly when the protection of human infrastructure is one of the objectives of management. These challenges are set to become harder as many researchers suggest that climate change will increase fire frequency (e.g., Cary 2002, Lenihan et al. 2003, Westerling et al. 2006). Nevertheless, we believe that the results of our study have some important implications for improved fire management practices.

First, because we found that observed species richness at a site was significantly negatively related to the

sequence of past fires (Fig. 2), we suggest that an informed approach to strategic spatial and temporal fire management may be to ensure that there are some areas exempt from additional planned prescribed fires. In particular, areas that have experienced several fires (e.g., three or more) over the past 35 years might be those where prescribed fire might be excluded. We also believe that there may be a need to target the protection of particular vegetation types such as those where the return of observed species richness (or particular individual taxa) to prefire levels is slowest. For example, in the case of Booderee National Park, efforts might be best focused on sedgeland and wet heathland, where our data suggest that the return to prefire bird species richness levels has been slowest (Table 2). Of course, this recommendation is not a generic one that can be applied uncritically to all ecosystems. For example, it would not apply in the many vegetation types around the world where prolonged fire suppression has had negative impacts on biodiversity and the proactive use of fire management is important (Zackrisson 1977, Harrington and Sanderson 1994, Covington 2003, Ehle and Baker 2003, Spies et al. 2004).

A second key finding from our work that has management implications is the relationship between the amount of unburned vegetation surrounding a site and the observed species richness, as well as the persistence of individual species on sites. Almost all wildfires are inherently patchy, leaving unburned and partially burned areas (Turner et al. 2003, Kulakowski and Veblen 2007). Such landscape heterogeneity is known to be important for the maintenance of biodiversity (De Long and Kessler 2000), although it is not always clear which spatial mosaic of patch types is the most appropriate one (Bradstock et al. 2005, Parr and Andersen 2006). To maintain landscape heterogeneity, we believe that one objective of prescribed burning might be to maintain some unburned areas with the perimeter of such controlled fires.

Our data on the importance of the amount of unburned vegetation surrounding a site also may have implications for the suppression of wildfires. In some jurisdictions, fire suppression activities involve "black-out" burning or burning out fuel between a fuel break and a fire. We believe that such practices might need to be carefully managed in places where the conservation of biodiversity is one of the objectives of management. This is because "blackout" burning may lead to a loss of landscape heterogeneity (Backer et al. 2004) with the potential to negatively influence postfire responses of some elements of the biota.

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APPENDIX A

Description of vegetation types at Booderee National Park (*Ecological Archives* A018-072-A1).

APPENDIX B

Covariates measured at the transect, plot, and subplot level and in polygons around each site (*Ecological Archives* A018-072-A2).

APPENDIX C

List of birds recorded in repeat surveys in Booderee National Park (*Ecological Archives A018-072-A3*).

APPENDIX D

Response curves highlighting temporal changes in detections of bird species as a function of fire severity (*Ecological Archives A018-072-A4*).