



Evaluating complementary networks of restoration plantings for landscape-scale occurrence of temporally dynamic species

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Abstract: *Multibillion dollar investments in land restoration make it critical that conservation goals are achieved cost-effectively. Approaches developed for systematic conservation planning offer opportunities to evaluate landscape-scale, temporally dynamic biodiversity outcomes from restoration and improve on traditional approaches that focus on the most species-rich plantings. We investigated whether it is possible to apply a complementarity-based approach to evaluate the extent to which an existing network of restoration plantings meets representation targets. Using a case study of woodland birds of conservation concern in southeastern Australia, we compared complementarity-based selections of plantings based on temporally dynamic species occurrences with selections based on static species occurrences and selections based on ranking plantings by species richness. The dynamic complementarity approach, which incorporated species occurrences over 5 years, resulted in higher species occurrences and proportion of targets met compared with the static complementarity approach, in which species occurrences were taken at a single point in time. For equivalent cost, the dynamic complementarity approach also always resulted in higher average minimum percent occurrence of species maintained through time and a higher proportion of the bird community meeting representation targets compared with the species-richness approach. Plantings selected under the complementarity approaches represented the full range of planting attributes, whereas those selected under the species-richness approach were larger in size. Our results suggest that future restoration policy should not attempt to achieve all conservation goals within individual plantings, but should instead capitalize on restoration opportunities as they arise to achieve collective value of multiple plantings across the landscape. Networks of restoration plantings with complementary attributes of age, size, vegetation structure, and landscape context lead to considerably better outcomes than conventional restoration objectives of site-scale species richness and are crucial for allocating restoration investment wisely to reach desired conservation goals.*

Keywords: agrienvironmental schemes, complementarity, dynamic distributions, Marxan, spatial prioritization, systematic conservation planning, vegetation restoration, woodland birds

Evaluación de Redes Complementarias de Plantaciones de Restauración para la Ocurrencia a Escala de Paisaje de Especies Temporalmente Dinámicas

Resumen: *Las inversiones multimillonarias de dólares en la restauración de suelos hacen que los objetivos de conservación se obtengan de manera rentable. Las estrategias desarrolladas para la planeación estratégica de la conservación ofrecen oportunidades para evaluar a escala de paisaje los resultados de biodiversidad temporalmente dinámica obtenidos de la restauración y para mejorar las estrategias tradicionales que se*

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Paper submitted September 15, 2015; revised manuscript accepted March 10, 2016.

enfocan en las plantaciones más ricas en especies. Investigamos si es posible aplicar una estrategia basada en la complementariedad para evaluar la extensión con la que una red de plantaciones de restauración cumple con los objetivos de representación. Con el uso de un estudio de caso de aves de bosque de importancia para la conservación en el sureste de Australia, comparamos las selecciones basadas en la complementariedad de las plantaciones basadas en la ocurrencia de especies dinámicas temporalmente con las selecciones basadas en la ocurrencia de especies estáticas y con las selecciones basadas en la clasificación por riqueza de especies de las plantaciones. La estrategia de complementariedad dinámica, que incorporó la ocurrencia de especies durante cinco años, resultó en una mayor ocurrencia de especies y en una mayor proporción de objetivos alcanzados en comparación con la estrategia de complementariedad estática, en la que la ocurrencia de las especies fue tomada en un punto único en el tiempo. En la equivalencia de costos, la estrategia de complementariedad dinámica también resultó siempre en un mayor porcentaje promedio mínimo de ocurrencia de especies mantenido en el tiempo y en una proporción mayor de la comunidad de aves que cumplían con los objetivos de representación en comparación con la estrategia de riqueza de especies. Las plantaciones seleccionadas bajo las estrategias de complementariedad representaron la extensión completa de atributos de plantación, mientras que aquellas seleccionadas bajo la estrategia de riqueza de especies tuvieron un mayor tamaño. Nuestros resultados sugieren que las futuras políticas de restauración no deberían intentar alcanzar todos los objetivos de conservación dentro de plantaciones individuales, sino que en su lugar, deberían capitalizar con las oportunidades de restauración conforme surgen para obtener así el valor colectivo de las plantaciones múltiples a lo largo del paisaje. Las redes de plantaciones de restauración con los atributos complementarios de edad, tamaño, estructura de la vegetación y contexto del paisaje llevan a resultados considerablemente mejores que los objetivos convencionales de restauración de riqueza de especies a escala de sitio y son cruciales para asignar sabiamente las inversiones de restauración para alcanzar los objetivos deseados de conservación.

Palabras Clave: aves de bosque, complementariedad, distribuciones dinámicas, esquemas agroambientales, Marxan, planeación sistemática de la conservación, priorización espacial, restauración de la vegetación

Introduction

Restoration plantings are a widely implemented approach to biodiversity conservation in agricultural landscapes (Bullock et al. 2011). Worldwide, international biodiversity targets for 2020 include the restoration of at least 15% of degraded ecosystems (Aichi Biodiversity Target 15, CBD COP 2010). Similar international targets for the restoration of 150 million ha of degraded lands by 2020 (Rio+20, UNCSD 2012) are estimated to cost nations globally US\$18 billion per year (Menz et al. 2013). Specific restoration targets have been set by the European Union (Bullock et al. 2011) and individual countries, including Australia, whose Biodiversity Fund aims to restore 18 million ha of native vegetation by 2020 with a budget of US\$1 billion (Australian Government 2013). Given this substantial investment, to maximize biodiversity outcomes it is important that restoration initiatives be both efficient and cost-effective (Menz et al. 2013).

Most research on biodiversity outcomes relative to restoration plantings (a form of active restoration) has focused on whether and how individual plantings achieve high levels of species occurrence, richness, or abundance (Munro et al. 2007). In addition to comparing the value of restoration plantings to that of reference sites (e.g., Gould et al. 2013), these studies have identified attributes of plantings that contribute to increased biodiversity at the site scale, including planting age (Vesk et al. 2008) and area and shape (Lindenmayer et al. 2010; Jellinek

et al. 2014) and vegetation structure (Munro et al. 2011). This earlier research recommends that future restoration investment be focused on maximizing site-scale attributes related to high individual planting biodiversity. Restoration plantings, however, also have value at the landscape scale (Thomson et al. 2009; Rappaport et al. 2015), and the collective features of different plantings across the landscape may be a better measure of biodiversity value than site-scale attributes. An alternative approach to restoration investment, therefore, is to maximize the number of species present across the entire landscape through a focus on networks of restoration plantings.

Systematic conservation planning, originally developed for locating and designing cost-effective protected areas (Margules & Pressey 2000), is increasingly being used for spatial prioritization of new restoration areas (Thomson et al. 2009; Lethbridge et al. 2010; McBride et al. 2010; Wilson et al. 2011; Yoshioka et al. 2014; Possingham et al. 2015). A key concept is complementarity, which ensures that each restoration planting contributes unrepresented features to the larger network of plantings (i.e., each planting complements the others in the network) (Margules & Pressey 2000). Complementarity approaches to the selection of restoration plantings thus differ from selection based on traditional measures of conservation value that focus on the most species-rich plantings. This is because plantings with high individual species richness may not necessarily contribute to overall conservation goals of maximizing diversity at a landscape

or regional scale (Margules & Pressey 2000; see also Chadès et al. 2015). Systematic conservation planning has frequently been used to evaluate the performance of an existing set of protected areas (e.g., Stewart et al. 2003), and the same approach might be useful to evaluate the performance of an existing network of restoration plantings. Undertaking such an evaluation would identify the best complementary subset of plantings that contribute the most to the biodiversity benefits of the network and might be afforded protection in cases of impact assessment and future landscape clearing and elucidate the attributes of plantings important for landscape-scale biodiversity outcomes. In doing so, landscapes undergoing restoration may have more efficient investment and conservation outcomes.

Most systematic conservation planning considers species occurrence only at a single point in time, but plant and animal communities (particularly those in disturbed landscapes) are temporally dynamic (Grantham et al. 2011; Runge et al. 2014; Tulloch et al. 2016). Failure to incorporate dynamics into spatial prioritizations (e.g., basing them on static species distributions derived from a single year of data or pooled over years) can lead to insufficient representation of species over time (Runge et al. 2016; Tulloch et al. 2016). Although previous spatial prioritizations for restoration have considered dynamics in the age and structural complexity of restored vegetation (e.g., Thomson et al. 2009), we are not aware of any spatial prioritization study that has accounted for temporal dynamics in the distribution or occurrence of species colonizing restoration plantings, an oversight that could undermine the success of restoration schemes.

We investigated whether a temporally dynamic complementarity approach can be used to evaluate the contribution of existing restoration plantings to achieve landscape-scale species occurrence. We used, as a case study, a network of plantings in the South West Slopes bioregion of southeastern Australia. Only 15% of this once-extensive temperate eucalypt woodland remains within this agricultural region (Benson 2008); consequently, many woodland bird species are of conservation concern (Rayner et al. 2014). Since 1990, however, concerted investment has been made to establish restoration plantings for a range of conservation- and land-management objectives, including increasing woodland bird habitat. Through extensive programs managed by multiple stakeholders, thousands of hectares of vegetation have been planted, corresponding to increases of 3–4% of vegetation cover in the landscape (Lindenmayer et al. 2012; Cunningham et al. 2014). As part of the South West Slopes Restoration Study (Cunningham et al. 2007), 61 plantings have been surveyed for birds and vegetation in 5 spring seasons since 2006.

Our first aim was to find the best complementary network (i.e., subset) of established restoration plantings to support landscape-scale occurrence of species of conser-

vation concern for minimal establishment cost. We accounted for temporally dynamic species occurrences by requiring representation targets for species occurrence to be met in every year (Runge et al. 2016). We compared the outcomes of taking a dynamic complementarity approach to find a network of plantings that met our desired representation target with networks selected using a static complementarity approach based on single years of data and with networks of plantings of an equivalent cost ranked by richness of species of conservation concern.

Our second aim was to identify the attributes of plantings that contributed most to the landscape-scale occurrence of species of conservation concern. The plantings in our study were established for a variety of reasons (e.g., wind breaks, soil erosion, and salinity); differed in age, area, shape, vegetation structure, and landscape context; and subsequently differed in their individual value for woodland birds (Lindenmayer et al. 2010). This opportunistically created a network of plantings that was ideal for exploring how subsets of plantings with different characteristics differed in terms of their ability to represent all bird species of conservation concern. Thus, we sought to quantify the value of evaluating biodiversity benefits of management at the landscape scale and incorporating temporally dynamic species distributions into restoration planning. The work seeks to inform future investment to ensure more efficient and cost-effective biodiversity outcomes across restoration landscapes.

Methods

Study Area, Experimental Design, and Data Collection

The South West Slopes Restoration Study is a 150 × 120 km area of the South West Slopes bioregion of New South Wales, Australia (Fig. 1). This region was once dominated by temperate box-gum *Eucalyptus* woodland but is now characterized by cropping and livestock grazing. Farms typically have 3–35% native vegetation cover, including old-growth woodland, regrowth, and plantings (Cunningham et al. 2014). We used data from 61 plantings distributed across 25 farms. Typically, plantings were a mix of local endemic and widely distributed Australian ground cover, understory, and overstory species and plants were spaced about 2 m apart. For each planting, we compiled data on variables important for bird species richness and occurrence in restoration plantings: years since establishment, area and width of plantings, vegetation structural complexity, surrounding woody vegetation cover (a proxy for connectivity), and landscape position (Supporting Information).

We used the area and shape of plantings to estimate the total establishment cost of each planting. Our estimates were based on 2015 pricing rates used by Greening

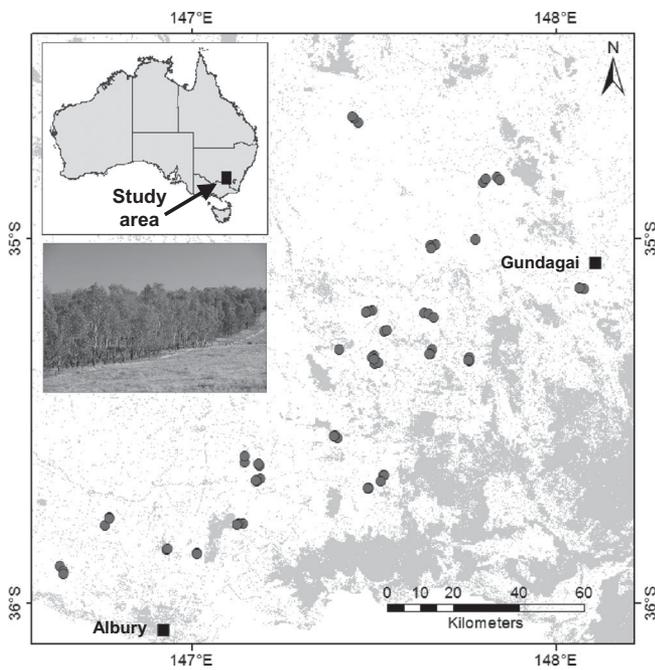


Figure 1. Map of study area showing restoration planting sites (points are not drawn to scale; gray shading, native woody vegetation cover). Insets show location of study area within Australia (top) and image of a typical planting site (bottom). Photo by D. Blair.

Australia, one of Australia's largest and longest running restoration practitioners. We calculated costs (\$AU) of materials and labor for fencing and direct-seeding of sites (Supporting Information). Because our focus was on biodiversity as a public benefit, we considered only public costs of establishing restoration sites. We acknowledge the importance of considering private opportunity costs and ongoing management costs in conservation planning on public land, but the inclusion of such information was beyond the scope of this study.

We collected bird occurrence data in the spring seasons of 2006, 2008, 2009, 2011, and 2013. In each year, every planting was visited twice within 4 days in early November (2 days by different observers), and a 5-min point count was conducted at the 0-, 100-, and 200-m points of a permanent transect. All birds seen or heard within 50 m of the point, excluding those flying overhead, were recorded as present. Surveys were conducted between sunrise and midmorning on days when the weather was not inclement. This strict survey protocol was designed to address biases in observer heterogeneity (Cunningham et al. 1999) and false-negative errors (i.e., failure to detect species that are present [Banks-Leite et al. 2014]).

We defined woodland birds of conservation concern as those species dependent on woodland for foraging or nesting (Silcocks et al. 2005) and listed as threatened

in New South Wales under the *Threatened Species Conservation Act 1995* (this also captured relevant nationally listed threatened species) or identified as having a >20% decrease in South West Slopes bioregion reporting rate between the first and second *Atlas of Australian Birds* (Barrett et al. 2003). Excluding very rare species (recorded only once during the 5 years), this definition resulted in 26 species of conservation concern for analysis (Supporting Information). We used permutational multivariate analysis of variance (PERMANOVA) to test for significant differences in species composition between years, based on a Bray–Curtis dissimilarity matrix adjusted for species presence–absence data, with the vegan package in R (R Development Core Team 2007).

Data Analyses

To identify targets of landscape-scale occurrence of species of conservation concern for the least investment, we compared the outcomes of using dynamic versus static complementarity approaches, and complementarity versus ranked approaches, to find the best subset network of restoration plantings. We set targets of 10–100% (in increments of 10) occurrence of each species per year in all years (equivalent to 10–100% of plantings where each species occurred in each year).

To find the best complementarity-based networks of plantings for each target, we used the decision-support software, Marxan, which uses a simulated annealing algorithm to solve the minimum-set problem (Ball et al. 2009). The objective was to minimize resources expended (i.e., cost of the planting network) while meeting prespecified representation targets (i.e., scenarios of 10–100% individual species occurrence per year in all years). To account for temporal variation in species occurrence between plantings (planting units), we created a conservation feature for each species for each survey year (5 conservation features per species of conservation concern for 130 conservation features in total), following Runge et al. (2016). Representation of conservation features in a given planting was based on presence–absence data (i.e., whether or not each species was recorded in each planting in each year). For each incremental increase in representation target, we compared the dynamic approach with 5 static approaches based on single years of data (i.e., 2006 only, 2008 only, 2009 only, 2011 only, and 2013 only). The objective of the static approaches was to meet representation targets only for that particular year. We parameterized Marxan to find the most cost-effective network irrespective of spatial configuration (by setting the boundary length modifier to zero) and performed 100 runs per scenario. We confirmed that the selected networks were not driven by planting cost by comparing the scenarios with baseline no-cost scenarios (Supporting Information). We considered 2 Marxan outputs for each scenario: the network of plantings that best met

the representation target for the least cost and the selection frequency (i.e., irreplaceability) of each planting (the number of times each planting was selected across the 100 runs). For our scenarios, these 2 values were strongly positively correlated (≥ 0.9), and the average selection frequency for plantings selected in the best network was close to 100% (Supporting Information). Because this indicates high irreplaceability in selected plantings, we used the identified best networks of plantings for subsequent analyses.

We paired each dynamic complementarity scenario with a ranked scenario of equivalent cost, creating 10 matched pairs of networks (i.e., one for each species occurrence target [10–100%]). To do this, we calculated total richness of species of conservation concern across the 5 survey years and ranked individual plantings from high to low species richness. We calculated the cumulative cost of the plantings based on these rankings and included in the best network only those plantings that cost less than or the same as the cost of the dynamic complementarity scenario.

For each network selected by the dynamic, static, and ranked approaches, we calculated the cumulative establishment cost, number of plantings in the network, and summary statistics for the minimum percentage of the occurrence of each species that was met over the 5 years. We also calculated Bray–Curtis dissimilarity (adjusted for presence–absence data) between networks to assess spatial concordance between the selected plantings (e.g., low Bray–Curtis dissimilarity between a pair of networks indicates that the spatial locations of the plantings in the networks were similar). We confirmed that differences between the dynamic complementarity and ranked networks were not driven by cost-effectiveness by comparing our results with networks of equivalent cost that were based on ranking plantings by cost-effectiveness but ignoring complementarity (dividing species richness by cost) (Supporting Information).

To identify the attributes of plantings that contributed to landscape-scale occurrence of species of conservation concern, we modeled the relationship between planting attributes and the probability of the planting being selected in the dynamic and static complementarity and ranked scenarios for 2 representation targets (30% and 60% species occurrence in all years). We also modeled the number of times (frequency) each planting was selected in the static networks for these targets over the 5 years. The first target (30% occurrence) was chosen to reflect typical targets for conservation assessments (Svancara et al. 2005). The second target (60% occurrence) was chosen based on the results of the Marxan analyses because there was a threshold jump in planting benefits at this target level for the dynamic complementarity approach. Planting attributes included standardized site-level variables (Supporting Information). Planting width was strongly and positively correlated with

planting area, so we excluded it from further analyses. We adopted an information-theoretic approach to model selection (Burnham & Anderson 2002) and compared a candidate set of 31 models that included single and additive combinations of all planting attributes (Supporting Information). We considered the univariate planting-area model the null model because previous research suggests that this attribute is of primary importance in restoration (e.g., Lindenmayer et al. 2010). We fitted generalized linear models with a binomial error distribution and log link (AICcmodavg package). We modeled each response variable against a distance-weighted spatial autocovariate (spdep package) to check for spatial autocorrelation between sites. For response variables that showed evidence of spatial autocorrelation, we included the distance-weighted spatial autocovariate in each alternative model. We ranked the candidate set of models with Akaike's information criterion corrected for small sample sizes (AICc). For top-ranked models (within 2 Δ AICc of the model with the lowest AICc), we assessed model support with Nagelkerke's coefficient of determination (R^2 ; fmsb package) and calculated model-averaged effect sizes for the model terms.

Results

Over the 5 survey years, we recorded 100 woodland bird species, including 26 of conservation concern (Supporting Information). Total richness of species of conservation concern ranged from 1 to 14 species per planting. Species composition differed significantly between years ($F = 2.723$, $p = 0.006$).

Dynamic Versus Static Complementary Restoration Planting Networks

The complementarity approach that incorporated dynamic species occurrences consistently resulted in higher mean minimum percent occurrence of species across the 5 survey years than the static complementarity approaches based on single years of data (Fig. 2a & Supporting Information). Although more expensive to achieve any given target than the static approaches, the dynamic approach always met the representation target for every species (Fig. 2b). In comparison, although plantings selected using a static single-year approach met the representation target for that year, they failed to meet the representation target over time (2006–2013) for more than one-third of species. This is because all 61 plantings were required to meet the dynamic representation target of 100% occurrence for each species over the period; for static targets, 42–54 plantings were required.

The spatial locations of the best network of selected plantings differed markedly between years. For example, for the 30% target, there was 44–78% Bray–Curtis

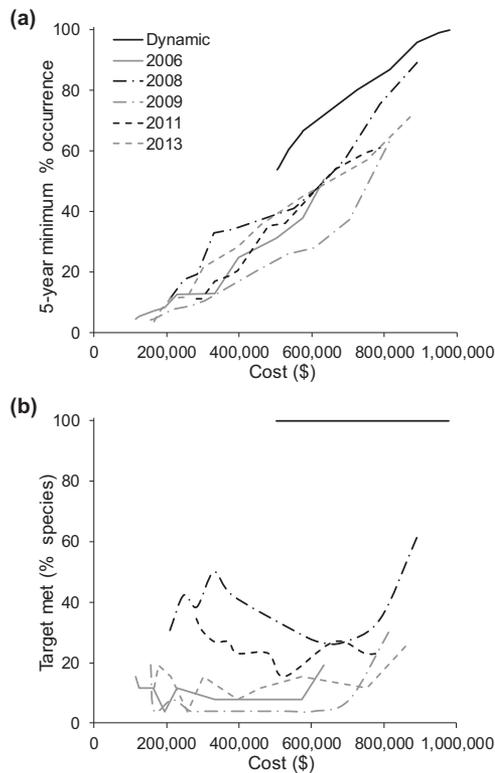


Figure 2. Comparison of 5-year outcomes under dynamic (incorporating species occurrences over 5 survey years) and static (based on single years of data, i.e., 2006, 2008, 2009, 2011, or 2013) complementarity approaches to maximize landscape-scale occurrence of species of conservation concern for (a) 5-year mean minimum percent species occurrence and (b) percentage of species meeting representation targets. Each line represents 10–100% representation targets.

Table 1. Percent Bray–Curtis dissimilarity between the spatial locations of plantings selected in the static (2006 only, 2008 only, 2009 only, 2011 only, and 2013 only) and dynamic complementarity restoration planting networks for the representation target of 30% occurrence for each species of conservation concern.

Network	2006	2008	2009	2011	2013
Static					
2008	44.44				
2009	52.94	57.89			
2011	54.29	48.72	78.38		
2013	43.75	50.00	58.82	54.29	
Dynamic	50.00	38.46	36.00	45.10	41.67

dissimilarity in selected plantings between years (Table 1). To meet this target, each planting was selected an average of 1.46 times (out of 5 possible static networks); 20 plantings were never selected and only 1 planting was always selected. The spatial locations of the selected plantings also differed between the dynamic and

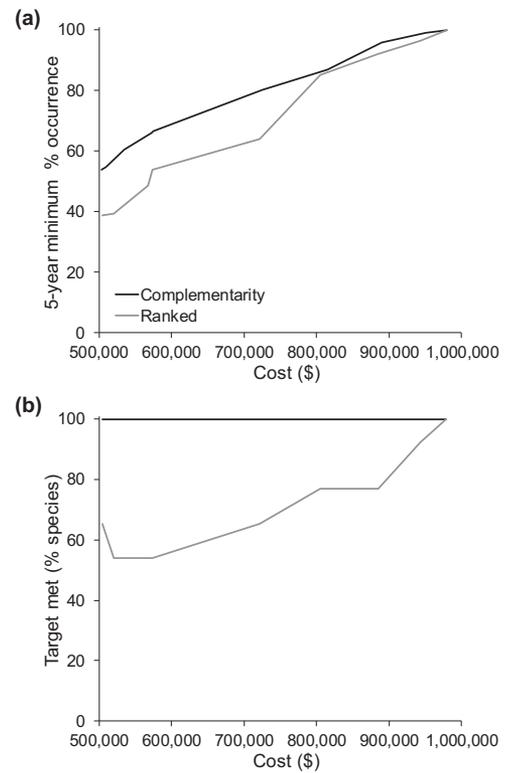


Figure 3. Comparison of dynamic complementarity (defined in the legend of Fig. 2) and species-richness ranked approaches to maximize landscape-scale occurrence of species of conservation concern for (a) 5-year mean minimum percent species occurrence and (b) percentage of species meeting representation targets. Each line represents 10–100% representation targets.

static approaches (average Bray–Curtis dissimilarity for the 30% target = 49%). However, within each approach, plantings selected under low representation targets were usually also selected under higher targets (average Bray–Curtis dissimilarity between increments = 12%).

Dynamic Complementary Versus Ranked Restoration Planting Networks

The dynamic complementarity approach consistently resulted in higher mean percent species occurrence than the species-richness-ranked approach (Fig. 3a & Supporting Information). For equivalent cost, mean minimum percent occurrence of species was up to 30% higher in the complementarity scenarios. Further, although the representation target was achieved in every complementarity scenario (i.e., all species met the specified target), up to 46% of species did not meet the target in the equivalent-cost ranked scenarios (Fig. 3b). On average, there was 78% overlap in the spatial location of plantings

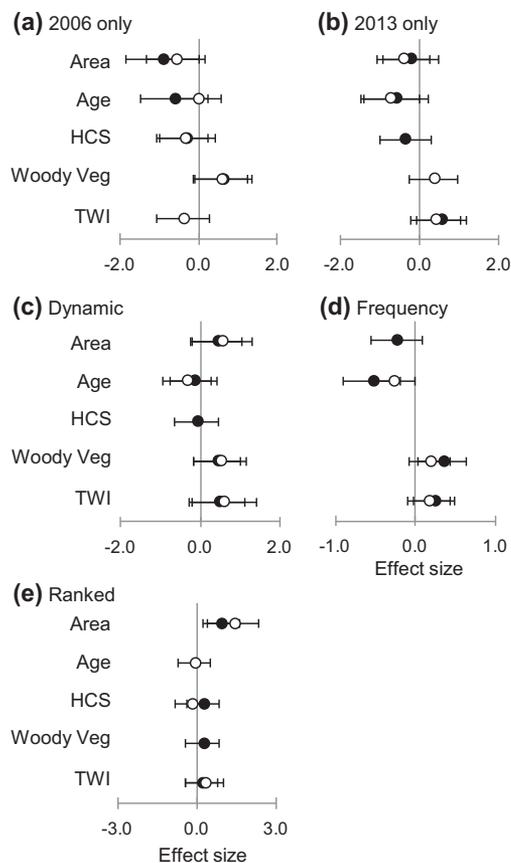


Figure 4. Summary of model-averaged effect sizes (and 95% CIs) for terms in the top-ranked models ($\Delta AIC_c \leq 2$) for 30% (closed circles) and 60% (open circles) representation targets. See Table 2 for a description of models and model terms. See Supporting Information for plots for 2008 only, 2009 only, and 2011 only models.

selected under the complementarity and ranked approaches (average Bray–Curtis dissimilarity = 22%).

Relationships with Planting Attributes

Plantings selected under the static and dynamic complementarity approach for the 30% and 60% targets did not consistently differ in their attributes from the plantings that were not selected. Model uncertainty was high because top-ranked models had relatively low R^2 values (Table 2). The effect sizes of terms in the models were generally small and variable (confidence intervals crossed 0) (Figs. 4a–c & Supporting Information). Similarly, there was no consistent relationship between the number of times each planting was selected in the static networks over the 5 years and planting attributes (Fig. 4d). Plantings selected more frequently to meet the 30% target were younger and surrounded by more woody vegetation cover, but effect sizes were small, and these

effects were variable for plantings selected to meet the 60% target. In comparison, plantings selected under the richness-ranked scenarios were larger than plantings that were not selected, and model certainty was relatively high (Table 2, Fig. 4e).

Discussion

The restoration of degraded lands is an international conservation goal with multibillion dollar annual investments that require wise allocation of resources (Bullock et al. 2011; Menz et al. 2013). We found that it is possible to apply the principles of systematic conservation planning to evaluate the extent to which an existing network of restoration plantings meets representation targets for woodland birds of conservation concern. Incorporating dynamics in species occurrences across a 5-year period resulted in higher species occurrences and proportion of targets met compared with using species occurrences that represented a single point in time. Importantly, we found that for equivalent cost, the dynamic complementarity approach always resulted in higher average minimum percent occurrence of species maintained through time and a higher proportion of the bird community meeting representation targets compared with ranking plantings by species richness (aim 1). We also found that plantings selected to achieve goals of both representation and complementarity represented the full range of planting attributes, whereas plantings selected under the richness approach were larger (aim 2).

Incorporating dynamic species occurrences led to more expensive networks of restoration plantings but considerably higher long-term species occurrences and achievement of representation targets compared with static approaches. This was because the bird community was highly spatially and temporally dynamic, and there was little overlap between networks selected based on single years of data. Compared with static-distribution approaches, incorporating temporally dynamic species' ranges in systematic conservation planning led to more expensive and less flexible networks but improved biodiversity outcomes (see also Grantham et al. 2011; Lourival et al. 2011; Van Teeffelen et al. 2012). For example, Runge et al. (2016) found that accounting for annual and seasonal range variation in nomadic bird species leads to greater areas of land needing to be conserved to achieve targets but greater levels of species protection. Similarly, in their case study of the South American Pantanal wetlands, Lourival et al. (2011) found that incorporating dynamic vegetation distributions, although it increases expense, improves the reliability and long-term adequacy of their reserve networks. A dynamic prioritization approach is thus crucial for allocating investment wisely to reach desired conservation goals (Tulloch et al. 2016).

Using a landscape-scale complementarity approach was critical to achieve cost-effective subsets of restoration plantings across the existing network. For example, to achieve similar species representation (for targets $\leq 90\%$ species occurrence), the complementarity approach required less investment, fewer plantings, and less combined restored area than the ranked approach based on site-scale species richness. Further, even with the substantial additional investment needed for the ranked approaches, many species still did not meet the representation target in every year (compared with all targets achieved under the complementarity approach). Complementarity approaches to reserve design have long been recognized as superior to ranked approaches (Chadès et al. 2015), and our study supports their utility in restoration programs (Yoshioka et al. 2014). However, by definition, the high efficiency that complementarity achieves may result in low redundancy across the network of restoration sites, with implications for network robustness to disturbance (O'Hanley et al. 2007). In our scenarios, we incorporated multiple years of data, including from severe drought (2006–2009) and postdrought recovery (2011–2013). Incorporating these dynamics within our system likely reduced the trade-off between complementarity and robustness by accounting for stochastic processes (Lourival et al. 2011; Van Teeffelen et al. 2012).

Our finding that no single attribute makes plantings best for bird occupancy over space and time challenges conventional thinking that there is a type of restoration planting best for woodland birds (Lindenmayer et al. 2010). Instead, our findings support previous research on the differing and complementary suitability of plantings for different functional groups (Loyn et al. 2007). By collectively considering occupancy of plantings by each species in our analyses, we specifically accounted for the variable habitat requirements of our bird community. However, it is difficult to evaluate to what extent the bird occurrence patterns within the best networks of plantings were influenced by bird occurrence in unselected plantings (to which highly mobile taxa like birds could disperse) or by other vegetation types (e.g., regrowth and remnant vegetation) in the study landscape (Lindenmayer et al. 2012). Future research should investigate complementarity and connectivity between restoration plantings, regrowth vegetation (i.e., passive restoration), and remnant vegetation for landscape-scale species persistence. Future research could also integrate dynamics in planting attributes with dynamics in species occurrences. For instance, we held planting attributes constant, yet some attributes such as age, structural complexity, and connectivity may change through time (Thomson et al. 2009). As such, the attributes of plantings that are likely to maximize complementarity may also change through time, as suggested by our findings from our static models. Ideally, any future research that uses cost-effectiveness

analysis to prioritize restored habitat in agricultural landscapes should also incorporate costs associated with lost farming opportunities in restored areas (Naidoo et al. 2006).

Translating our findings into future restoration policy involves some challenges. Our results show that it is desirable from a complementarity perspective to encourage a mixed portfolio of restoration projects that differ in the attributes of plantings and landscape context. Given real-world social, economic, and political constraints on biologically-driven conservation planning, “informed opportunism” (sensu Noss et al. 2002) may be appropriate. That is, in addition to available biodiversity knowledge, future investment in restoration initiatives should also be guided by the capacity and willingness of land owners to participate (Knight et al. 2010). A key difficulty is developing policy that can capitalize on informed opportunism to achieve complementary planting networks. One approach may be to implement policies that support consistent, incremental funding of restoration plantings in a region, so that a breadth of planting ages and structural attributes is maintained. Another more resource-intensive approach could be to allocate funding for new plantings that would complement the attributes of existing restoration plantings.

We found that a complementarity approach can be used to find the best network of established restoration plantings and that this network is more cost-effective and represents more of species' landscape occupancy than a traditional species-richness approach. Further, incorporating temporally dynamic species occurrences leads to a more cost-effective and robust restoration-plantings network compared with using static single-year data (Grantham et al. 2011; Lourival et al. 2011; Van Teeffelen et al. 2012; Runge et al. 2014). Substantial resources will continue to be invested in restoration initiatives in response to international and national policy and as part of wider agrienvironmental schemes (Bullock et al. 2011; Menz et al. 2013). This investment should not attempt to achieve all conservation goals within individual plantings but could instead be implemented incrementally to capitalize on restoration opportunities as they arise (Noss et al. 2002) to achieve collective value of multiple plantings across the landscape. Adopting a landscape-scale temporally dynamic approach leads to considerably better outcomes for a faunal community of conservation concern than applying conventional site-scale metrics and is crucial for the wise allocation of restoration investment to reach desired conservation goals.

Acknowledgments

We thank the Australian Research Council, the Murray and Riverina Local Land Services, and the Caring for Our Country Program for funding for this project. We thank

D. Michael, M. Crane, S. Okada, C. MacGregor, L. McBurney, D. Blair, and D. Florence for their important contribution to the collection of the field data, and C. Foster and the Conservation and Landscape Ecology Group for discussion of ideas.

Supporting Information

Summary and definition of planting attributes (Appendix S1), habitat-complexity score calculation (Appendix S2), establishment costs of planting (Appendix S3), list of woodland bird species of conservation concern (Appendix S4), comparison with no-cost scenarios (Appendix S5), mean selection frequencies of selected plantings (Appendix S6), candidate set of models considered in model selection (Appendix S7), summary of dynamic and static complementarity scenarios (Appendix S8), summary of dynamic complementarity and ranked scenarios (Appendix S9), and summary of the 2008, 2009, and 2011 static complementarity models (Appendix S10) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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