

# Where and when to revegetate: a quantitative method for scheduling landscape reconstruction

J. R. THOMSON,<sup>1,5</sup> A. J. MOILANEN,<sup>2</sup> P. A. VESK,<sup>3</sup> A. F. BENNETT,<sup>4</sup> AND R. MAC NALLY<sup>1</sup>

<sup>1</sup>*Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Clayton, Victoria 3800 Australia*

<sup>2</sup>*Department of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Helsinki, Finland*

<sup>3</sup>*School of Botany, University of Melbourne, Parkville, Victoria 3010 Australia*

<sup>4</sup>*School of Life and Environmental Sciences, Deakin University, Burwood, Victoria 3125 Australia*

**Abstract.** Restoration of native vegetation is required in many regions of the world, but determining priority locations for revegetation is a complex problem. We consider the problem of determining spatial and temporal priorities for revegetation to maximize habitat for 62 bird species within a heavily cleared agricultural region, 11 000 km<sup>2</sup> in area. We show how a reserve-selection framework can be applied to a complex, large-scale restoration-planning problem to account for multi-species objectives and connectivity requirements at a spatial extent and resolution relevant to management. Our approach explicitly accounts for time lags in planting and development of habitat resources, which is intended to avoid future population bottlenecks caused by delayed provision of critical resources, such as tree hollows. We coupled species-specific models of expected habitat quality and fragmentation effects with the dynamics of habitat suitability following replanting to produce species-specific maps for future times. Spatial priorities for restoration were determined by ranking locations (150-m grid cells) by their expected contribution to species habitat through time using the conservation planning tool, “Zonation.” We evaluated solutions by calculating expected trajectories of habitat availability for each species. We produced a spatially explicit revegetation schedule for the region that resulted in a balanced increase in habitat for all species. Priority areas for revegetation generally were clustered around existing vegetation, although not always. Areas on richer soils and with high rainfall were more highly ranked, reflecting their potential to support high-quality habitats that have been disproportionately cleared for agriculture. Accounting for delayed development of habitat resources altered the rank-order of locations in the derived revegetation plan and led to improved expected outcomes for fragmentation-sensitive species. This work demonstrates the potential for systematic restoration planning at large scales that accounts for multiple objectives, which is urgently needed by land and natural resource managers.

**Key words:** *birds; connectivity; conservation prioritization; habitat suitability; landscape-scale optimization for revegetation; restoration planning; time delay; Zonation software.*

## INTRODUCTION

In many regions of the world, restoration of native vegetation is central to rebuilding functioning landscapes and reversing biodiversity declines (Saunders et al. 1993, Hobbs and Harris 2001, Vesik and Mac Nally 2006). Quantitative planning tools are required to prioritize the location and timing of revegetation, given multiple ecological objectives and constraints (Westphal et al. 2003, 2007, Crossman and Bryan 2006, Bryan and Crossman 2008).

Restoration planning poses a similar challenge to systematic planning for reserve selection (Margules and Pressey 2000, Cabeza and Moilanen 2001, Pressey et al. 2007, Wilson et al. 2007) because sites are chosen to maximize one or more biodiversity objectives (or

objective functions), such as abundance or persistence of multiple species across landscapes (Moilanen et al. 2005, Nicholson et al. 2006, Mac Nally 2008). An important difference is that restoration planning must consider locations that currently do not provide habitat (e.g., cleared land) but would do so in the future given sufficient and timely actions. Given the vast areas that potentially could be revegetated, the number of possible landscape configurations is enormous. The problem becomes even more complex when time is considered. Financial and social constraints mean that landscape-scale restoration can occur only over long periods (decades), and lags in vegetation development mean that “restored” habitat for many species may take centuries to mature (Martinez-Garza and Howe 2003, Vesik and Mac Nally 2006, Vesik et al. 2008a, b). Climate change (Cai and Cowan 2008) may retard even these slow schedules of vegetation maturation. Therefore, optimal revegetation planning must consider both spatial and temporal aspects of habitat quality.

Manuscript received 16 May 2008; accepted 13 August 2008.  
Corresponding Editor: R. L. Knight.

<sup>5</sup> E-mail: jim.thomson@sci.monash.edu.au

The future suitability of a site for any species depends on the site's location relative to surrounding habitat, but crucially also depends on local environmental conditions and resources that will change through time as vegetation matures (Barrett et al. 2008, Vesik et al. 2008a, b). Spatial and temporal variability in local habitat suitability largely have been ignored in previous studies on optimal landscape reconstruction (e.g., Westphal et al. 2003, 2007), which have treated habitat as either present or absent. Spatial variability in habitat quality will, along with landscape context, affect optimal placement of new plantings. Optimal spatial configurations and planting schedules also may depend on relative rates of provision of habitat resources, depending on the time frame of interest. For example, immature plantings that provide food but not breeding resources (Mac Nally et al. 2009; Selwood et al. 2009) may need to be located close to remnant vegetation to benefit some species in the short term (decades). An assumption that revegetation "instantly" acts as high-quality habitat may result in plantings that have little biodiversity value until that vegetation "matures" (>100 years), which may be too late for populations of conservation concern (Morris et al. 2006).

Here we consider the problem of large-scale revegetation for bird biodiversity conservation in a rural region in southeastern Australia. Our study focuses on an area of ~11 000 km<sup>2</sup> of the Box-Ironbark region of central Victoria, Australia, where only 14% of original vegetation cover remains (ECC 1997). We seek a quantitatively justified, spatially explicit strategy for landscape restoration based around existing vegetation, which accounts for expected time lags in planting and development of habitat resources. We use the conservation-planning software *Zonation* to determine priority areas for revegetation based upon models of bird distribution (Thomson et al. 2007) coupled with habitat dynamics resulting from revegetation (Vesik et al. 2008a, b).

## METHODS

### *Determining priority areas for conservation using Zonation*

The *Zonation* framework and software for spatial conservation planning includes a range of methods for identifying and evaluating conservation areas (Moilanen et al. 2005, Moilanen 2007). Biodiversity features analyzed using *Zonation* can include predicted or observed distribution data for species or habitat types, including presence/absence, probability of occurrence, and abundance or density. Data usually are input as GIS-based grid maps (raster format), but observed point locations also may be entered. *Zonation* algorithms determine hierarchical conservation priorities for a landscape by starting with the entire landscape and iteratively removing grid cells while minimizing the rate of loss of conservation value. This process can include considerations such as species-specific variation in habitat quality, species priorities (weights), land cost, planning units, species-specific measures of connectivity

(Moilanen et al. 2005, 2008, Moilanen and Wintle 2006, 2007), uncertainty of occurrences (Moilanen et al. 2006a, b), and interactions among conservation features (Moilanen and Kujala 2008). *Zonation* can accommodate comparatively large data sets (Kremen et al. 2008) and is freely available (Moilanen and Kujala 2006, 2008).

### *Application to revegetation planning*

*Zonation* typically is used to rank areas of existing habitat on the basis of distribution maps for many features (Moilanen et al. 2005, Kremen et al. 2008) to produce spatial configurations that retain maximum conservation value for different proportions of habitat loss, while accounting for given connectivity responses and species weights.

Here we address a related but more complex task. We seek to rank areas within the landscape by their potential contribution to future biodiversity, assuming large-scale revegetation. Further, we wish to determine a revegetation schedule that benefits all species over both short and long time frames, and that avoids bottlenecks in population expansion caused by delays in resource provision from the revegetated habitats.

Our basic approach is to start from the hypothetical situation where all candidate areas have been revegetated. We note that complete landscape revegetation is not a realistic or intended objective but is a necessary starting point to evaluate all candidate areas in the approach we have adopted. We then use *Zonation* to simulate "clearing" of candidate revegetation cells iteratively, while minimizing the loss rate of predicted biodiversity, down to the current extent of native vegetation. The resulting cell rankings indicate the expected contribution of each location to future biodiversity, given the current landscape configuration.

### *Analysis outline*

Here, we outline the main steps of the analysis, which are summarized in Fig. 1. Subsequent sections explain the creation of necessary inputs and the results for our case study.

*Step 1.*—Predict the habitat suitability for each species at each location in the landscape at multiple time slices in the future, assuming the entire landscape is planted immediately with native vegetation and that suitability changes as plants grow and the vegetation matures.

*Step 2.*—Perform core-area *Zonation* analysis (Moilanen et al. 2005, Moilanen 2007) based on maps of potential habitat suitability.

A key innovation of our approach is that multiple habitat maps for each species, corresponding to different time slices, are entered together into the same analysis. *Zonation* treats each time-specific habitat map for a species as a separate conservation feature (entity to be conserved), and the core-area algorithm ensures that all such features retain balanced proportional representa-

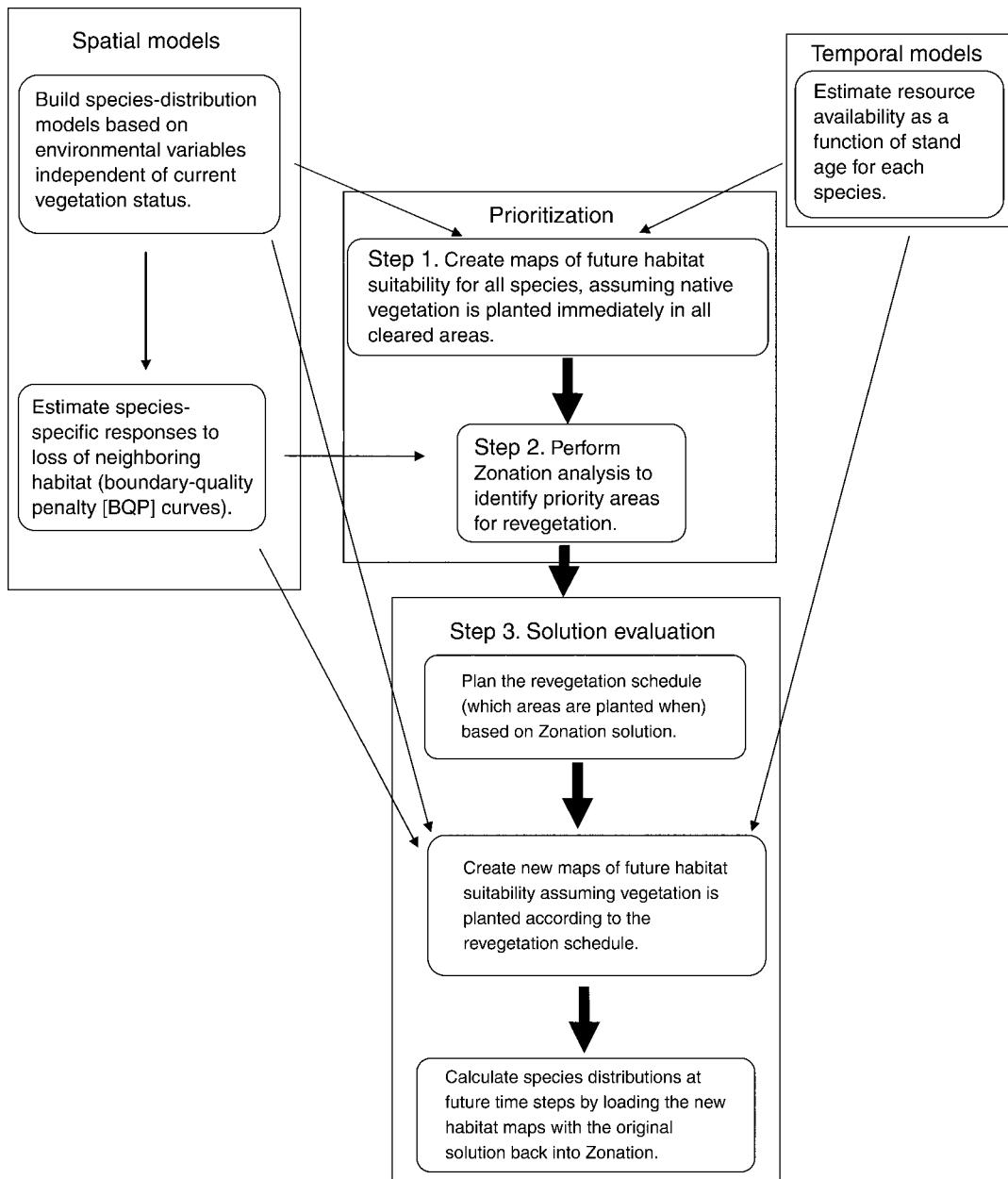


FIG. 1. Flow diagram showing the sequence of analyses and required inputs for determination of an optimal revegetation schedule with the Zonation framework.

tion as (potential) habitat is removed from the landscape (Kremen et al. 2008, Leathwick et al. 2008). The combination of the core-area algorithm and multiple, time-specific habitat maps for each species ensures that all species maintain high-quality areas through all time slices. This promotes stable population trajectories for all species through time.

This approach has two components that together promote the extension of existing patches of native vegetation and the connectivity within and among remnant and restored patches. First, extant vegetation is protected from removal (“masked in”) until all other cells

in the landscape have been removed. Second, individual habitat-connectivity requirements are given for each species (Moilanen and Wintle 2007). Consequently, the iterative cell-removal strategy progressively “shrinks” the vegetation cover from the hypothetical 100% condition towards an extension of actual remaining vegetation that satisfies the habitat and connectivity requirements of all species. The ranking of cells in the landscape indicates the order in which areas should be revegetated to maximize biodiversity outcomes through time.

*Step 3.*—Evaluate the Zonation solution by estimating the habitat availability for each species through time,

accounting for staggered planting and delayed resource provision.

In Step 2 we assume that all selected habitat would be instantly replanted, which is not realistic. Rather, the priority areas identified for revegetation would be restored by land managers over many years. Therefore, we evaluate the solution of Step 2 by calculating the total habitat available to each species at each future time step assuming that plantings are scheduled according to the cell ranks. This step involves calculating a second set of time-specific maps of habitat suitability in which the age of planted vegetation varies spatially according to the recommended sequence of planting. These maps then are loaded into Zonation along with the priority ranks (solution from Step 2) to calculate total habitat availability through time.

Here, *total habitat* for each species at each time step is the sum over all grid cells of that species' probabilities of occurrence, which depend on local environmental conditions, landscape context and age of vegetation. Total habitat is an overall measure of the quality and quantity of habitat for each species that accounts for configuration (absolute and relative location) and age of vegetation. We equate maximizing total habitat at each time step for a species to maximizing population size, and hence probability of persistence. Note that the core-area algorithm ranks cells for removal according to their maximum (across species) proportional contribution to total habitat at any time. Therefore, areas with highest habitat quality for each species, called *core areas*, are preferred over larger areas of lower habitat quality (20 locations with  $P = 0.05$  is not the same as one location with  $P = 1.0$ , Moilanen et al. 2005, Moilanen 2007).

Our analyses identify a set of locations at which restoration action will produce a balanced set of species' representation levels through time. *Balanced* means that no species does poorly compared to the others, accounting for species weights and connectivity requirements (see next section, below). Heuristically, the greatest gains from restoration should be expected for species whose habitat has been most reduced by clearing or that have a narrow distribution that is easily extended. Higher-than-average gains also may accrue for species with distributions nested within those of other species. The smallest gains should be expected for species that have large range sizes and that have experienced relatively little habitat loss.

#### Implementation in the Box-Ironbark region

*Step 1. Predicting habitat suitability for woodland bird species.*—

1. *Local habitat models.*—Habitat-suitability maps were derived from statistical models relating species occurrences at 2-ha sites within large ( $\geq 40$  ha) blocks of remnant native vegetation to local environmental attributes (Thomson et al. 2007). We used Bayesian model averaging (BMA) with binomial regression to predict probabilities of occurrence from topographic,

edaphic, and climatic variables. This suite of predictor variables, detailed in Thomson et al. (2007), together influence local vegetation characteristics (some also influence birds directly) and, therefore, allow predictions of habitat quality in presently cleared areas, assuming these were to be vegetated. The models used here improve on those described by Thomson et al. (2007) in two respects. First, data from another 74 sites (Radford et al. 2005) were combined with the original model-building data (101 sites) to increase sample size and spatial representativeness. Second, penalized regression splines (low-rank, thin plate splines, Crainiceanu et al. 2005) were incorporated into the model-averaging procedure to allow more flexible functional responses to predictor variables. We implemented BMA with the reversible jump Markov chain Monte Carlo add-on (Lunn et al. 2006) for WinBUGS (Spiegelhalter et al. 2003), which necessitated use of the probit link function instead of the logit link used in the original models. Apart from computational tractability (Lunn et al. 2006), there usually is no practical difference between probit and logit link functions, McCullagh and Nelder 1990:109). The modified models outperformed the original models in independent validation tests (J. Thomson, *unpublished data*).

2. *Landscape context: boundary-quality penalty (Steps 1 and 2).*—We quantified the effects of neighborhood habitat loss on habitat quality (i.e., measured as probability of occurrence) by combining predictions from the local habitat models described above with a measure of landscape context. Specifically, we used the predictions from the local habitat models as an offset term (i.e., a variable having no coefficient) in a binomial regression model relating species occurrence to the proportion of native vegetation (PVEG) in the surrounding 0.5 km radius of a site. We calculated PVEG with three other radii (1, 2, and 5 km), but found that a 0.5 km radius produced the best (equal or absolute) predictive performance for each species (details of independent model validation appear below). The model was

$$\text{probit}(p_i) = \alpha + \eta_{Li} + f(\text{PVEG}).$$

Here  $\eta_{Li}$  is the probit-transformed probability of occurrence for site  $i$  as predicted by the local variable models described above, and  $f(\text{PVEG})$  is a nonlinear, penalized spline function of PVEG. This landscape model predicts local occurrence by modifying the local habitat quality expected on the basis of local variables by a nonlinear function of PVEG. We parameterized the landscape model by combining the model-building data ( $n = 175$  survey sites) with data from another 200 surveyed sites (38 sites of Mac Nally and Horrocks [2002], 162 sites of Radford et al. [2005]) located in remnant wooded patches of  $< 40$  ha (range: 2–38 ha). Data from patches  $< 40$  ha were not used to parameterize the local habitat models because such patches are known to have a depauperate avifauna (i.e., a species absence from a small patch may be unrelated to local conditions; Mac Nally 2007).

Using the predictions of local habitat models as offsets in a landscape model avoided confounding the effects of landscape context with local topographic or edaphic variables, which often were correlated because of past preferential clearing of productive lowlands (Mac Nally et al. 2000). This two-stage procedure also facilitated production of separate maps of local habitat quality and boundary-quality penalty curves (BQP; Moilanen and Wintle 2007) for use in Zonation.

We converted  $f(\text{PVEG})$  for each species into appropriate boundary-quality penalty response curves for input to Zonation. BQP curves give the proportion remaining  $R(j)$  of the original habitat value of a focal cell when that cell has fraction  $j$  of its neighbors intact (i.e., vegetated). For each species, we calculated the expected proportion of habitat value remaining for a site with average local habitat conditions and fraction  $j$  neighbors remaining as follows:

$$R(j) = p_j/p_1 \quad \text{probit}(p_j) = \alpha + \eta_L + f(j)$$

where  $\eta_L$  is the overall mean of the local linear predictors for each site from the relevant local habitat model, and  $p_1$  is the expected probability of occurrence when all neighbors are vegetated. BQP functions ( $R(j)$  values) for all species are given in Appendix A, along with plotted curves for selected species.

We validated predictions from the combined landscape models using two independent data sets. The first comprised 90 2-ha sites within large (>40 ha) remnant blocks, each surveyed 8 times over 18 mo (Thomson et al. 2007). The second validation data set was 280 2-ha sites located in remnants >2 ha and surveyed by volunteers on at least two occasions (Birds Australia second atlas project; Barrett et al. 2003). Prediction success was assessed using the area under receiver operator characteristic curves (AUC) calculated for each validation data set separately. We included in Zonation analyses only those species for which models achieved AUC > 0.7 for at least one validation data set (62 species).

3. *Vegetation maturation.*—To incorporate a temporal component into the prioritization process, we created multiple maps of habitat suitability for each species corresponding to vegetation maturity for multiple time slices. First, we used the models of local habitat suitability to map the potential local habitat value for each species across the entire landscape, assuming mature vegetation was present. We denote the predicted habitat suitability (occurrence probability) of cell  $i$  for species  $s$  as  $H_{si}$ . We then modified these maps of habitat potential for each of five future time slices (20, 40, 60, 100, 140 years hence) by multiplying  $H_{si}$  values of presently cleared cells (i.e., candidate revegetation sites) by species-specific, time-dependent coefficients of resource suitability  $S_{st}$ . Resource coefficients reflect the probability that plantings of age  $t$  provide sufficient breeding and foraging resources for species  $s$ . The habitat suitability of the  $i$ th cell at time  $t$  for species  $s$  was given by the following:

$$H_{sti} = S_{st}H_{si} \quad S_{st} = \min(S_{Fst}, S_{Bst}).$$

Here  $S_{Fst}$  and  $S_{Bst}$  are the coefficients of foraging and breeding suitability, respectively, for species  $s$  after  $t$  years. We treated all extant vegetation as “mature” ( $S_s = 1$  for all  $t$ ). Resource scores were derived from the resource provision model of Vesik et al. (2008a, b). These scores are based on estimated species’ requirements for, and rates of development of, 22 resources, which included structural and consumable ground-story, shrub, and tree-layer components and prey, where appropriate. Resource provision is estimated to be sufficient for all species within 140 years of planting (i.e.,  $S_{s140} = 1$  and  $H_{s140} = H_s$ ), but many species’ requirements are met much sooner (e.g.,  $S_{s20} = 1$  for some species). Resource coefficients for each species and time slice are listed in Appendix B.

*Step 2. Running Zonation.*—We carried out the analysis using habitat suitability ( $H_{sti}$ ) maps with  $150 \times 150$  m cell size for 62 species with five time slices. The cell size (2.25 ha) corresponds approximately to the size of bird survey sites (2 ha) and, therefore, to the minimum resolution at which the models reasonably can be expected to predict occurrences. All extant native vegetation was masked in (hence removed last). Urban centers, sealed roads, waterways, and lakes were excluded, leaving 466 924 grid cells (10 506 km<sup>2</sup>) for ranking, of which 406 444 grid cells (9155 km<sup>2</sup>) were candidate cells for revegetation. BQP curves derived from landscape context models were included with neighborhoods of  $5 \times 5$  grid cells (56 ha) for each species. This neighborhood area is consistent with the 0.5 km radius within which we found the proportion of native vegetation to be a useful predictor for all species in the landscape-context models. Note that species-specific BQP neighborhood areas can be specified if appropriate.

We weighted species maps in Zonation according to validation AUC values for corresponding predictive models. This weighting scheme means that highest priority is assigned to areas with high potential habitat value for species with relatively high prediction confidence. Species with AUC > 0.7 (Pearce and Ferrier 2000) for both validation data sets ( $n = 30$  species) were assigned maximum weight (1). Species with AUC > 0.7 for one data set and  $0.6 < \text{AUC} < 0.7$  for the other ( $n = 20$  species) were assigned weight = 0.75. Species with AUC > 0.7 for one data set and AUC < 0.6 for the other ( $n = 12$  species) were assigned weight = 0.5.

We used a warp factor (i.e., the number of cells removed at each iteration, Moilanen and Kujala 2008) of 100 cells and specified that cells be removed only from the edges of contiguous blocks of remaining grid cells at each iteration. Warp 100 and edge-only removal reduced Zonation run times from an estimated many weeks to ~10 days. Edge removal may also promote habitat continuity (Moilanen and Kujala 2008). In preliminary trials with reduced numbers of species layers and grid

cells, we found negligible differences in selected spatial patterns and resulting species performances using warp 100 and warp 1 (similar results were observed by Moilanen and Kujala [2008]).

*Step 3. Solution evaluation.*—The evaluation step is required to estimate trajectories of habitat availability for individual species and to verify that revegetating areas in order of their Zonation ranks leads to balanced increases in habitat for all species, even when planting is staggered over many years. We scheduled a hypothetical planting sequence based on the cell rankings returned by Zonation and then predicted species occurrences at future time slices based on the approximate ages of planted vegetation. We assumed a long-term goal of increasing the extent of native vegetation from the current 14% cover to 50% cover over a 70-year period, with intermediate targets of 24%, 34%, and 44% cover after 20, 40, and 60 years, respectively. Planting times were assigned such that the highest ranked, unvegetated cells were planted first, and cells ranked  $<0.5$  were never planted. The assumed targets are broadly consistent with current ecological understanding and land-use trends. For example, Bennett and Radford (2009) estimated that at least 30–35% (40-year target) vegetation cover is required to maintain populations of most woodland bird species in northern Victoria, Australia. More extensive revegetation (e.g., 50% cover) is possible in the longer term in parts of the region, if continued planting occurs for carbon storage, salinity amelioration and conservation (Brereton et al. 1995). Note that the cell ranks derived from the core-area algorithm do not depend on specific revegetation targets.

We created a new set of habitat suitability maps for each species corresponding to 0 (current), 20, 40, 60, 80, 140, and 220-year time slices. The inclusion of year 220 in the evaluation step allowed estimation of total habitat values when all planted vegetation was at least 140 years “mature” (latest planting occurred at year 70). Cell values were given by

$$H_{sti} = S_{sz(i)} H_{is} \quad S_{sz(i)} = \begin{cases} \min[S_{Fsz(i)}, S_{Bsz(i)}] & z > 0 \\ 0 & z \leq 0. \end{cases}$$

Here,  $z(i)$  is the age ( $t - \text{year planted}$ ) of any planted vegetation in cell  $i$  and  $S_{sz}$  is the corresponding resource sufficiency coefficient. We assumed constant resource suitability  $S_{sz} = 1$  for extant vegetation. We then loaded this set of suitability maps into Zonation using the solution rankings from the initial run to recompute total habitat values for each species at each time step under the explicit planting schedule. We obtained the total habitat values for each species at each time step by looking up the estimated value remaining for the relevant time-specific habitat maps at the corresponding landscape fractions. For example, the total habitat for species  $s$  at  $t = 40$  years was the habitat remaining for map  $H_{s40}$  using the top-ranked 34% of the landscape (assuming 34% of the landscape is vegetated after 40 years).

### Comparison of maturing and “instant” vegetation

To examine how explicit accounting for delayed maturation of vegetation affected the ranking of sites for revegetation, and resulting species performances, we repeated the analysis and solution evaluation procedures described above using only maps of mature-habitat suitability ( $H_{s140}$ ) as inputs (analysis Step 2). That is, we derived a planting schedule from cell rankings based on mature-habitat quality only (with extant vegetation masked in) and then evaluated species’ performances (Step 3) under that schedule by reloading a new set of time-specific habitat maps that accounted for the corresponding planting times and expected delays in resource provision.

## RESULTS

Revegetation schedules derived from Zonation cell ranks are shown in Fig. 2. The upper map (Fig. 2A) shows the solution based on multiple, time-dependent maps of habitat suitability (hereafter termed the *maturing-habitat* solution). The lower map (Fig. 2B) shows the solution based on maps of mature habitat suitability only (hereafter the *instant-habitat* solution). Both solutions give highest priority to revegetation in the neighborhood of present patches of remnant vegetation and in areas of higher rainfall on more-fertile soils, especially along the southern margin.

The solutions diverged substantially once  $\sim 25\text{--}30\%$  of the landscape is vegetated, which is after 20 years of plantings under our hypothetical planting schedule. The maturing-habitat solution favored continued expansion of areas in the west to create a very large patch of continuous vegetation, whereas the instant-habitat solution suggested later plantings (after  $\sim 30\%$  of the total landscape is vegetated) should be more evenly distributed (although generally still concentrated around existing and already-expanded patches).

### Solution evaluation

Species’ responses (changes in estimated total habitat values) to the planting schedules, allowing for estimated rates of resource maturation, are summarized in Figs. 3 and 4 (species-specific performance curves are shown in Appendix C). Total habitat for the majority of species doubles by the time one-third of the landscape is vegetated (within 40 years under the planting schedule). In general, the rate of increase in a species total habitat was proportional to the rate at which that species’ resources develop and inversely proportional to that species’ sensitivity to fragmentation (Fig. 3). Increases are most rapid for species, such as Brown Thornbill (*Acanthiza pusilla*) and Buff-rumped Thornbill (*A. reguloides*), that are fragmentation sensitive but use relatively fast-developing resources (Fig. 3). Plantings are assumed to benefit such species through rapid provision of new habitat and immediate enhancement of neighboring remnant patches. In contrast, species such as the Laughing Kookaburra (*Dacelo novaegu-*

*nae*), which are favored by fragmentation but rely on slow-developing tree hollows for nesting, are estimated to have initial reductions in total habitat because young plantings do not provide suitable habitat and reduce fragmentation (Fig. 3, Appendix C). Proportional increases in total habitat were greatest for species whose habitats have been most depleted since European settlement (Fig. 4).

Species performances were similar under the maturing habitat and instant habitat solutions, especially in the first 60 years (Fig. 3). Fragmentation-sensitive species did better eventually under the maturing-habitat solution because vegetation is more aggregated at 50% overall cover. Species that benefit from fragmentation did worse under the maturing habitat solution for the same reason.

#### DISCUSSION

The use of decision modeling tools is a major step forward in systematic planning of revegetation for landscape restoration (Westphal et al. 2003, 2007, Bryan and Crossman 2008). To date, revegetation in heavily cleared regions in southern Australia, for example, has been based on the application of general principles (e.g., Hobbs 1993, Barrett 2000, Wilson and Lowe 2003), or the inferred requirements of selected threat-sensitive focal species (Lambeck 1997, Watson et al. 2001). Alternatively, revegetation has been driven from the “bottom up” by the actions of local community groups and individual land holders at the property scale, leading to nonstrategic outcomes (Campbell 1994, Bennett and Mac Nally 2004). Multispecies optimization provides land managers with spatially explicit priorities for restoration based on quantitative models of habitat use by a large number of species, while potentially accounting for other objectives and costs (Westphal et al. 2007).

To our knowledge, this study is the first to undertake landscape-scale optimization for revegetation that accounts explicitly for spatial and temporal variability in local habitat conditions in addition to landscape contextual effects. Westphal et al. (2003) used stochastic dynamic programming to optimize the sequence of reconstruction actions for a single species, but such an approach is infeasible for larger problems (many sites, many species). Westphal et al. (2007) used simulated annealing to optimize placement of revegetation for 22 bird species in a 5000-km<sup>2</sup> landscape by treating habitat as binary (present or absent) and estimating occurrence probabilities from landscape contextual effects alone. Our work extends this basic approach, although using a different optimization algorithm, to incorporate spatial and temporal variability in local habitat conditions. Our analysis includes relatively many (62) species and was conducted over a large spatial extent (11 000 km<sup>2</sup> with fine grid resolution (>400 000 candidate revegetation locations), demonstrating the applicability of the approach to real-world problems.

Our analysis ignores revegetation costs and assumes the sole purpose of revegetation is to increase habitat for

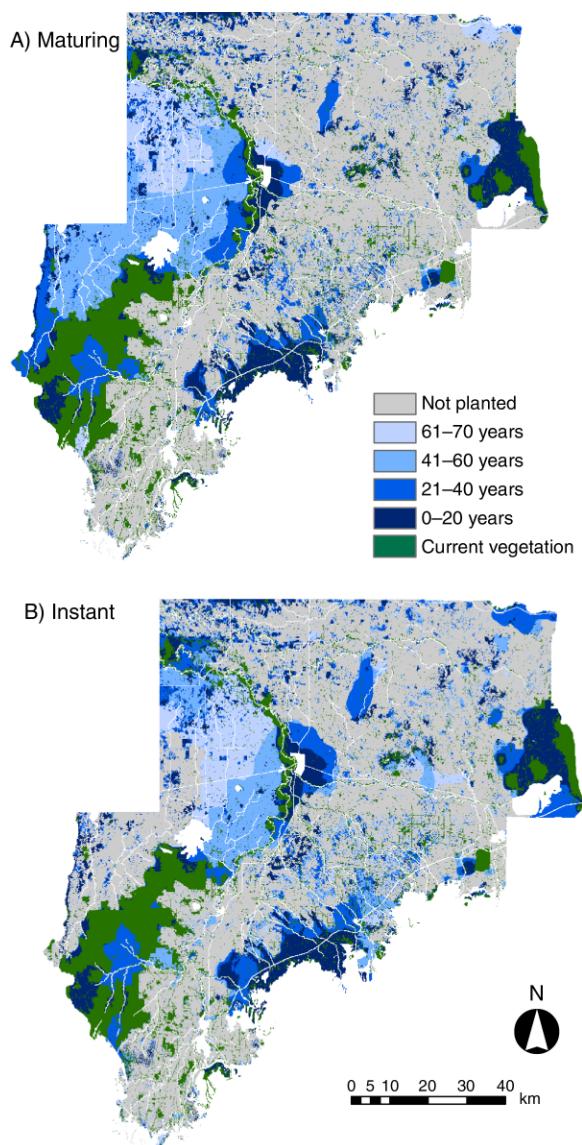


FIG. 2. Proposed revegetation schedules for optimal outcomes for bird biodiversity based on Zonation cell ranks: (A) the solution based on multiple, time-dependent maps of habitat suitability for bird species (the “maturing-habitat” solution) and (B) the solution based on maps of mature habitat suitability only (the “instant-habitat” solution). Colors indicate cell ranks grouped into 20-year planting periods. The highest-ranked areas would be planted within the first 20 years under the derived planting schedule, which would achieve total vegetation covers of 24%, 34%, 44%, and 50% after 20, 40, 60, and 70 years, respectively.

bird species. In reality, large-scale revegetation will have multiple objectives, including multiple taxa (flora and fauna) and land-management goals (e.g., salinity control, carbon sequestration; Harper et al. 2007). Spatial priorities may be influenced by local revegetation costs, which will vary with opportunity costs (lost production) and other local factors (Dorrrough et al. 2008). These considerations can be included in the analysis frame-

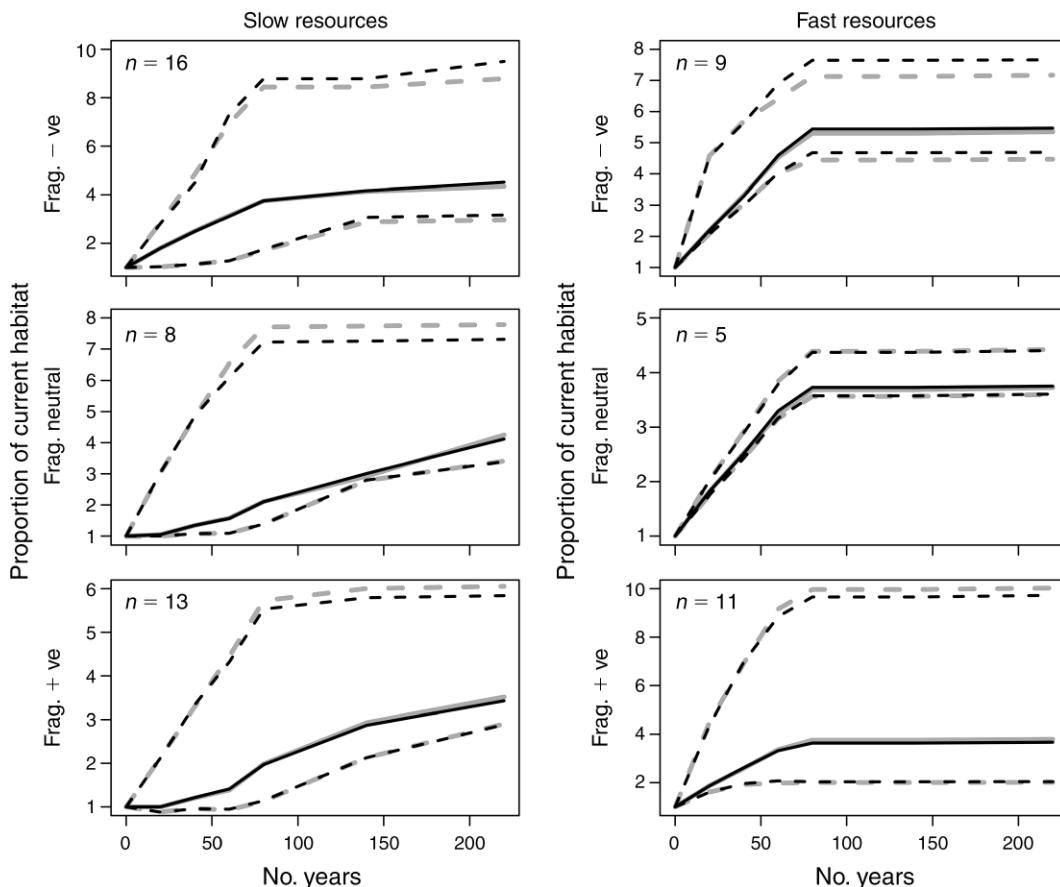


FIG. 3. Typical changes in species' total-habitat values assuming revegetation schedules derived from the "maturing-habitat" solution (black lines) and the "instant-habitat" solution (gray lines). The maturing-habitat solution explicitly recognizes time-dependent changes in habitat suitability. Habitat values are expressed as fractions of current estimated total habitats (i.e., summed occurrence probabilities) for each species. Species were grouped into six categories to reflect their estimated sensitivities to fragmentation (based on boundary-quality penalty [BQP] curves) and expected rates of response to development of resources in revegetated habitats: "Frag. - ve," species negatively affected by local loss of vegetation (i.e., local habitat quality declines with the proportion of surrounding vegetation lost); "Frag. neutral," species not affected by changes in the vegetation of neighboring cells; "Frag. + ve," species that benefit from clearing of some neighboring cells; "slow resources," species that rely on slowly developing resources, such as tree hollows; "fast resources," species that rely only on more rapidly developing resources, such as canopy foliage. Solid lines are median values for species in a group; dashed lines are minima and maxima;  $n$  is the number of species.

work, given sufficient spatially explicit information. Other taxa can be incorporated by including appropriate maps of habitat potential. A cost layer also can be included as an input, in which case the habitat value of a cell is adjusted by the relative cost of securing and restoring that vegetation. Cells then can be ranked according to expected biodiversity returns on investment. Work in progress will extend the current study to include estimated values of agricultural output as a cost layer, and modeled, pre-European distributions of vegetation communities as additional conservation features (one binary habitat map for each vegetation community). With these inputs, we seek a cost-effective revegetation plan that simultaneously expands distributions of depleted vegetation types and increases habitat for multiple bird species.

Other constraints or management objectives could be included through the "mask" input layer, which allows

specification of cells that should be removed first (e.g., areas that cannot be revegetated) or last (e.g., extant vegetation, or areas where revegetation is required regardless of potential value to species in the analysis). For example, areas that are critical for salinity amelioration might be masked in to ensure high priority for revegetation. Some objectives might also be included as additional conservation features through "habitat" maps that indicate the potential for local vegetation to contribute to those objectives. For example, a map of stream buffers could be included so that riparian restoration would be given priority over non-riparian plantings, all else being equal. It is preferable to incorporate all known constraints in the analysis a priori so that the solution is as close to optimal (and robust) as possible given those constraints and competing objectives. If certain areas are excluded from the suggested configuration

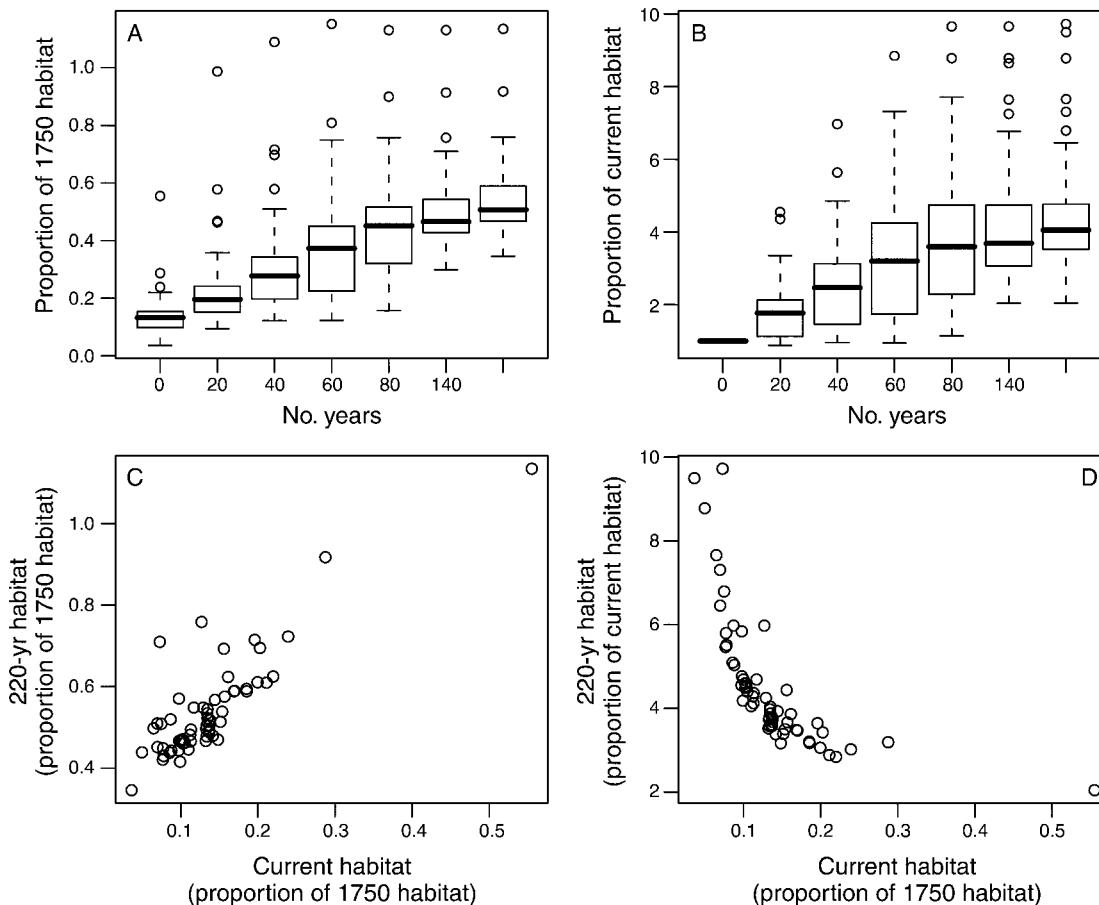


FIG. 4. Summary of total-habitat values at future time steps assuming a revegetation schedule derived from the maturing-habitat solution (i.e., recognizing time-dependent changes in the habitat suitability of revegetation). Top row: box plots of total-habitat values expressed as proportions of (A) estimates for a fully vegetated landscape; and (B) estimated current values. Bottom row: final (220 yr) total-habitat values as proportions of values for (C) a fully vegetated landscape and (D) current values plotted against current total-habitat values as proportions of values for a fully vegetated landscape.

after the analysis to meet other objectives (e.g., for economic, political, or other reasons such as hydrology or salinity control), then the remaining configuration probably no longer will be near optimal from a biodiversity perspective.

An assumption in our analysis is that vegetation matures at the same rate across the entire region. However, maturation rates depend on local environmental conditions such as soil productivity and climate. Land-acquisition costs, vegetation-maturation rates and future habitat quality are likely to be correlated (Vesk and Mac Nally 2006), leading to trade-offs between costs and biodiversity benefits. Given sufficient information, spatially varying rates of maturation could be incorporated by using spatially explicit resource coefficients ( $S_{st}$ ;  $S_{s=(t)}$ ) to calculate time-dependent habitat maps used to rank cells and verify solutions. This would require appropriate models of vegetation maturation as functions of local environmental attributes, but no changes would be required for the prioritization phase implemented using Zonation.

The rate of vegetation maturation and costs of revegetation will depend in part on the revegetation method(s) used (e.g., active planting vs. passive regeneration; Vesk et al. 2008b). The present capabilities of the Zonation software do not allow for selection from among multiple alternative conservation actions (and times) for specific areas in a single analysis. However, alternative strategies can be compared by performing analyses on each strategy and comparing the resulting species' outcomes. The best restoration strategy would be that which produced the highest absolute increases in species' distributions for a given cost. A strategy might include a set of rules defining which revegetation methods should be applied in different parts of the landscape. For example, a strategy employing active replanting in high-productivity areas and passive regeneration in low-productivity areas could be compared to exclusive use of active replanting (Dorrough et al. 2008). This analysis would require a specific set of input maps and cost layers for each strategy. Habitat suitability maps would be calculated according to expected

maturation rates given the revegetation method used at each location under each strategy.

The assumption of constant maturation rate explains in part the apparent similarity of species' performances under the maturing-habitat and instant-habitat solutions. Despite large differences in the final spatial configurations at 50% vegetation cover, the maturing and instant solutions produced similar gains in expected habitat quality for most species. Greater differences in species' outcomes would be expected if vegetation matures at different rates at different locations. Another reason for the similarity of species' performances is that areas assigned highest priority for revegetation (top 10% of landscape, excluding extant vegetation) were very similar for both solutions. This suggests that initially there was little trade-off between short-term enhancement of existing habitat and eventual quality of mature habitat, at least for species with the most depleted habitats, which determine areas with highest revegetation priorities.

In the Box-Ironbark region, the most depleted habitats (or vegetation communities) are associated with relatively productive plains and riparian areas that have been cleared almost completely for agriculture. The few remnant patches of these habitats are surrounded by productive soils that would yield similar, high-quality habitats. The more productive areas often have been cleared right up to the poorer soils and their associated vegetation communities (i.e., habitats), leaving relatively large remnants on poor soils. Plantings adjacent to those remnants potentially achieve both rapid enhancement of the remnant and longer-term provision of high-quality mature habitat for the more depleted, productive-habitat types.

We stress that the similarity of species' performances under maturing-habitat and instant-habitat solutions is unlikely to be a general result even if maturation rates were spatially invariant. This result does not imply that lags in resource provision can be ignored in revegetation planning. If mature-habitat values of locations only are used as inputs to Zonation, or any other optimization algorithm, then priorities for revegetation are identified solely on the basis of the expected quality of the mature habitat for species and context effects. Highest priority will be given to areas that eventually will be high-quality mature habitat for species whose current habitat is much reduced. While this seems an intuitively desirable result—we should start restoring the most depleted habitat first—it ignores potential variation in the rate at which planted vegetation provides critical resources for different species. Revegetation strategies that target species dependent on slow-developing resources, such as tree hollows (Vesk et al. 2008a), may differ from strategies that target species whose habitat requirements can be met more rapidly. The former may require earlier planting and greater enhancement of existing vegetation through buffers or increased foraging sites close to breeding sites, even if those areas will not produce the highest quality habitat in the longer term. Our inclusion

of different stages of vegetation development provides an explicit and objective consideration of these spatio-temporal trade-offs within and among species.

An assumption in our use of boundary-quality penalty functions is that planted vegetation has immediate neighborhood effects on any adjacent remnant vegetation. Although the local quality of planted vegetation develops over time in our analysis, neighboring vegetation immediately becomes better or worse habitat for fragmentation-sensitive and tolerant species, respectively. We lack empirical data to test these assumptions for any taxa, but their validity will be context and species dependent. While some benefits of planted buffers (e.g., reduced cattle and sheep access) may be rapid, especially in intensive-agricultural areas, others (e.g., provision of additional foraging resources close to breeding sites) may take longer. Therefore, the analysis may overestimate the rate of increase in total habitat for some species. Similarly, the suitability of remnant patches for species that nest or roost in woodlands but that forage in open paddocks (e.g., many parrots) may be unaffected or even enhanced by planted buffers, in which case some "open tolerant" species would do better than models predict in the early stages of revegetation. Further work is required to improve understanding of species' responses to revegetation over short and long time scales and to determine the planning implications of those responses.

We masked in all extant remnant vegetation on the assumption that land clearing in Victoria effectively has ceased and that remnant patches would be protected and, where necessary, restored. This assumption could be relaxed within the current framework to explore trade-offs between planting new vegetation and improving or protecting remnant vegetation. Instead of masking in remnant vegetation, one could include a cost layer that reflected the relative costs of achieving good-condition native vegetation in each cell. That cost would be very low for remnant patches already in good condition, higher for remnant patches in poor condition, and very high (and varying with land use) for cleared agricultural land. Cleared areas that represented very high potential value might then be ranked above remnant vegetation in poor condition with low potential value for regional biodiversity.

### Conclusions

Landscape-planning algorithms that deal with very large landscapes are rare, especially when long-term scheduling of conservation action is required. In our work, we implemented restoration planning and scheduling of restoration action using a particular setup of a method and software, Zonation, originally developed for the design of large-scale, high-resolution reserve networks. We show how creative use of the analysis setup allows us to approximate a solution to a complex, large-scale restoration-planning problem, accounting for multi-species objectives and connectivity requirements at

spatial extents and grain sizes relevant to management. We used validated, species-specific, habitat models that included local habitat and landscape contextual effects, and we accounted for species-specific lags in habitat suitability following planting. While solutions generated by this method cannot be guaranteed to be globally optimal, the expected outcomes for all species and objectives can be evaluated to ensure that solutions are good. Uncertainty analyses also can be performed to ensure robust solutions (e.g., Moilanen and Wintle 2006, Moilanen et al. 2006a, b). Last, we note that the verification procedure (analysis Step 3) can be used to estimate species' outcomes under any revegetation plan, whether the plan is derived from a Zonation solution or from another method (e.g., Wilson and Lowe 2003), provided models of habitat potential and resource provision are available. Therefore, this approach has potential to contribute to regional planning and to inform investment decisions (Stoneham et al. 2003) both through the development of optimal revegetation plans and by evaluating the expected biodiversity outcomes of alternative management options.

#### ACKNOWLEDGMENTS

This research was supported by several grants from the Australian Research Council, including the focal grant LP0560518 (with co-funding from Victorian Department of Sustainability and Environment, Victorian Department of Primary Industries, North-Central, Goulburn-Broken, Mallee and North-East Catchment Management Authorities, and contributes to the Key Project 1.1 under the Our Rural Landscapes Initiative of the Victorian Department of Primary Industries) and DP0343898 and A19531268. A. J. Moilanen was supported by the Academy of Finland, project 202870, and by the Australian Centre of Excellence in Risk Analysis (ACERA) where he was visiting at the time this work was initiated. We thank Jim Radford and Josh Dorrrough for valuable discussions and access to data, and two anonymous reviewers for helpful comments on the manuscript. This paper is number 165 from the Australian Centre for Biodiversity.

#### LITERATURE CITED

- Barrett, G. 2000. Birds on farms: ecological management for agricultural sustainability. *Wingspan* 10(4)Supplement:I–XV.
- Barrett, G. W., D. Freudenberger, A. Drew, J. Stol, A. O. Nicholls, and E. M. Cawsey. 2008. Colonisation of native tree and shrub plantings by woodland birds in an agricultural landscape. *Wildlife Research* 35:19–32.
- Barrett, G., A. Silcocks, S. Barry, R. Cunningham, and R. Poulter. 2003. *The New Atlas of Australian birds*. Birds Australia/Royal Australasian Ornithologists Union, Melbourne, Victoria, Australia.
- Bennett, A. F., and R. Mac Nally. 2004. Identifying priority areas for conservation action in agricultural landscapes. *Pacific Conservation Biology* 10:106–123.
- Bennett, A. F., and J. Q. Radford. 2009. Thresholds, incidence functions, and species-specific cues: responses of woodland birds to landscape structure in south-eastern Australia. Pages 161–184 *in* M.-A. Villard and B. G. Jonsson, editors. *Setting conservation targets for managed forest landscapes*. Cambridge University Press, Cambridge, UK.
- Brereton, R., S. Bennett, and I. Mansergh. 1995. Enhanced greenhouse climate change and its potential effect on selected fauna of south-eastern Australia: a trend analysis. *Biological Conservation* 72:339–354.
- Bryan, B. A., and N. D. Crossman. 2008. Systematic regional planning for multiple objective natural resource management. *Journal of Environmental Management* 88:1175–1189.
- Cabeza, M., and A. Moilanen. 2001. Design of reserve networks and the persistence of biodiversity. *Trends in Ecology and Evolution* 16:242–248.
- Cai, W., and T. Cowan. 2008. Dynamics of late autumn rainfall reduction over southeastern Australia. *Geophysical Research Letters* 35, L09708.
- Campbell, A. 1994. *Landcare. Communities Shaping the Land and the Future*. Allen & Unwin, St Leonards, New South Wales, Australia.
- Crainiceanu, C. M., D. Ruppert, and M. P. Wand. 2005. Bayesian analysis for penalized spline regression using WinBUGS. *Journal of Statistical Software* 14:1–24.
- Crossman, N. D., and B. A. Bryan. 2006. Systematic landscape restoration using integer programming. *Biological Conservation* 128:369–383.
- Dorrrough, J., P. A. Vesik, and J. Moll. 2008. Integrating ecological uncertainty and farm-scale economics when planning restoration. *Journal of Applied Ecology* 45:288–295.
- ECC [Environment Conservation Council]. 1997. *Box-Ironbark forests and woodlands investigation. Resources and issues report*. Environment Conservation Council, East Melbourne, Victoria, Australia.
- Harper, R. J., A. C. Beck, P. Ritson, M. J. Hill, C. D. Mitchell, D. J. Barrett, K. R. J. Smettem, and S. S. Mann. 2007. The potential of greenhouse sinks to underwrite improved land management. *Ecological Engineering* 29:329–341.
- Hobbs, R. J. 1993. Can revegetation assist in the conservation of biodiversity in agricultural areas? *Pacific Conservation Biology* 1:29–38.
- Hobbs, R. J., and J. A. Harris. 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. *Restoration Ecology* 9:239–246.
- Kremen, C., et al. 2008. Aligning conservation priorities across taxa in Madagascar, a biodiversity hotspot, with high-resolution planning tools. *Science* 320:222–226.
- Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* 11:849–856.
- Leathwick, J. R., A. Moilanen, M. Francis, J. Elith, P. Taylor, K. Julian, and T. Hastie. 2008. Novel methods for the design and evaluation of marine protected areas in offshore waters. *Conservation Letters* 1:91–102.
- Lunn, D. J., J. C. Whittaker, and N. Best. 2006. A Bayesian toolkit for genetic association studies. *Genetic Epidemiology* 30:231–247.
- Mac Nally, R. 2007. Use of the abundance spectrum and relative-abundance distributions to analyze assemblage change in massively altered landscapes. *American Naturalist* 170:319–330.
- Mac Nally, R. 2008. The lag daemon: Hysteresis in rebuilding landscapes and implications for biodiversity futures. *Journal of Environmental Management* 88:1202–1221.
- Mac Nally, R., A. F. Bennett, and G. Horrocks. 2000. Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the Box-Ironbark forests of central Victoria, Australia. *Biological Conservation* 95:7–29.
- Mac Nally, R., L. De Vries, and J. Thomson. 2009. Are replanted floodplain forests in south-eastern Australia providing biodiversity benefits? *Restoration Ecology*, *in press*.
- Mac Nally, R., and G. Horrocks. 2002. Relative influences of site, landscape and historical factors on birds in a fragmented landscape. *Journal of Biogeography* 29:395–410.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243–253.
- Martínez-Garza, C., and H. F. Howe. 2003. Restoring tropical diversity: beating the time tax on species loss. *Journal of Applied Ecology* 40:423–429.

- McCullagh, P., and J. A. Nelder. 1990. Generalized linear models. Second edition. Chapman and Hall, New York, New York, USA.
- Moilanen, A. 2007. Landscape Zonation, benefit functions and target-based planning: unifying reserve selection strategies. *Biological Conservation* 134:571–579.
- Moilanen, A., A. Franco, R. Early, R. Fox, B. Wintle, and C. Thomas. 2005. Prioritizing multiple-use landscapes for conservation. *Proceedings of the Royal Society of London Series B* 272:1885–1891.
- Moilanen, A., and H. Kujala. 2006. The Zonation spatial conservation planning framework and software v. 1.0: user manual. Edita, Helsinki, Finland. ([www.helsinki.fi/science/metapop/software](http://www.helsinki.fi/science/metapop/software))
- Moilanen, A., and H. Kujala. 2008. Zonation spatial conservation planning framework and software v. 2.0: user manual. ([www.helsinki.fi/bioscience/consplan](http://www.helsinki.fi/bioscience/consplan))
- Moilanen, A., J. R. Leathwick, and J. Elith. 2008. A method for freshwater conservation prioritization. *Freshwater Biology* 53:577–592.
- Moilanen, A., M. Runge, J. Elith, A. Tyre, Y. Carmel, E. Fegraus, B. Wintle, M. Burgman, and Y. Ben-Haim. 2006a. Planning for robust reserve networks using uncertainty analysis. *Ecological Modeling* 199:115–124.
- Moilanen, A., and B. A. Wintle. 2006. Uncertainty analysis favours selection of spatially aggregated reserve networks. *Biological Conservation* 129:427–434.
- Moilanen, A., and B. A. Wintle. 2007. The boundary-quality penalty: a quantitative method for approximating species responses to fragmentation in reserve selection. *Conservation Biology* 21:355–364.
- Moilanen, A., B. A. Wintle, J. Elith, and M. Burgman. 2006b. Uncertainty analysis for regional-scale reserve selection. *Conservation Biology* 20:1688–1697.
- Morris, R. K. A., I. Alonso, R. G. Jefferson, and K. J. Kirby. 2006. The creation of compensatory habitat—Can it secure sustainable development? *Journal for Nature Conservation* 14:106–116.
- Nicholson, E., M. I. Westphal, K. Frank, W. A. Rochester, R. L. Pressey, D. Lindenmayer, and H. P. Possingham. 2006. A new method for conservation planning for the persistence of multiple species. *Ecology Letters* 9:1049–1060.
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models using logistic regression. *Ecological Modeling* 133:225–245.
- Pressey, R. L., M. Cabeza, M. E. Watts, and R. M. Cowling. and K. A. Wilson. 2007. Conservation planning in a changing world. *Trends in Ecology and Evolution* 22:583–592.
- Radford, J. Q., A. F. Bennett, and G. J. Cheers. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124:317–337.
- Saunders, D., R. Hobbs, and P. Ehrlich, editors. 1993. *Nature conservation 3: reconstruction of fragmented ecosystems, global and regional perspectives*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Selwood, K., R. Mac Nally, and J. R. Thomson. 2009. Native bird breeding in a chronosequence of revegetated sites. *Oecologia* 159:435–446.
- Spielgelhalter, D., A. Thomas, and N. Best. 2003. WinBUGS version 1.4. Bayesian inference using Gibbs sampling. Manual. MRC Biostatistics Unit, Institute for Public Health, Cambridge, UK.
- Stoneham, G., V. Chaudhri, A. Ha, and L. Strappazzon. 2003. Auctions for conservation contracts: an empirical examination of Victoria's BushTender trial. *Australian Journal of Agricultural and Resource Economics* 47:477–500.
- Thomson, J. R., R. Mac Nally, E. Fleishman, and G. Horrocks. 2007. Predicting bird species distributions in reconstructed landscapes. *Conservation Biology* 21:752–766.
- Vesk, P. A., and R. Mac Nally. 2006. The clock is ticking: revegetation and habitat for birds and arboreal mammals in rural landscapes of southern Australia. *Agriculture, Ecosystems & Environment* 112:356–366.
- Vesk, P. A., R. Mac Nally, G. Horrocks, and J. R. Thomson. 2008a. Revegetation and the significance of lags in the provision of habitat resources for birds. Pages 183–209 in C. Pettit, W. Cartwright, K. Lowell, I. Bishop, D. Duncan, and D. Pullar, editors. *Landscape analysis and visualisation. Spatial Models for Natural Resource Management and Planning*. Springer-Verlag, Berlin/Heidelberg, Germany.
- Vesk, P. A., R. Nolan, J. R. Thomson, J. W. Dorrrough, and R. Mac Nally. 2008b. Time lags in provision of habitat resources through revegetation. *Biological Conservation* 141: 174–186.
- Watson, J., D. Freudenberger, and D. J. Paull. 2001. An assessment of the focal-species approach for conserving birds in variegated landscapes in southeastern Australia. *Conservation Biology* 15:1364–1373.
- Westphal, M. I., S. A. Field, and H. P. Possingham. 2007. Optimizing landscape configuration: a case study of woodland birds in the Mount Lofty Ranges, South Australia. *Landscape and Urban Planning* 81:56–66.
- Westphal, M. I., M. Pickett, W. M. Getz, and H. Possingham. 2003. The use of stochastic dynamic programming in optimal landscape reconstruction for metapopulations. *Ecological Applications* 13:543–555.
- Wilson, J. A., and K. W. Lowe. 2003. Planning for the restoration of native biodiversity within the Goulburn Broken Catchment, Victoria, using spatial modeling. *Ecological Management and Restoration* 4:212–219.
- Wilson, K. A., E. C. Underwood, S. A. Morrison, K. R. Klausmeyer, W. W. Murdoch, and B. Reyers. et al. 2007. Conserving biodiversity efficiently: what to do, where, and when. *PLoS Biology* 5:1850–1861.

#### APPENDIX A

Boundary-quality penalty (BQP) functions for bird species used in Zonation analysis (*Ecological Archives* A019-033-A1).

#### APPENDIX B

Estimated suitability for woodland bird species of restored native vegetation as a function of time (*Ecological Archives* A019-033-A2).

#### APPENDIX C

Estimated changes in habitat availability for each species under revegetation schedules derived from Zonation cell ranks (*Ecological Archives* A019-033-A3).