

Draft of Vesk, P.A., Mac Nally, R., Thomson, J.R., Horrocks, G., 2008. Revegetation and the significance of lags in the provision of habitat resources for birds, In *Landscape Analysis and Visualisation: Spatial Models for Natural Resource Management and Planning* eds C. Pettit, W. Cartwright, I. Bishop, K. Lowell, D. Pullar, D. Duncan, pp. 183-210. Springer, Berlin.

## **Revegetation and the significance of timelags in provision of habitat resources for birds**

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Running Header: *Revegetation and bird resources*

**Keywords:** landscape reconstruction, habitat suitability, woodland birds, land use decision, restoration, biodiversity

### **Abstract**

In many approaches to landscape visualisation and reconstruction for biodiversity management, vegetation is represented as being either present or absent. Revegetation is assumed to be possible, and new vegetation appears ‘immediately’ in a mature state, which is likely to drastically overestimate habitat suitability in the short-term. We constructed a simple temporal model of resource provision from revegetated agricultural land to estimate habitat suitability indices for woodland birds in south-eastern Australia. We used this model to illustrate the trajectory of change in biodiversity benefits of revegetation. As vegetation matures, its suitability for a given species changes, so a time-integrated assessment of habitat value is needed. Spatial allocation strategies, such as offsets, that may provide high value habitat in the long-term but imply shorter term population bottlenecks from a paucity of key resources (e.g. tree hollows) must be avoided. Given that vegetation may not meet both foraging and breeding requirements of a given species, populations may be limited continuously — by foraging constraints at some times, and by breeding constraints at other times. Animal species differ in their resource requirements so that optimisation involves compromises among species. Temporal processes associated with revegetation and differences in resource requirements of species complicate landscape reconstruction. Nevertheless, our analyses suggest that the time course of vegetation development must be incorporated in models for optimising landscape reconstruction and for calculating revegetation offsets.

### **Introduction**

Land use decisions rest upon models of system responses. These models may be implicit or explicit and their focus may range from social and economic to physicochemical and ecological. In this volume are many contributions emphasising spatial or visualisation approaches to modelling land use change with a view to decision support. These have tremendous potential as humans are visual creatures and landscapes are inherently spatial.

Envisioning the outcomes of land use decisions could have massive potential for supporting better

decisions. Our point of departure in this chapter is to ask what revegetated landscapes might look like *for biodiversity* 20, 50, 100 or 200 years in the future. We don't know how other organisms see the world (Smith this volume), but through habitat modelling we can try to project the suitability of a landscape for supporting persistence of one or more species.

Most of the contributions to this volume that are concerned with visualisation are necessarily simplistic in their treatment of the ecological aspects; areas are selected for revegetation, trees grow, animals return and thrive. In this contribution we emphasise the ecological detail and necessarily ignore spatial and visualisation aspects. Importantly, we point out how thinking about what species need in landscapes and the time course of change helps to understand the outcomes of land use decisions and to point to making effective decisions for improving the status of biodiversity in agricultural landscapes. In time, the ecological and visualisation approaches will inevitably become better integrated, for the benefit of understanding landscape change.

The limited extent of native vegetation in the 'wheat-sheep' regions of south-eastern and south-western Australia is insufficient to sustain native biodiversity (Barrett et al. 2003; Mac Nally 2007; Recher 1999; Robinson and Traill 1996), and extensive revegetation is needed (Mac Nally 2008; Saunders and Hobbs 1995; Vesk and Mac Nally 2006). While some progress toward broad-scale revegetation has been made, areas revegetated are orders of magnitude too small (Freudenberger et al. 2004; Huggett 2007). If we assume that responsible agencies must act to counter the potential meltdown of terrestrial biodiversity in these regions of southern Australia, we now must consider how to plan for 'landscape-scale' restoration, which we call *landscape reconstruction* (Bennett and Mac Nally 2004; Huxel and Hastings 1999; Lambeck 1997; Westphal and Possingham 2003; Westphal et al. 2007).

In most existing approaches to landscape reconstruction, vegetation is represented as a binary variable (present/absent), revegetation is assumed to be feasible, and new vegetation appears 'immediately' in a mature state (Mac Nally 2008). Timelags in reconstruction can translate to substantial declines of biota in fragments (Martínez-Garza and Howe 2003; Vesk and Mac Nally 2006). Explicitly factoring maturation time into restoration planning becomes imperative when we contemplate areas where regrowth of native vegetation is likely to be very slow (due to poor nutrients or little water) and where existing vegetation is senescing. These conditions are widespread in southern Australia, as well as many parts of Africa, Eurasia and North and South America. Empirical models of habitat resource provision demonstrate century-scale timelags in development of some key resources in Victorian woodlands, such as large boughs for nesting, tree hollows and fallen timber (Vesk et al. 2008).

Here, we recognise explicitly that timelags and species-specific habitat requirements strongly influence the success of landscape reconstruction for biodiversity conservation. Therefore, we examine the temporal dimension of habitat restoration through revegetation on potentially retirable agricultural land. We use a simple model of habitat suitability for woodland bird species defined by breeding and foraging resources provided by *Eucalyptus* woodland habitats during revegetation. We believe birds are a useful taxon for this approach because:

- birds respond to the amount and arrangement of vegetation at the scales of human activity, for example, clearing, retention and revegetation (10–10,000 ha) (Radford et al. 2005; Trzcinski et al. 1999)
- birds are the most species-rich vertebrate taxon in these regions
- knowledge of ecological requirements of bird species is rich
- data on species' distributions is extensive (Barrett et al. 2003; Radford and Bennett 2007; Thomson et al. 2007).

We define 'habitat' as a set of resources provided by vegetation (Dennis et al. 2003), focussing on vegetation structure through time rather than floristic succession. We construct a generalised 'Habitat Suitability Index' (O'Connell et al. 2000), which we parameterise for different species individually based on literature accounts of species ecology. We then use this model to identify temporal dynamics that are crucial for planning revegetation actions in box-ironbark (*Eucalyptus* spp.) woodlands of northern Victoria, Australia.

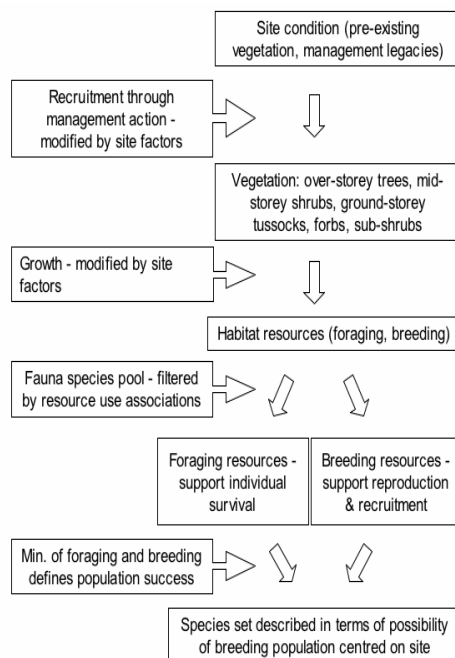
## Methodology

Model details are extensive so we have gathered these together in the Appendices. This means that the minutiae will not detract from the general flow. We are generally concerned with the agricultural landscapes of southern Australia which are primarily woodlands and open forests dominated by eucalypt trees. Specifically, here we model the responses of grazed or cropped grassy box-ironbark forests and woodlands of northern Victoria (Lunt and Bennett 2000). These were extensively cleared for grazing and cropping over the past 200 years of European agriculture. More information about the study system can be found in Vesk and Mac Nally (2006), and about historical modification of vegetation structure in Lunt et al. (2006).

## Model description

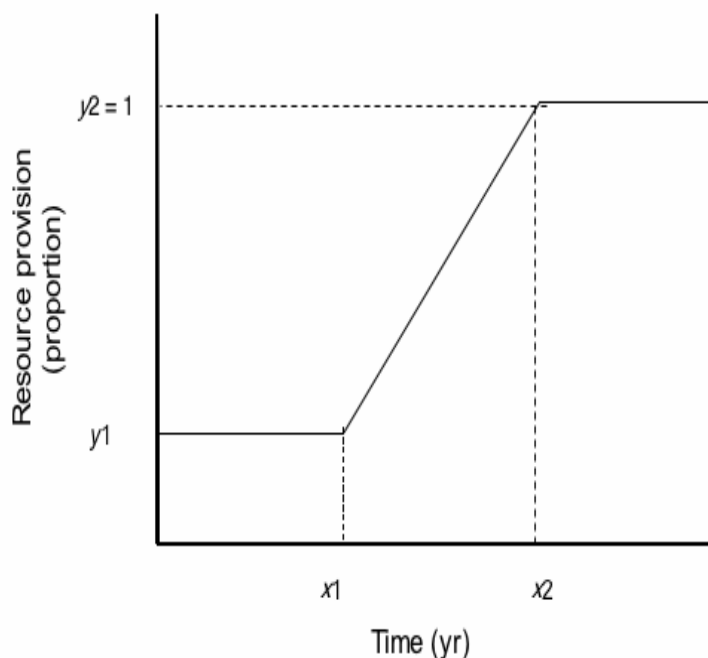
As vegetation grows it provides required habitat resources for birds (Fig. 1). The better these requirements are satisfied by the resources produced by vegetation, the higher the suitability for the bird species. The model is focused on local resource provision through time. Spatial configuration was not considered, although clearly it is important for some species (Radford et al. 2005). The 'unit' modelled was a site of approximately 1 ha, which frequently is the area of revegetation sites (Freudenberger et al. 2004).

We modelled two cohorts of vegetation, an extant mature cohort and a cohort recruiting from revegetation actions on land formerly cleared for agriculture. Site conditions reflect management legacies through effects on soil structure (including compaction) and fertility (including sodicity and acidity), seed banks and weed loads. Recruitment of new vegetation results from two possibilities: active revegetation (direct seeding, planting tubestock) and from natural recruitment. These were combined into a recruiting cohort. Ongoing management ('business as usual', exclusion of stock) also modifies recruitment rate (Vesk and Dorrough 2006). The detailed model scenarios for sites and management are outlined in Appendix 1.



**Fig. 1.** Flow chart of model of structural dynamics of revegetation and suitability for bird species use

Vegetation was modelled as three layers: ground-storey, shrubs and trees. Each layer grows and provides consumable resources for birds, such as nectar and seeds, and structural resources, such as boughs and tree hollows for nesting (Fig. 1). The same resources could act as both foraging and breeding resources (e.g. fallen timber). Prey resources emerging from vegetation growth — invertebrates, small mammals and birds — also were modelled. Resources were depicted on a proportional scale and accumulated as simple ramp functions of time (delay, linear increase and maximum, Fig. 2). As we accumulate further empirical data on habitat resources, these functions can be replaced with ones resulting from statistical modelling (Vesk et al. 2008).



**Fig. 2.** Diagram of habitat resources through time provided by revegetation. Resources are provided at some initial level,  $y_1$  (usually zero), until time  $x_1$ , when they increase linearly to a maximum,  $y_2$  (usually one), at time  $x_2$ , thereafter remaining at the maximum

Table 1 shows the modelled relationships for habitat resources supplied by new vegetation in the default case, equivalent to seeding of bare ground. The delay is equivalent to  $x_1$  in Fig. 1, time to maximum is time from  $x_1$  to  $x_2$  in Fig. 1. Maximum provision of resources is 1 for all resources; open ground decreases with vegetation growth. Initial provision of all resources is 0; open ground is initially 1.

Ground dwelling and aerial invertebrate abundances do not change with different vegetation and land use, despite compositional changes, and are maintained at 1.

The frequency with which bird species use the resources was expressed proportionally. We coded resource use,  $u$  (0: never, 0.15: rarely or occasionally, 0.65: regularly, 1: most frequently or obligate) from autecological accounts in Marchant and Higgins (1990–2002) (see Appendix 3). These values for resource use frequency were derived using a set of simple rules (see Appendix 4).

**Table 1.** Modelled relationships for habitat resources supplied by new vegetation in default case, equivalent to seeding of bare ground

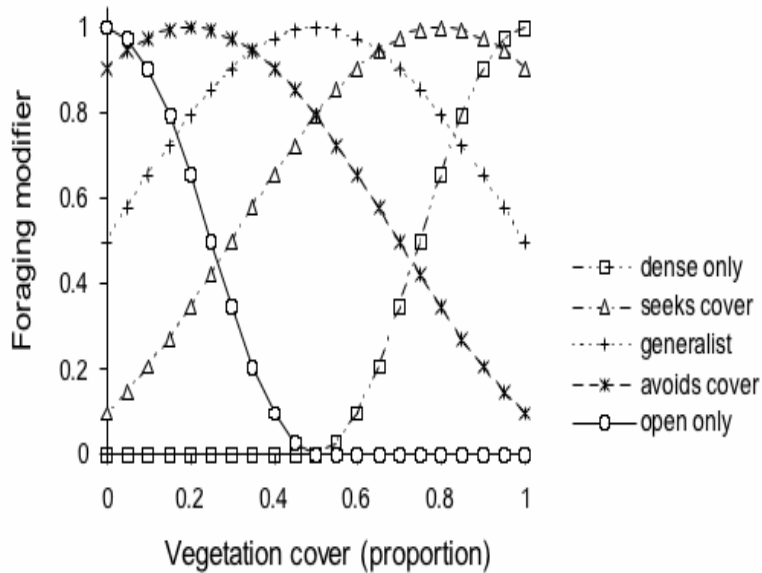
Resource	Delay [yr]	Time to max [yr]	Slope of increase	Basis for relationship <sup>a</sup>
<i>Ground-storey foraging</i>				
Leaves, flowers, seeds	0	4	2.00	
Fallen timber	114	305	0.043	= small hollows
Soil and litter	0	10	0.797	2 <sup>o</sup> , $\Sigma(\text{gl, ml, ol})$
Open ground	1	24	-0.357	
<i>Mid-storey foraging</i>				
leaves, flowers, seeds	0	29	0.286	
Invertebrates	0	29	0.286	2 <sup>o</sup> , (ml)
<i>Over-storey foraging</i>				
Leaves	0	77	0.106	
Flowers/seeds	29	257	0.036	
Canopy invertebrates	0	115	0.071	2 <sup>o</sup> , $\Sigma(\text{ol, ofs})$
Stem invertebrates				2 <sup>o</sup> , $\Sigma(\text{ol, ob})$
Higher prey				
Small ground vertebrates				2 <sup>o</sup> , $\Sigma(\text{gf, gi, gsl, gl})$
Medium arboreal vertebrates				2 <sup>o</sup> , $\Sigma(\text{ol, ofs, ml, mf, oi})$
Small insectivorous birds				2 <sup>o</sup> , $\Sigma(\text{mi, ml, ol, of, oi})$
<i>Ground-storey breeding</i>				
Tussocks	0	4	2.0	= gl
Fallen timber	114	305	0.043	= small hollows
<i>Mid-storey breeding</i>				
Shrub branches	0	29	0.286	= ml
<i>Over-storey breeding</i>				
Leaves and twigs	0	77	0.106	= ol
Tree boughs	43	233	0.043	
Stem bark and fissures	29	138	0.074	
Small hollows <10 cm	114	305	0.043	
Large hollows >10 cm	171	362	0.043	

<sup>a</sup>Relationship codes: g=ground-storey, m=mid-storey, o=over-storey, l=leaves, f=flowers/seeds, i=invertebrates, 2<sup>o</sup>=secondarily supplied from,  $\Sigma$ =sum of.

For a given point in time ( $t$ ) for species  $j$  and a set of resources  $r_i$ , we derived a ‘sufficiency’ ( $S_{jt}$ ) as the summed product of the resources  $r_{it}$  provided by the vegetation and the frequency of use  $u_{ij}$  over the set of resources. This was constrained to a maximum of unity. For tractability, we assume that foraging resources are substitutable. Thus, sufficiency is defined by:

$$S_{jt} = \sum_i (u_{ij} \times r_{it}) \leq 1 \quad (2)$$

Sufficiencies for foraging ( $S_{fjt}$ ) and for breeding ( $S_{bjt}$ ) were estimated separately. Foraging sufficiency was modified by known preferences of bird species for foraging in open or closed vegetation (Appendix 5). Nest site availability is described in Appendix 6. Summed foraging sufficiency  $S_{fjt}$  was multiplied by the foraging cover modifier,  $m_j$ .



**Fig. 3.** Modification of foraging suitability by vegetation cover

A breeding population can occupy the site at a given time only if its minimum requirements for foraging and breeding resources are both provided. That is, we expect foraging and breeding resources to be non-substitutable. Hence, we used the minimum of the values for sufficiency of foraging and breeding resources to estimate the habitat suitability ( $HS$ ) for a species  $j$  as:

$$HS_{jt} = \min(S_{fjt}, S_{bjt}) \quad (3)$$

The model is implemented as a series of look-up tables in a Microsoft Excel® spreadsheet.

Three forms of pre-existing vegetation were used:

- over-grazed, transformed pastures
- croplands
- lightly grazed, grassy woodlands.

Cropping is thought to increase soil erosion and deplete soil seed banks, but increase soil nitrogen from fertilization (Prober et al. 2002).

Overgrazing is thought to reduce soil fertility because of biomass off-take and to degrade soil structure via compaction by livestock (Prober et al. 2002).

## Case study

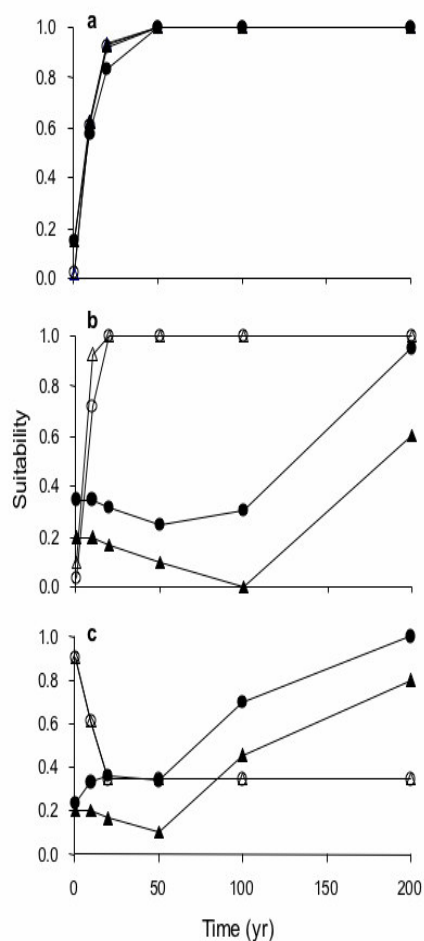
We consider the case of intensive revegetation on grazed grassy box-ironbark (*Eucalyptus* spp.) woodland of northern Victoria, Australia (Lunt and Bennett 2000). The landscape between 150 m and 350 m above sea level, mean annual rainfall ranges from 400mm to 750 mm, and mean daily maximum temperatures vary from approximately 30°C in summer to 12–13°C in winter. We assumed the site initially had remnant, scattered, mature trees following clearing (approximately 1–2 trees/ha), but no juvenile trees or shrubs, as typical of the region. Ground-storey was assumed to be initially a mixture of native perennial and annual grasses and forbs and annual exotic grasses. We assumed intense restoration effort (Schirmer and Field 2000), that is, sites are ripped to improve soil structural characteristics, herbicides are applied, dominant native species in ground-storey, shrubs and trees are direct seeded or planted as tubestock, and management is ongoing (weed control, replacement plantings, thinning, maintenance of shrub and grass populations). Existing mature trees were assumed to die by 100 years from now (Appendix 2; Gibbons and Boak 2002). We modelled 133 bird species

recorded during surveys of the box-ironbark woodlands (Mac Nally et al. 2000; Mac Nally and Horrocks 2002). Species nomenclature follows Marchant and Higgins (1990–2002).

## Results

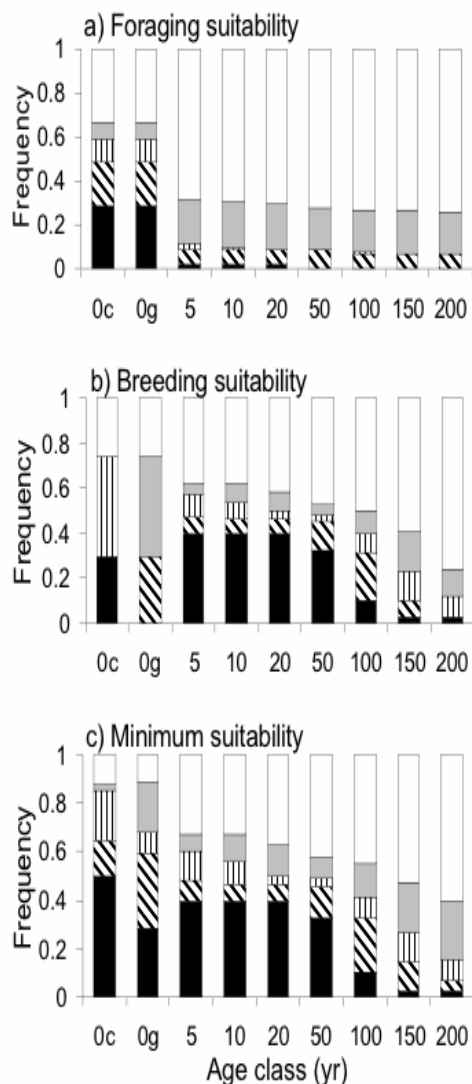
### *Bird species differ in their ability to use revegetation*

We identified several broad patterns of bird species responses to vegetation maturation. Some species benefited from revegetation because both foraging and breeding resources were provided quickly by the maturation of shrubs and trees. These included the yellow thornbill and rufous whistler (Fig. 4a). For other species (e.g. striated pardalote and southern boobook Fig. 4b), foraging requirements were met soon after revegetation but breeding resources, such as tree hollows, developed only after long delays (approximately 150 years). Foraging resources for birds tolerant of open country, such as the Australian magpie and wedge-tailed eagle, were already satisfied, but the suitability of those resources declined as vegetation matured and cover increased (Fig. 4c). Availability of large boughs for nesting decreased as mature trees senesced, but gradually increased with growth of the new cohort of trees.



**Fig. 4.** Habitat suitability for six bird species following revegetation. Suitability of resources for foraging (open symbols) and for breeding (filled symbols). Examples are for a lightly grazed site with 1–2 trees/ha planted with tubestock. (a) Species for which suitability for both foraging and breeding initially is low and increases rapidly; yellow thornbill (△, ▲), rufous whistler (○, ●). (b) Species for which foraging resources initially are poor but increase rapidly, whereas breeding resources initially decline before a slow increase; southern boobook (△, ▲), striated pardalote (○, ●). (c) Species characteristic of open country for which foraging suitability initially is high but declines as vegetation matures and cover increases, whereas breeding resources gradually increase after an initial delay; wedge-tailed eagle (△, ▲), Australian magpie (○, ●)

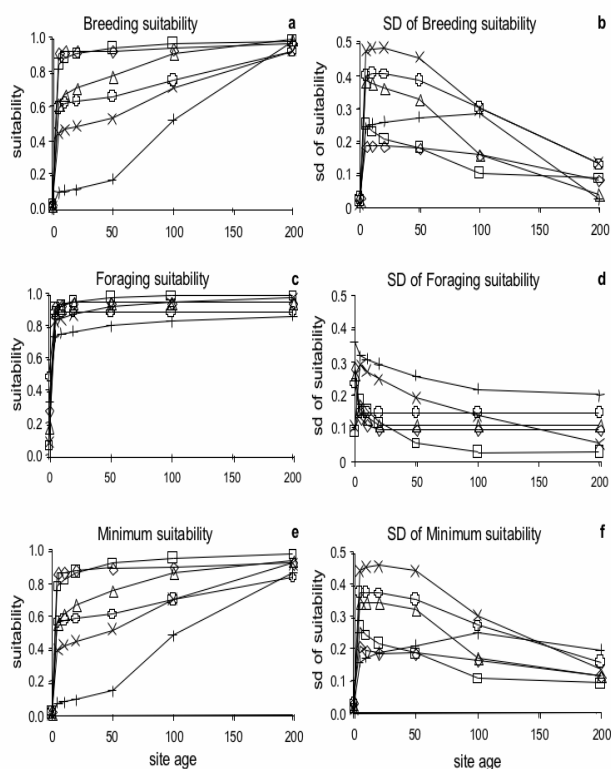
Summaries over the whole avifauna show that foraging sufficiency increased rapidly for most species, but suitability increased more slowly for a small number of species (Fig. 5a). Breeding suitability was much slower to improve over the entire avifauna (Fig. 5b). The minimum of foraging and breeding broadly reflected the change in suitability for breeding (Fig. 5c).



**Fig. 5.** Habitat suitability for 134 bird species of box-ironbark forests and woodlands over time after intensive revegetation on an overgrazed site, lacking shrubs and trees, summarised in classes. Suitability values classed as follows, black–very low,  $S < 0.2$ ; diagonal hatching–low,  $0.2 \leq S < 0.4$ ; vertical hatching–medium,  $0.4 \leq S < 0.6$ ; grey–high,  $0.6 \leq S < 0.8$ ; white–very high,  $0.8 \leq S < 1.0$ . Age classes 0c and 0g are cropped site and grazed grassy woodland, respectively.

Representations of habitat suitability for selected functional groups demonstrated that expected suitability is more variable for breeding than for foraging, and the minimum suitability reflects suitability for breeding (Fig. 6a, 6c, 6e). This echoes the pattern in overall suitability and highlights the importance of breeding resources. Breeding suitability for hollow-nesting birds and frugivores is slow to increase, while suitability for canopy foragers and ground foragers improves more rapidly. The

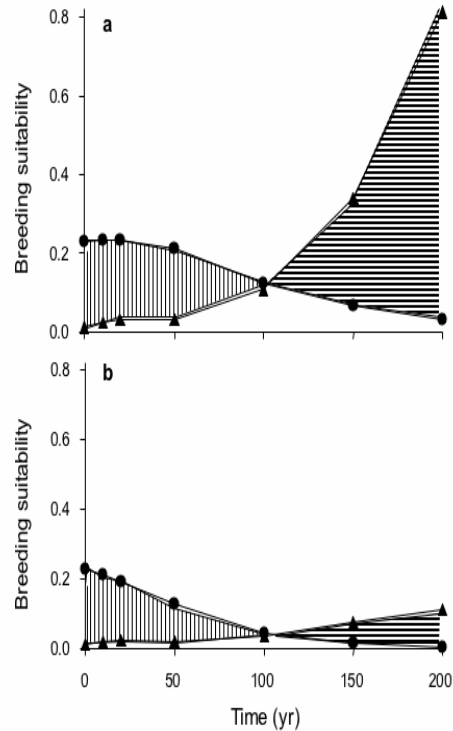
variation of breeding suitability within functional groups tends to be greater for groups defined by foraging than by groups defined by breeding (Fig. 6b), whereas foraging suitability is more variable within a group defined by breeding than those groups defined by foraging (Fig. 6d).



**Fig. 6.** Average suitability (a, c, e) and standard deviation of suitability (b, d, f) for breeding, foraging and their minimum for selected functional groups of 96 species of box-ironbark woodland birds. The modelled scenario was for intensive revegetation on an overgrazed site, lacking shrubs and trees. Symbols as follows: 41 species of ground foragers,  $\diamond$ ; 26 species of small birds (<30 g) foraging amongst canopy,  $\square$ ; 18 species of small birds that forage on bark,  $\triangle$ ; 18 species of mid-storey foragers,  $\circ$ ; 18 species of frugivores,  $\times$ ; 13 species of hollow-nesters,  $+$

### **Comparing strategies over time: species that require old trees**

Here we consider the decision whether to actively revegetate a cropland site or to destock a lightly-grazed site (see also Dorrrough et al. 2008). In cleared lands being grazed, there are few trees and therefore few large boughs and tree hollows; large boughs and tree hollows are absent from cropland. Many bird species nest in large boughs or tree hollows that develop after 50–150 years (see Fig. 6, Gibbons and Lindenmayer 2002). These birds are of conservation concern because boughs and hollows upon which they depend are few and declining, and quick replacement is unlikely. Availability of these resources declines as mature trees senesce, even were grazing livestock removed (‘destocking’, Fig. 7a), because of low recruitment and long timelags in resource development. The aim of planting trees is to replace senescing trees and supplement low rates of natural recruitment. However, breeding resources from revegetated cropland sites will not be available for a long time. A comparison of the provision of breeding resources for large-bough- and hollow-nesters by destocking a grazed site (cheap) against intensively planting a cropland site (expensive) is shown in Fig. 7a. Destocking a grazed site is superior over the first century before old trees senesce, but intensively planting a cropland site is superior after 100 years when the planted cohort matures (Fig. 7a).



**Fig. 7.** Average breeding suitability for 26 bird species that nest in either large boughs or in tree hollows. Triangles represent an intensively revegetated cropland (ploughing, weed control, tubestock and replacement). Circles represent a lightly grazed, low productivity site with scattered trees that has been fenced and destocked. (a) Integrating over time (the areas under the curves) demonstrates that revegetation on the broad-scale crop site has greater value (horizontal hatching) than destocking the grazed site (vertical hatching). (b) Discounting future value at 1% p.a. reduces the value of the planting on broad-scale cropland relative to vegetation on destocked grazing land.

We believe that for assessing the value of vegetation, or for comparing revegetation alternatives, integration of resource suitability over time (e.g. 200 years) is better than calculating suitability at any single time (Gibbons and Lindenmayer 2007; Mac Nally 2008). A trajectory of habitat quality over time provides a curve, the area beneath which can be used to compare strategies (Fig. 7a). In this example, intensive replanting provides a greater time-integrated value than destocking alone (Fig. 7a). However, future value should be discounted because populations cannot take advantage of the resources unless they persist until the resources become available. Bottlenecks in the medium term may lead to local extinction irrespective of the quality of habitat in the more distant future. Using a future discount rate of 1% per annum, the distant future value of intensive planting is substantially decreased whereas the near future value of destocking is little changed (Fig. 7b) (Drechsler and Burgman 2004). Under this logic, destocking is preferred.

## Discussion

When envisioning landscapes for natural resource management, vegetation is a surrogate for native biodiversity. In essence this requires that future landscapes support viable populations of species. For the general public, biodiversity concepts often translate most strongly to mammals and birds, rather than insects, for example. Species' responses to changing landscapes can be modelled through a rules-based approach as used here, with population demographic models, or statistical models of spatial distribution. Our work highlights the opportunity to use extensive existing knowledge on bird species'

ecology together with a simple model of habitat suitability, that is, animals need to feed and to breed to maintain viable populations. This is appropriate when there is no sound reason to select one focal species over others.

Explicit population demographic modelling, which explicitly addresses population viability, requires intensive study to estimate demographic parameters, and thus is likely to be limited to one or few species. Statistical modelling of species distribution requires substantial surveys of species occurrence across the landscape and is limited in extrapolation beyond the sample population, that is, we can't project to 100 year old revegetation if we have none in the landscape currently. Also, occurrence does not necessarily imply population viability. All these approaches are useful for projecting biodiversity benefits of revegetation and constraints thereupon, and all move us away from a simplistic conceptualisation where biodiversity restoration is assumed possible, instant and perfect. The challenge then is to integrate this into envisioning of spatial land use scenarios.

In this work, we have demonstrated how important ecological processes and principles can be when analysing land use change scenarios. Our model is heuristic so we would not have great confidence in the precision or accuracy of predictions about any particular species and scenario. However, by making reasonable assumptions about how vegetation develops, and how bird species use habitat resources based on textbook ecology, we have drawn out some implications of temporal change in vegetation resulting from revegetation activities that we believe are quite general. We see this as contributing to a future integration of spatial models of vegetation change and ecological responses into spatial scenario analyses.

We emphasise five main ecological points based on these analyses:

- First, as revegetation matures, availability of habitat resources increases and the proportion of open ground decreases, so suitability of revegetation for different native species changes through time.
- Second, species differ in responses to habitat change, and so, particular revegetation actions will favour species differentially.
- Third, at any given time, and at any given site, vegetation may not provide both foraging and breeding resources for a single species. If foraging resources are limited at some times, and breeding resources at others in the maturation sequence, the population may remain continuously limited (Fig. 4c).
- Fourth, time lags in development of some resources, such as peak floral production by eucalypt trees and tree-hollow formation, are considerable, in the order of decades to centuries (Gibbons and Lindenmayer 2002; Wilson and Bennett 1999; Vesik et al. 2008).
- Fifth, assessing suitability of revegetation for target species requires integration over time-to-maturation and perhaps should include consideration of future discounting, or some form of complex future benefit function, to avoid solutions that may be good in the distant future but that pass through a prior (deleterious) bottleneck.

As restored vegetation matures, its suitability for different species of birds shifts. This leads to management compromises between species. Summing of suitability values for many species can be unweighted, or weighted by species' conservation concern. Models based on species occurrences may lead to planning of revegetation that satisfies foraging needs but not breeding requirements, and so will allow survival of an individual but not population persistence (Thomson et al. 2007). Long timelags and bottlenecks for crucial habitat resources, coupled with future-discounting, requires acceleration of the development of certain resources, such as hollows, or artificial supplements. The latter option may be very expensive or, in some cases, infeasible (Spring et al. 2001).

## **Caveats and extensions**

We have assumed successful revegetation, yet this is not certain. Many efforts are only partially successful and the ensuing suitability for birds would likely reflect that. Anecdotally, the least successful restoration is of the ground-storey. We have also assumed replacement of ground- and mid-storey species after senescence, which will be over relatively short terms (approximately 30 years). Replacement may require planned disturbance treatments to encourage recruitment. We also have not accounted for recruitment of a second generation of trees after the initial revegetation action.

However, in practice it always is desirable to establish self-recruiting populations because subsequent management may not occur and a key aim should be sustainable systems. Observations suggest limited regeneration occurs in extant plantings (Vesk et al. 2008). We have not modelled disturbances that reset succession, such as wildfires. Although these disturbances would complicate the model, their omission is unlikely to invalidate our main conclusions.

The chosen future discount rates will greatly affect the preferred options (Drechsler and Burgman 2004). It seems necessary to avoid allocation strategies whereby revegetation actions that provide high value habitat in the long-term are proposed to offset loss of current habitat and which lead to short-term population bottlenecks from a paucity of key resources such as tree hollows. Moilanen et al. (in press) highlight the importance of future discounting in calculating habitat offsets.

There are several ways to extend this work. Our spreadsheet model needs to be migrated to computational GIS layers that can be combined with knowledge about individual species' spatial requirements (minimum areas, connections, spatial configurations of breeding and non-breeding habitats) to make better assessments of probable population viabilities through time. We currently are working towards this goal. Some compromises between foraging and breeding resources can be addressed in a spatially explicit model. For example, some birds may use a dense patch of vegetation for breeding and adjacent more open areas for foraging (Law and Dickman 1998). However, other birds and less mobile organisms, such as small mammals and reptiles, may have to use the same patch for foraging and breeding. The use of different patches of habitat implies that scheduling of revegetation activities on sites might be required to maintain a matrix of successional stages (Richards et al. 1999). Existing approaches to scheduling of silvicultural operations and fire management may be helpful (Bever and Hof 1999; Hansen et al. 1993; Richards et al. 1999). Size and isolation of revegetated patches will clearly influence colonisation, population size and time to local extinction (Huxel and Hastings 1999; Lambeck 1997).

Another way forward would be to introduce a vegetation-dynamic element to the spatially efficient landscape reconstruction approach developed by Westphal and Possingham (2003). That work used statistical species-occurrence models based on landscape metrics coupled with estimates of bird densities to model population sizes (and hence persistence) in a reconstructed landscape (Westphal and Possingham 2003; Westphal et al. 2007). The species-occurrence probabilities for each patch could be modified by values for vegetation resources, which in turn, would be dependent on time. Desirable landscapes would have high values for time integrated (future discounted), landscape-level bird populations aggregated across species.

Further extension would be to account for interspecific interactions such as predation and competition, which are known to have strong effects on bird community composition. Given that habitat restoration involves decade- and century-scale ecological processes, we must also consider climate change (Hobbs and Hopkins 1990), which will shift climatic envelopes of plants and animals across the landscape (Root et al. 2003). In 50 years, the climatic envelopes of many species of *Eucalyptus* — the dominant trees in south-eastern Australian woodlands — may not overlap with their current distributions (Hughes 2003; Hughes et al. 1996). Future climates should be considered when selecting long-lived species for revegetation.

In conclusion, we see much scope for the development of spatial analysis and visualisation tools that incorporate ecological processes. This will enable planners and stakeholders to make better informed decisions about land use to accommodate social, economic and ecological concerns. We hope that this chapter contributes to this goal.

## Acknowledgements

We appreciate the contributions of Josh Dorrrough and Erica Fleishman to the development of ideas presented here and for comments on drafts, for which we also thank David Duncan and an anonymous reviewer. We acknowledge funding from the Monash University Research Fund: New Research Areas and from the Australian Research Council LP 0560518 with co-funding from the Victorian Department of Sustainability and Environment, Victorian Department of Primary Industries, North Central CMA, Goulburn-Broken CMA, Mallee CMA and North East CMA, and contributes to the

Key Project 1.1 under the Our Rural Landscapes Initiative of the Victorian Department of Primary Industries. This is contribution number 57 from the Australian Centre for Biodiversity: Analysis, Policy and Management.

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# Appendices

## Appendix 1: Scenarios for sites and management activities

### ***Business-as-usual scenario***

A good condition site assumes 'moderate' grazing history. Initial vegetation: 50% of native ground-storey vegetation, 20% of scattered mature shrubs and trees. Propagule supply is proportional to density, but recruitment, and thus rate of increase, is halved by ongoing grazing. Potential maximum native vegetation components are limited by ongoing grazing and weed competition: 50% in ground-storey and 20% in each of shrub- and tree-storeys.

Cropped sites have no native vegetation. Propagule supply from distant vegetation is 5%, as is recruitment. Maximum native vegetation for each stratum is 0%. Land is subjected to ongoing cropping, removing all native vegetation periodically.

Grazed sites have no native shrubs or trees, but have 20% native ground-storey. Propagule supply is proportional to vegetative density, with 10% of possible tree seeds (assuming well dispersed). Rate of increase (recruitment) is very low, 0.1%, due to continuing intense grazing. Potential maximum native vegetation components are limited by ongoing grazing and weed competition: 20% in ground-storey and 5% in each of shrub- and tree-storeys.

### ***Fencing and destocking***

Fencing and destocking on a good site result in checks of recruitment being removed, so rate of increase is 50% in ground-storey and 20% in each of shrub- and tree-storeys. Fencing and destocking a cropped site results in the cap on native vegetation being relaxed, allowing up to 50% native ground-storey and 80% of shrub- and tree-storeys. Weeds comprise the remainder. Propagule supply still is minimal, as is resultant rate of increase, 5% each stratum. Destocking benefits grazed sites and the rate of increase climbs to 20% in ground-storey, shrubs are unchanged as few propagules arrive and none are present in the seedbank. Trees increase at 10%, matching propagule supply of small seeds.

### ***Direct seeding***

Maximum propagule supply is achieved, as is rate of increase on a good site. On a cropped site, although maximum propagules are supplied, recruitment is reduced by competition with weeds. Rate of increase is 50% in native ground-storey and 80% in shrub and tree strata. Maximum native vegetation cover is capped at 50% ground-storey and 80% shrub and tree strata by weeds abetted by residual fertilizers. On grazed sites, direct seeding saturates propagule supply, but rate of increase is reduced by poor soil structure and fertility due to years of grazer hooves and production off-take (Prober et al. 2002).

### ***Planting tubestock after site preparation and follow up weed control***

Good sites have saturated propagule supply, achieve maximum rate of increase and have enhanced initial vegetation due to planting advanced seedlings: 60% ground-storey, 30% shrub- and 25% tree-storeys. Weed control removes cap on native vegetation in cropped sites, maximum growth rate is achieved, and planting advanced seedling enhances the initial vegetation: 20% ground-storey, 10% shrubs and 5% trees. Grazed sites have soil structure improved by ripping and spot fertilization under planting. So maximum growth rate is achieved and planting tubestock enhances initial vegetation: 25% ground-storey, 10% shrubs and 5% trees.

## Appendix 2: Tree senescence

We follow the reasoning of Gibbons and Boak (2002). Extensive clearing (tree and shrub removal) of woodlands and forests of south-eastern Australia occurred between approximately 1850 and 1900 (Woodgate and Black 1988). We assume that scattered trees remaining in paddocks today were retained because of their value as shade for livestock (Gibbons and Boak 2002). This would mean that the trees were large and mature ( $\geq 100$  years old) when clearing was occurring (1850–1900, at latest). This would result in trees of 200 to 400 years of age in 2000. If we also assume that the lifespan of *Eucalyptus* spp. trees is approximately 400 to 500 years (Boland et al. 1984), then all trees would be expected to die between 2000 and 2300. Most trees would be dead by 2150. Gibbons and Boak (2002) estimated annual mortality rate of paddock trees from a number of studies was 0.54–2.5%. We assume a mid-range value loss of 1.5% of trees per year. For scattered trees at 20% of capacity, this means that decline to 5% of original density will occur by 2090. Even where scattered trees at 50% of tree capacity, a fall to 5% occurs by 2150. Taking these two approaches, we assume that trees will die at 2150.

For shrub- and ground-storeys, we assume that management has established a new equilibrium, that is, population and structure are maintained at current levels by ongoing recruitment.

## Appendix 3: Bird species' resource use

A list of bird species and their resource use compiled from autecological accounts in the Handbook of Australian, New Zealand and Antarctic Birds (Marchant and Higgins 1990–2002) is available from the senior author upon request. Volume 7 (Yellow-breasted Boatbill to Starlings) was unavailable, so for some *Passerinidae* (fam. *Artamidae*, *Pardalotidae*), accounts in field guides and atlases were used (Blakers et al. 1984; Emison et al. 1987; Pizzey and Doyle 1980).

## Appendix 4: Weights

Resource use sufficiency,  $S_j$ , for species  $j$  was estimated using the formula:

$$S_j = \sum_i (u_{ij} \times r_i) \quad (4)$$

for resources  $r_{i=1, \dots, n}$  with resource use frequency,  $u_i$ , at time  $t$ . Values for the  $u_i$  were derived by first classifying resource use frequency from bird species' autecological accounts, such that  $a$  = obligate or most frequently used,  $b$  = used regularly,  $c$  = used occasionally or rarely. Then, values of  $a = 1$ ,  $b = 0.65$ ,  $c = 0.15$  were derived such that the following conditions were met (Table 2).

Table 2. Rules for determining weightings for resources

Verbal rule (to be read as 'when the resource/s is/are maximally abundant ...')	Equation
one most frequently used or obligate resource should suffice	$a_i \times r_i = 1, r_1 = 1$
two regular resources should suffice	$(b_1 \times r_1) + (b_2 \times r_2) \geq 1, r_1 = r_2 = 1$
one regular resource and one-half abundance of a second regular resource should suffice	$(b_1 \times r_1) + (b_2 \times r_2) \geq 1, r_1 = 1, r_2 = 0.5$
less than four occasional resources should not suffice	$\sum_{i=1}^3 c_i \times r_i < 1, r_1 = r_2 = r_3 = 1$

ten occasional resources should suffice	$\sum_{i=1}^{10} c_i \times r_i \geq 1, r_1 = \dots = r_{10} = 1$
One regular and two occasional resources should almost suffice	$0.7 \leq (b_1 \times r_1) + (c_2 \times r_2) + (c_3 \times r_3) \leq 0.95, r_1 = r_2 = r_3 = 1$
One regular and one occasional resource should not suffice	$(b_1 \times r_1) + (c_2 \times r_2) < 1, r_1 = r_2 = 1$
One regular should be better than three occasional resources	$(b_1 \times r_1) > \sum_{i=2}^4 (c_i \times r_i), r_1 = r_2 = r_3 = r_4 = 1$
Five occasional resources should be at least as good as one regular resource	$(b_1 \times r_1) \leq \sum_{i=2}^6 (c_i \times r_i), r_1 = \dots = r_6 = 1$

## Appendix 5: Effects of cover on foraging resource use

Because birds display varied preferences for foraging in different cover environments, the availability of a resources to a bird should be modified accordingly. Bird species were categorised according to foraging responses to shrub and tree cover. We considered whether they require vertical structure, like perches, from which to pounce. Effect of cover on foraging was assigned by Peter Vesk using data from abovementioned literature sources, and Gregory Horrocks using expert opinion. Conflicts were resolved by re-examining bases for the categorisation. If conflict remained and assignments differed by two categories, the middle category was used. If assignments differed by one category, the category closer to the middle (occasional use of open areas) was used. Sine curves were used to characterise foraging responses to vegetation cover. Open areas refer to open grassy areas or bare ground with patchy ground cover (> 100 m x 100 m). Dense cover ( $C \sim 1.0$ ) refers to areas of dense shrub and or tree cover (e.g. closed heath and closed forest, >70% foliage projective cover). Summed foraging sufficiency was multiplied by the foraging cover modifier,  $m$ . These functions appear in Fig 3.

Table 3. Formulae used to modify foraging suitability due to vegetation cover

Foraging response to mid- and over-storey vegetation cover	Formula for foraging modifier $m$ to account for cover $C$
Forages exclusively in open areas or bare ground with patchy grass.	If $C > 0.5$ then $m = 0$ , otherwise $m = \frac{1}{2} \left[ \sin \pi \left( 2C + \frac{1}{2} \right) + 1 \right]$
Regularly forages in open areas but requires some over-storey structure.	$m = \frac{1}{2} [\sin \pi C + 1]$
Occasionally forages in open areas and in dense cover but neither actively avoids nor actively seeks those areas.	$m = \frac{1}{2} [\sin \pi (C - 0.3) + 1]$
Actively avoids open areas.	$m = \frac{1}{2} [\sin \pi (C + 0.3) + 1]$
Forages exclusively in dense cover. If sighted in open areas, only crossing to suitable habitat.	If $C < 0.5$ then $m = 0$ , otherwise $m = \frac{1}{2} \left[ \sin \pi \left( 2C + \frac{1}{2} \right) + 1 \right]$

## Appendix 6: Nesting requirements

### *Ground nesting*

For species that nest on the ground in open areas, increases in vegetation cover reduce nest-site availability. Otherwise, ground nesting sites are assumed to be unlimited. For species that nest in earthen banks, the model assumes there is a bank nearby.

For species that nest on the ground but often under/next to/among tussocks/logs/trees, then nest site availability is not to be determined solely by ground (i.e. unlimited) but by the supplementary resource too. We use 0.65 contribution from ground, which means 0.5 of the supporting resource will suffice, but that 0.25 of the supporting resource will not suffice.

Some species that nest on or near the ground respond either positively or negatively to vegetation cover. Therefore, we used a modifier for the summed nesting sufficiency from ground, tussocks and fallen timber. Species were categorised for their use of open ground nest sites:

- restricted to very open sites (<10% mid- and tree-storey),  $g = 1$ .
- nesting is favoured by some mid- and tree-storeys but is less likely in <10%, less likely at >70% cover,  $g = 0.5$ .
- nesting is reduced at <70% cover and is best at high cover (> 70%),  $g = 0$
- unaffected, not ground nester.

The following formula was used to modify nesting sufficiency for ground nesting birds by the amount of vegetation cover:

$$O = 1 - 1.8 \times |1 - C - g| \quad (5)$$

where  $O$  is the open ground modifier for nesting,  $C$  is cover,  $g$  is the value appropriate for the class of use of open ground nest sites.

### *Cuckoos*

Cuckoos should be not be limited by nest sites providing hosts are present. Hosts are diverse, but particular cuckoos have specific suites of host species:

- pallid and fan-tailed cuckoos parasitise honeyeaters
- Horsefield's bronze, shining bronze and black-eared cuckoos parasitise thornbills, fairy wrens and speckled warblers.