

Joining the dots versus growing the blobs: optimal spatial targeting of ecological restoration.

Maksym Polyakov ^a, Fiona Gibson ^a, and David J. Pannell ^a

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Abstract: The primary causes of biodiversity decline worldwide are the destruction, alteration, and fragmentation of habitat resulting from human economic activities such as agriculture or property development. In regions with highly cleared and fragmented landscapes, biodiversity conservation efforts typically involve the restoration of native habitat and the rebuilding of functioning ecosystems. In this study, we use simulation to compare several commonly used strategies for spatially targeting ecological restoration efforts when creating conservation networks on private lands in a fragmented agricultural landscape. The evaluated targeting strategies are Aggregation, Connectivity, and Representativeness. We compare the effectiveness of these targeting strategies to the effectiveness of ecological restoration without targeting. We allow for heterogeneity in landowners' willingness to participate in restoration projects and explicitly assume that not all parcels within target areas will be restored. We model the probability of participation in restoration projects as a function of the private benefits of ecological restoration captured by the landowner. Results show that regardless of which targeting strategy is used, targeted ecological restoration outperforms untargeted ecological restoration. Relative effectiveness of the targeting strategies depends on landscape characteristics, species characteristics, restoration effort, and assumption about private benefits of ecological restoration. At low levels of restoration effort and in highly cleared landscapes, Aggregation and Representativeness perform better. With larger restoration effort and in less fragmented landscapes, Connectivity becomes more effective. Accounting for the landowners' behavior through a private benefits function improves the biodiversity outcome for most species and improves the relative effectiveness of connectivity-focused strategies.

Keywords: Ecological restoration; Spatial targeting; Private benefits; Simulation;

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JEL Classification: Q15, Q57, Q58

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^a Centre for Environmental Economics and Policy, UWA School of Agriculture and Environment, The University of Western Australia, Perth WA 6009, Australia

Introduction

The primary causes of biodiversity decline worldwide are destruction, alteration and fragmentation of habitat resulting from human economic activities such as agriculture or development (Fahrig, 2003, Foley et al., 2005). Public- and private-sector organizations allocate considerable resources to slow biodiversity decline by conserving the remaining natural vegetation for habitat. However, achievement of biodiversity goals may require not just retention of existing vegetation, but also restoration of vegetation on currently cleared land, especially in a landscape that is highly cleared and fragmented (meaning that remaining native vegetation is in disconnected patches) (Moilanen et al., 2005, Thomson et al., 2009). The quality of vegetation as habitat depends on its spatial pattern, particularly the size of contiguous patches, the distances between patches and the composition of patches in terms of their vegetation types (Polyakov et al., 2015). Therefore, attention to spatial context is essential when planning the restoration of habitat. The effectiveness of voluntary conservation programs can be improved by appropriate targeting (Babcock et al., 1997, Khanna et al., 2003, Sutton and Armsworth, 2014, Wu, Zilberman, and Babcock, 2001).

Various strategies have been proposed and used for targeting habitat restoration spatially. One is to restore vegetation on the edge of existing patches, increasing the contiguous area of habitat suitable for certain species (Cowling et al., 1999). Some species require large contiguous areas of habitat and are likely to be benefited by this strategy, which is variously known as the patch-size-focused strategy (Lee and Thompson, 2005), contiguity (Fooks et al., 2016), or aggregation (Mokany, Harwood, and Ferrier, 2013).

A second strategy is to restore vegetation in such a way that it connects existing patches, in so-called “corridors”. This is known as the isolation-focused strategy (Lee and Thompson, 2005) or connectivity (Mokany, Harwood, and Ferrier, 2013). This approach benefits species

that will not cross unvegetated areas by allowing them to move between patches, effectively increasing the area of habitat available to them. Some species also prefer to occupy the edges of habitat, and corridors have a high ratio of edges to interior.

Thirdly, environmental managers may aim to restore vegetation so as to achieve high “representativeness” of habitat types (Mokany, Harwood, and Ferrier, 2013). The aim here is to achieve a high heterogeneity of habitat features to support a wide range of species with different preferences and needs.

Spatial targeting of land retirement to improve water quality can substantially increase the cost-effectiveness of voluntary conservation programs (Khanna et al., 2003, Yang, Khanna, and Farnsworth, 2005, Yang et al., 2005). Spatial targeting of parcels to increase biodiversity improves the aggregate environmental and social welfare outcomes (Fooks et al., 2016).

Lewis, Plantinga, and Wu (2009) analyzed spatial prioritization of incentives to reduce fragmentation of a forest landscape. They found that the corner solution (to achieve either full reforestation or none) would be optimal for a section of landscape due to the convexity of expected marginal benefits and inability of the regulator to control exact locations of reforestation.

Choice of a specific spatial targeting strategy, such as connectivity, aggregation or representativeness, has implications for the biodiversity outcome. The effectiveness of these targeting strategies in the design of conservation reserves was compared by Mokany, Harwood, and Ferrier (2013), but without consideration of socioeconomic factors such as ownership structure and the probability of landowners’ participation in conservation. Land tenure can be important because of issues with getting private landowners to participate in restoration schemes and the significant implications that non-participation can have for biodiversity outcomes. Tenure may have a different implications for different targeting

strategy, especially in fragmented landscapes. Among economic studies that analyzed spatial targeting of biodiversity conservation or ecological restoration, the alternative strategies identified above (aggregation, connectivity, and representativeness) were not compared. For example, Fooks et al. (2016) evaluated contiguity targeting, while Lewis, Plantinga, and Wu (2009) analyzed targeting to reduce fragmentation. Both studies found that targeting improves the effectiveness of conservation effort. Whilst the results of these two studies are useful to practitioners of ecological restoration tasked with selecting a targeting strategy, a direct comparison of the three strategies would be even more useful.

In our study, we set out to bridge this gap. We use simulation to compare spatial targeting strategies for ecological restoration on private lands in a fragmented agricultural landscape. The effectiveness of the three targeting strategies is compared to the effectiveness of ecological restoration without targeting. We allow for heterogeneity of landowners' willingness to participate in restoration projects and assume that not all parcels within the target area will be restored. We model the probability of participation in restoration projects as a function of the private benefits of ecological restoration that are captured by the landowner, following Polyakov et al. (2015). We model biodiversity benefit using the approach proposed by Polasky et al. (2005). We overcome the issue of scale identified by Lewis, Plantinga, and Wu (2009) by modeling land-use decisions at the property scale while evaluating ecological outcome using spatial processes at the landscape scale.

Biodiversity benefit of the habitat in fragmented landscapes

Assume a fragmented landscape consisting of the matrix (cleared land) and N patches of habitat with areas A_n , $n \in [1 \dots N]$. Benefit B^x for species x is derived from the landscape's ability to support a population of this species. Specifically it is measured as the number of

breeding pairs of species x that the landscape can support. For simplicity of presentation, we assume that the matrix is not suitable for the species and that the species cannot travel between patches, although the second restriction could be relaxed by expressing propensity of travel as a function of the distance between the patches and species characteristics. The carrying capacity of habitat per unit area C_n^x for vegetation patch n for species x is determined by the habitat requirement of a breeding pair H^x and the minimum viable population P^x of breeding pairs. If the area is too small to support population P^x we assume that the carrying capacity is zero.

$$(1) \quad C_n^x = \begin{cases} 0 & \text{if } A < H^x P^x \\ A_n / H^x & \text{if } A \geq H^x P^x \end{cases} .$$

However, due to the uncertain nature of the parameters, including the minimal viable population, the carrying capacity function is better expressed probabilistically as a sigmoid-shape (e.g., logistic) function of the patch size: $C_n^x = F^x(A_n)$; $F^{x'}(A) > 0$ (figure 1). Figure 1 is divided into three parts. Part I indicates the patch sizes that do not provide habitat for a viable population, part II indicates patch sizes where carrying capacity is diminished because the size of the patch is close to supporting the minimum viable population, and part III indicates patch sizes that provide habitat for a viable population.

[Insert Figure 1 here]

Furthermore, existing and restored habitats differ by quality Q , which can take values between 0 and 1 (Polasky et al., 2008). It is measured as a fraction of ideal habitat quality for species x . Thus, the value of benefit of the current landscape for species x is

$$B_0^x = \sum_{n=1}^N A_n Q_n^x F^x(A_n).$$

Effectiveness of targeting strategies of ecological restoration

To illustrate the consequence of restoration, assume that there are two patches of existing habitat with areas A_1 hectares and A_2 hectares in the landscape, and that there are resources to restore A_3 hectares of the matrix. The location of restoration sites can be selected using one of the three spatial targeting strategies, S : *Aggregation* (a), *Connectivity* (c) and *Representativeness* (r). *Aggregation* prioritizes restoration of the sites immediately adjacent to either of the existing patches 1 and 2. If restored sites are adjacent to patch 1, the new biodiversity benefit becomes $B_a = (A_1Q_1 + A_3Q_3)F(A_1 + A_3) + A_2Q_2F(A_2)$. *Connectivity* prioritizes selection of restoration sites that connect existing patches. After implementing a restoration project using the connectivity strategy (i.e., A_3 is located such that when it is restored, it connects existing patches A_1 and A_2), the biodiversity benefit becomes $B_c = (A_1Q_1 + A_2Q_2 + A_3Q_3)F(A_1 + A_2 + A_3)$. *Representativeness* prioritizes restoration of sites that have the most suitable habitat type for the target species (sites with the highest Q^x value), without regard to a location relative to the existing habitat. In the worst case, if sites with the highest potential habitat quality are not adjacent to the existing patches of habitat, the biodiversity benefit becomes $B_r = A_1Q_1F(A_1) + A_2Q_2F(A_2) + A_3Q_3F(A_3)$. In better cases, if sites with the highest potential habitat quality are adjacent or connecting, then $B_r = B_a$ or $B_r = B_c$.

Now consider a comparison of the benefits of ecological restoration using the above strategies in a situation when restoration is successful. For example, when the targeting strategy is *aggregation*, either patch 1 or 2 is enlarged by A_3 hectares of adjacent restored habitat; when the targeting strategy is *connectivity*, two patches of habitat become connected;

and when the targeting strategy is *representativeness*, an A_3 -hectare patch of high-quality habitat is created. The difference between the connectivity strategy and the aggregation strategy depends on the species characteristics (habitat requirements H^x and the minimal viable population P^x), the degree of fragmentation of the landscape (patch sizes A_1 and A_2), and the restoration area (A_3). Habitat requirement and viable population determine the shape of the function $F^x(A)$.

When A_1 and A_2 are in part III of the graph in figure 1, ecological restoration using *aggregation* and *connectivity* spatial targeting strategies result in similar benefit. Because the sizes of the initial patches A_1 and A_2 are large, the suitability of a patch is not particularly sensitive to further increases in patch size. If A_3 is also in part III, implementing the *representativeness* strategy may result in greater benefit than connectivity and aggregation strategies, because $F(A_3) \approx F(A_1)$ while $Q_{3r} \geq Q_{3c}$. When A_1 and A_2 are in the part II of the graph, $B_c > B_a$ because $F(A_1 + A_2 + A_3) > F(A_1 + A_3)$. Whether $B_r > B_c$ or $B_r < B_c$ depends on how large are $F'(A)$ and Q_{3r}/Q_{3a} .

Effectiveness of targeting strategies when participation of landowners is uncertain

Consider ecological restoration being implemented by multiple private landowners. The environmental manager cannot force landowners to participate and relies on incentives to encourage voluntary participation. The manager needs to identify a sufficiently large target area that non-participation by some landowners does not jeopardize the achievement of biodiversity goals. We define expected benefit of a strategy as the benefit of its successful implementation times probability of the strategy being successfully implemented:

$$E(B_s) = \Pr(s) B_s \text{ where strategy } s \in \{a, c, r\}.$$

Under an *aggregation* strategy, only areas immediately adjacent to existing patches of habitat are targeted. Therefore, if some targeted landowners do not participate, the restoration projects of participating landowners will still be immediately adjacent to the existing habitat and will contribute to the benefit of the strategy. Therefore, $\Pr(a) = 1$ and

$$E(B_a) = \Pr(a)B_a = B_a.$$

According to the *connectivity* strategy, the target area is a corridor that connects two patches of existing habitat. The probability of success of this strategy depends on enough landowners participating to create a linking corridor of vegetation. The link could be broken by any of a number of landowners declining to participate. If participation of individual landowners is random, the probability of success of the connectivity strategy decreases as the length of the corridor D increases and as the number of landowners L in the corridor increases:

$\Pr(c) < 1$; $\Pr(c) = F(D, L)$; $\partial \Pr(c) / \partial D < 0$; $\partial \Pr(c) / \partial L < 0$. Given that $\Pr(a) = 1$ then depending on $\Pr(c)$ (i.e., how much < 1 it is), then it may be that $E(B_c) < E(B_a)$, even if A_1 and A_2 are in part II of the graph.

Implementing a *representativeness* strategy when there are multiple landowners may result in multiple disconnected patches, which reduces the benefit of implementing the strategy.

Depending on the number of landowners, it is possible that $E(B_r) < E(B_c)$ and

$E(B_r) < E(B_a)$ when A_3 is in parts II or III of figure 1.

Effectiveness of targeting strategies when landowners derive private benefits from ecological restoration

Landholders may benefit from ecological restoration in at least two ways: through improvements in economic productivity (e.g. provision of shelter to livestock), or through

enhancing environmental outcomes that increase the landholder's utility. We now introduce an assumption that the probability of a particular landowner's participation in an ecological restoration program depends on the private benefits of restored habitat:

$\Pr(c, r) = F(D, L, PB)$; $\partial \Pr(c, r) / \partial PB > 0$. Following the empirical evidence of Polyakov et al. (2015), private benefits of additional native vegetation on private property increases as property size (PS) decreases, and as the area of existing native vegetation (NV) decreases, therefore, $\partial \Pr(c, r) / \partial PS < 0$ and $\partial \Pr(c, r) / \partial NV < 0$. Earlier we concluded that $\Pr(c)$ is negatively related to both the length of a corridor and the number of landowners along its length. As the number of landowners in a given area or region is inversely related to average property size (for a given corridor length) and, *ceteris paribus*, the average length of the corridors is inversely related to the area of native vegetation in a landscape, private benefits of restoration can partly mitigate the negative impact of large of landowners and length of the corridors on the success of the Connectivity strategy.

Empirical model

Based on the conceptual model above, an empirical model of this problem needs to include a biological model predicting the populations of a set of species supported by a particular landscape, given a land-use pattern, and a model of landowner participation in ecological restoration.

The biological model

In developing the biological model, we follow Polasky et al. (2008). We use the number of breeding pairs of a species supported by a landscape, rather than the probability that a species will be sustained by a landscape, as our measure of ecological benefit. Consistent with the

way that environmental programs typically operate, we assume that there is a given budget available and the objective is to maximize the environmental benefits for that budget.

The population of species x depends on the spatial arrangement and suitability of habitat in the landscape, and on species-specific characteristics: the amount of land area required for a breeding pair, minimum viable population size, and the species' ability to disperse between suitable patches of habitat. We break the landscape into I cells. Adjacent cells of suitable habitat form a patch n . The number of breeding pairs Z_n^x of species x that patch n can support is calculated:

$$(2) \quad Z_n^x = \sum_{j \in n} \frac{A_j S_j^x}{R^x},$$

where A_j is the area of cell j , S_j^x is the suitability of habitat in cell j for species x , and R^x is the habitat requirement (area of suitable habitat per breeding pair) for species x .

The number of breeding pairs of a species that the landscape can support depends on the number of breeding pairs that could be supported by habitat patches in isolation, the distances between habitat patches, and the species' ability to disperse between the patches. Assuming no minimum viable population constraint, the maximum number of breeding pairs of species x that a landscape can support is the sum of the number of breeding pairs for species s supported by all habitat patches:

$$(3) \quad Z_{\max}^x = \sum_{n=1}^{N_s} Z_n^x.$$

The minimum number of breeding pairs is calculated accounting for the minimum viable population in a patch and assuming no dispersion between patches:

$$(4) \quad Z_{\min}^x = \sum_{n=1}^{N_s} Z_n^x \times (Z_n^x \geq \gamma^x),$$

where γ^x is the minimum number of breeding pairs required for a population of species x to survive in a patch. The connectivity of the landscape D^x for species x depends on the distances between patches of habitat in the landscape and on the dispersal abilities of a species:

$$(4) \quad D^x = \frac{\left(\sum_{n=1}^N \sum_{m=1}^N \exp\left(-\frac{d_{nm}}{\alpha^x}\right) Z_m^x \right)}{NZ_{\max}^x},$$

where N is the number of patches, d_{nm} is the shortest distance between patches n and m and α^x is dispersal ability of species x . The value of D^x varies between 0, when patches are so far apart that species cannot travel between them, and 1 where their habitat patches are adjacent. The number of breeding pairs that a landscape can support is calculated as

$$(4) \quad Z^x = D^x Z_{\max}^x + (1 - D^x) Z_{\min}^x.$$

In an entirely connected landscape, the number of breeding pairs supported by the landscape is Z_{\max}^x , while in a completely fragmented landscape, with no possibility for species to travel between patches (and thus $D^x=0$), the number of breeding pairs is Z_{\min}^x .

The model of landowner participation

Native vegetation in fragmented, agriculture-dominated landscapes generates both public benefits to the society as well as private benefits to the landowners. Examples of public benefits are support of biodiversity and regulation of water flows. Examples of private benefits are shade for livestock, pollination services, and aesthetics. Private benefits

generated by native vegetation are an important factor influencing participation of private landowners in conservation (Raymond and Brown, 2011), and knowledge of the magnitude of private benefits can enhance the efficiency of policy instruments used to promote ecological restoration (Pannell, 2008). The value of private benefits depends on the landowner's goal for owning land, being lower for the owners of production-oriented properties (which are typically larger in area), and likely to exhibit diminishing marginal benefits as area increases (Polyakov et al., 2015). In this study, we assume that the probability of participation in ecological restoration by a randomly selected landowner, as well as the level of participation, depends on the benefit of restored native vegetation captured by the landowner.

The private benefit of native vegetation is calculated using the model and associated parameters developed by Polyakov et al. (2015), which was estimated using a hedonic pricing method. The value of a property i is modeled as $P_i = P(w_i, v_i, X_i, \varepsilon_i)$, where w_i is the area of the property; v_i is the area of native vegetation; X_i are other characteristics of the property such as location, soil, slope; and ε_i is the error term. We predict the private benefit of restoring Δv of habitat as

$$(4) \quad P_i(\Delta v) = P(w_i, v_i + \Delta v, X_i, \varepsilon_i) - P(w_i, v_i, X_i, \varepsilon_i).$$

For each simulation, ε_i is drawn from the normal distribution with zero mean and standard deviation obtained from the estimate of the hedonic model.

Simulation

For simulations we parameterize the model to a particular case-study area: the North-Central region of the state of Victoria in Australia (described in the next section). During the

simulations, ecological restoration is allocated on the landscape based on the relevant targeting strategy, the probability of landowners' participation, and amount of area targeted for restoration. In this study, we use a set of 10,000 hectares representative landscapes and a set of three restoration area targets: 10, 30 and 100 hectares in each of the representative landscapes. This corresponds to revegetation of 0.1% to 1% of the modelled landscape, which is consistent with the total extent of revegetation projects completed in the study region from 1999 to 2013 (Shaddick, 2014). The modeling unit is a 1-hectare cell that is characterized by land cover and vegetation type, and belongs to a particular property. The simulation is repeated 50 times for each combination of scenarios.

We test four targeting strategies as outlined earlier: aggregation, connectivity, representativeness, and no targeting of the restoration effort. In each 10,000-hectare landscape, we identify target regions using each strategy. The total area identified as being targeted for the region are greater than the modeled restoration area targets. For the aggregation strategy, the targeting region consists of cells immediately adjacent to the existing patches of habitat. For the connectivity strategy, the targeting region includes groups of cells ("corridors") that connect existing patches. These corridors were selected along roads, streams, and other linear patches of existing vegetation as much as possible. For the representativeness strategy, the targeting region includes locations with pre-clearance vegetation types that have high suitability for all modeled species. Finally, under the no-targeting strategy, restoration can be allocated anywhere at random on the cleared portion of the landscape.

We use two different assumptions about landowners' participation in ecological restoration. The base case assumption is that participation in ecological restoration does not depend on private benefit, but is instead random within the population of landholders. The alternative

assumption is that that probability of participation is higher for the landowners who have a higher value of private benefit from ecological restoration. Under the base assumption, cells belonging to each targeting region (i.e., that satisfy each targeting strategy) are randomly allocated to restoration. In the private-benefit assumption, for each cell available for ecological restoration in the landscape, we evaluate the private benefit of restoring this cell to its landowner. When then add a random component to the private benefits based on the distribution of the residual from the hedonic model (Polyakov et al., 2015). The cell with highest private benefits within the targeted region is selected for restoration. Note that restoring a cell changes the private benefit of restoring the next cell within the same property, due to diminishing marginal utility of restoration (Polyakov et al., 2015). The evaluation of private benefit and allocation of cells to restoration is repeated until the restoration area target is exhausted.

After each simulation (restoration area target, targeting scenario, private benefit scenario, and iteration), we calculate the number of breeding pairs that can be supported in each landscape (equation 4) and the increase, if any, in the number of breeding pairs for each species as a result of ecological restoration.

Regression analysis

We analyzed results of the simulation using regression. The dependent variable is the change of the number of breeding pairs of a species in a landscape. The explanatory variables of primary interest are dummy variables representing spatial targeting strategies and a dummy variable indicating whether private benefits of ecological restoration are taken into account. The estimated parameters for dummy variables representing spatial targeting strategies (*Aggregation, Connectivity, Representativeness*) indicate the impact of respective targeting strategy relatively to random (no targeting) ecological restoration. The other explanatory

variables are characteristic of the landscape (area of native vegetation before restoration), restoration area target, and a characteristic of the species: the size of the isolated patch that can sustain a local minimum viable population (MVP) patch size. MVP patch size is calculated as a product of the number of breeding pairs that are necessary to sustain a population of species in an isolated patch and the area required by a breeding pair.

Continuous explanatory variables are normalized (median scaled) and log transformed.

Normalization allows interpretation of the coefficients of dummy variables as effects at the median of the sample.

The functional relationship is assumed to be log-log (a) because the dependent variable (change in the number of breeding pairs) is nonnegative with a highly right-skewed distribution, and (b) to reflect the multiplicative relationship between the factors impacting the biodiversity outcome. Log-transforming the dependent variable and using ordinary least squares (OLS) for non-negative continuous dependent variables has a number of well documented disadvantages (Manning and Mullahy, 2001, Polyakov and Teeter, 2007, Santos Silva and Tenreyro, 2006, Thomson, 2014). Specifically, log-linear OLS estimates are biased, inconsistent in the presence of heteroskedasticity, and the log transformation is undefined for zero values of dependent variable. Santos Silva and Tenreyro (2006) propose using models suitable for count data, such as Poisson. Manning and Mullahy (2001) and Thomson (2014) use Generalized Linear Model with a log link and gamma distribution. Gamma distribution is defined over sets of positive real numbers. We use a Generalized Linear Mixed Model with a log link and an exponential distribution, which is a right-skewed distribution defined over nonnegative real numbers. Landscape-specific and species-specific random intercepts are used to capture unobservable characteristics of the landscapes that may affect the habitat of individual species. Furthermore, we estimate robust standard errors. Because there are both

log-link and log-transformed explanatory variables, the coefficients of continuous variables are interpreted as elasticities.

Study area and Data

The study sites are located in a fragmented, agriculture-dominated landscape in the north-central region of Victoria, Australia (figure 2), in the Southern part of the area managed by North Central Catchment Management Authority. (The Authority plays an important role in coordinating and implementing a range of environmental projects.) The study area ranges from 150 to 300 m above sea level and has a Mediterranean climate, with hot, dry summers and cool winters. Most annual rainfall is received in Southern Hemisphere winter/spring, and annual precipitation ranges from 400 to 600 mm, increasing across the study area from the north-west to the south-east (Radford and Bennett, 2007, Radford, Bennett, and Cheers, 2005). The area was mostly cleared for extensive agriculture in the late 19th and early 20th centuries; only about 17% of the area remains covered with the original endemic woody vegetation. Approximately 13% of the region is public land, including national, state and regional parks.

[Insert Figure 2 here]

Within the study area, we use 14 10×10 km (10,000 hectares) “landscapes” that were selected as representative of the study area by Radford and Bennett (2007) to conduct surveys of woodland birds. These landscapes were split into 100×100 m (1 hectare) grids cells that are used as modeling units. Each cell was assigned values for land cover (matrix or native vegetation), pre-clearance ecological vegetation class (DSE, 2007), and tenure (private or public). Also, each cell was allocated to a specific property.

We selected five woodland-dependent animal species that represent mammals, birds, and reptiles and display a variety of characteristics (dispersal, breeding pair requirement) and habitat requirements (Table 1). The species chosen are Yellow Footed Antechinus (a shrew-like marsupial), Brush-tailed Phascogale (a rat-sized arboreal carnivorous marsupial), Diamond Firetail (a small bird of the finch family), Lace Monitor (a large lizard, up to 2 meters in length) and Marbled Gecko (a small nocturnal gecko). The parameters required in the model for each species are the number of breeding pairs necessary to sustain a population of species in an isolated patch (minimum viable population size), the dispersal ability of species, and the area needed by a breeding pair of species for typical breeding and feeding activities (Table 1) Selected species' habitat suitability scores were assigned by local experts to each of the 17 pre-land-clearing vegetation classes found within the representative landscapes. Habitat suitability scores take values of 0 (not suitable), 0.5 (moderately suitable), and 1 (suitable).

[Insert Table 1 here]

Results

We conducted 50 simulations for each representative landscape and each combination of the assumptions (total number of simulation is $50 \times 4 \times 2 \times 3 \times 14 = 16,800$). We analyzed the simulated data using a GLMM with a log link and an exponential distribution, to predict the number of breeding pairs. First, we estimated a separate model for each species (Table 2). These initial models do not include species characteristics and their interaction effects; they are included in the model in the next section (Table 3).

With one exception, the aggregation strategy results in the largest or equal largest increase in the number of breeding pairs for all species (evidenced by the regression coefficient and

robust errors). For the exception, the Marbled Gecko, the aggregation strategy reduces the number of breeding pairs relative to no targeting. Again with the exception of Marbled Gecko, the connectivity strategy outperforms the representativeness strategy for all species.

When the private benefits of ecological restoration are assumed to impact the probability of landowners' participation, there is an increase in the number of breeding pairs for all species except for the Lace Monitor.

[Insert Table 2 here]

The responsiveness of the number of breeding pairs to an increase in the restoration area target is positive but varies by species. The elasticity of the change in the number of breeding pairs with respect to restoration area target is close to unity for Marbled Gecko and greater than unity for rest of the species, although for Brush Tailed Phascogale the difference is not statistically significant.

Accounting for private benefits to landowners when evaluating restoration strategies has a positive impact on the outcome of ecological restoration of two species: Diamond Firetail and Yellow Footed Antechinus. These species have medium area requirements (20 ha required for minimum viable population), and our results indicate that, for these species in our study area, private benefits are positively correlated with the biodiversity outcome.

We estimate a pooled regression model to allow generalization of our results to a range of species and conditions (Table 3). The additional variables used in this model are characteristics of species (i.e., MVP patch size) and interaction effects for each targeting strategy and landscape characteristics, species characteristics, restoration area target and private benefits. As we mentioned earlier, the coefficients of continuous variables can be interpreted as elasticities. However, the coefficients for a continuous variable interacted with

a targeting strategy dummy is a deviations of elasticity from the elasticity of un-interacted continuous variable. Therefore, we add elasticities for continuous variables interacted with targeting strategies.

[Insert Table 3 here]

At the median values of all variables, the greatest increase in ecological benefit is delivered by the aggregation strategy, followed by the connectivity strategy and then the representativeness strategy. This is consistent with the findings of the individual species models. The coefficients for each targeting strategy (*Aggregation*, *Connectivity* and *Representativeness*) indicate that for a species with median habitat area requirement (MVP patch size 280 hectares), median pre-restoration levels of native vegetation in the landscape (23%), restoration area target of 30 hectares, and assuming that private benefits do not affect the probability of a landholder's participation in restoration, *Aggregation* is the best targeting strategy ($\exp(1.78)=5.9$ times improvement of the outcome comparing to no targeting), followed by *Connectivity* ($\exp(1.34)=3.8$ times improvement) and *Representativeness* ($\exp(0.57)=1.8$ times improvement).

The response to restoration (increase in the number of breeding pairs) decreases with the increase in MVP patch size. This is expected as given the same intervention; there are fewer additional breeding pairs for a species with a larger area requirement. The elasticities indicate that the aggregation strategy is more likely to produce the better biodiversity outcome for a species with larger area requirement and the representativeness strategy is more likely to produce the best biodiversity outcome for a species with smaller area requirement.

Restoration effort is more effective in landscapes with greater initial level of native vegetation. Without targeting, the elasticity of ecological benefit with respect to initial area of native vegetation in the landscape is 1.04. This means that if the same restoration effort is

applied to a landscape with 1% more native vegetation, the biodiversity outcome would be 1.04% greater.

When spatial targeting is used, the impact of initial level of native vegetation is positive but lower than for the restoration without targeting (elasticities are 0.63, 0.80, and 0.65 for *Aggregation*, *Connectivity*, and *Representativeness*, respectively). However spatial targeting substantially improves biodiversity outcome in the first place.

The elasticity of the biodiversity outcome with respect to an increase in the amount of area targeted for restoration is close to unity for no spatial targeting (1.01) and the *Aggregation* strategy (1.06). The response to an increase in the size of the restoration target is elastic for *Connectivity* and *Representativeness* strategies (elasticities 1.29 and 1.14, respectively), meaning an increase in area targeted makes these strategies more effective relative to the *Aggregation* strategy.

Under the assumption that the landowners who value private benefits of native vegetation are more likely to participate in ecological restoration, the biodiversity outcome of restoration without targeting is 1.6 times greater than without such an assumption. This effect is still positive but smaller with *Representativeness* and *Connectivity* targeting strategies. Under the *Aggregation* targeting strategy, accounting for private benefits does not change the biodiversity outcome.

The shading in the different plots in figure 3 shows which of the three targeting strategies provides the best biodiversity outcome (increase in breeding pairs) under different conditions (proportion of initial native vegetation in a landscape, a species' MVP patch size, restoration area target and with and without private benefits to landowners). Untargeted restoration is not optimal under any combination of conditions. Across all plots in Figure 3, as the proportion of initial native vegetation increases the optimal targeting strategy shifts from

Representativeness and *Aggregation* to *Connectivity*. This is consistent with the results of the pooled regression model. Furthermore, as the proportion of native vegetation in a landscape increases, the *Connectivity* strategy becomes optimal over a greater range of MVP patch size values. *Connectivity* also tends to become optimal more often as the size of the restoration target increases. Under the assumption that private benefits increase the probability of landowner participation in restoration, *Representativeness* and *Connectivity* strategies are optimal more frequently and *Aggregation* is optimal less often.

[Insert Figure 3 here]

Discussion

The purpose of this study was to evaluate three commonly used spatial strategies for targeting ecological restoration when land is privately owned, and participation of landowners in restoration programs is voluntary and uncertain. Compared to no targeting, all targeting strategies we tested (*Connectivity*, *Aggregation*, and *Representativeness*) substantially improve the effectiveness of ecological restoration in increasing number of breeding pairs of woodland-dependent species relative to untargeted restoration. However, which of the targeting strategies performs better, depends on the characteristics of a species, conditions of a landscape, the intensity of restoration effort and preferences of landowners. Specifically, restoring native vegetation in a way that generates connectivity between patches does not always produce better outcomes than a strategy that increases sizes of existing patches or a strategy that restores valuable vegetation types without regard to spatial context.

Our model and empirical results suggest two explanations. The first is that in fragmented landscapes with multiple landowners, the success of ecological restoration under different strategies depends to some extent on landowners participating simultaneously in the

restoration effort. The uncertainty about landowners' participation affects the efficacy of the Connectivity strategy the most. While we anticipated this outcome in the theoretical model, using simulation we can quantify the magnitude of the difference and to do so for a range of landscapes and species. The finding supports the use of incentives to encourage landowner participation, such as an agglomeration bonus mechanism (Parkhurst et al., 2002).

The second reason is that the species' characteristics, such as the area requirement, minimum viable population, and dispersal ability, determine the effectiveness of a particular targeting strategy to deliver a better biodiversity outcome, with these characteristics affecting the relative efficacy of the strategies. Specifically, while Connectivity is rarely the best strategy with a low level of restoration effort and/or in highly cleared landscapes, it becomes dominant with high restoration effort in less cleared landscapes.

For the Marbled Gecko the representativeness strategy is best while aggregation is worst. This is different to all other species, but is explained by the Marbled Gecko's minimum habitat requirement being close to the size of the modeling unit (i.e. 1 hectare). As one modeling unit is sufficient to sustain a viable number of breeding pairs, under our assumptions, the most important factor in restoration becomes suitable habitat type. Gibbons and Boak (2002) demonstrate that biodiversity outcomes for woodland-dependent small fauna can be achieved through the protection of individual trees and small patches, in the Paddock Trees program.

Another key finding is that the effectiveness of restoration (biodiversity outcome per unit of restoration effort) increases with the restoration effort and with the initial area of native vegetation in a landscape. This suggests that to achieve greatest benefits, restoration effort should be concentrated in the parts of a landscape with a large proportion of existing native vegetation. This is consistent with the results of Lewis, Plantinga, and Wu (2009) who found

that converting either none or all of the agricultural land in a section to forest is optimal, and Polyakov et al. (2015) suggesting that spreading restoration effort equally across landscape leads to a suboptimal outcome. In addition, concentrated restoration effort would result in the Connectivity being optimal for a larger number of species.

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Tables

Table 1. List of species used in the modelling and their characteristics

Scientific Species Name	Common Species Name	Area needed by a breeding pair, ha	Dispersal ability, km	Minimum viable population, breeding pairs
<i>Antechinus flavipes</i>	Yellow Footed Antechinus	0.78 ¹	0.352 ²	360 ³
<i>Phascogale tapoatafa</i>	Brush-tailed Phascogale	40.0 ⁴	1.400 ⁴	25 ⁴
<i>Stagonopleura guttata</i>	Diamond Firetail	1.0 ⁵	1.000 ⁵	20 ⁶
<i>Varanus varius</i>	Lace Monitor	64.0 ⁷	2.000 ⁸	5 ⁸
<i>Christinus marmoratus</i>	Marbled Gecko	0.04 ⁸	0.040 ⁸	5 ⁸

Sources of data: ¹Coates (1995), ²Marchesan and Carthew (2008); ³Lada, Mac Nally, and Taylor (2008), ⁴Humphries and Seebeck (1997); ⁵Paton, Rogers, and Harris (2004) ; ⁶Park (2014); ⁷Weavers (1993); ⁸Kay (2014)

Table 2. Results of estimating separate generalized linear mixed model of the impact of spatial targeting strategies on the change in number of breeding pairs for each species.

Parameters	Species									
	Brush-tailed Phascogale		Diamond Firetail		Lace Monitor		Marbled Gecko		Yellow Footed Antechinus	
Intercept	-1.87***	(0.31)	1.88***	(0.12)	-2.48***	(0.35)	6.50***	(0.02)	1.30***	(0.21)
Aggregation	1.46***	(0.21)	1.13***	(0.18)	1.52***	(0.19)	-0.19***	(0.04)	1.94***	(0.26)
Connectivity	1.36***	(0.21)	1.14***	(0.15)	0.97***	(0.17)	0.01	(0.01)	1.46***	(0.24)
Representativeness	0.57***	(0.22)	0.60***	(0.14)	0.74**	(0.30)	0.10***	(0.02)	-0.12	(0.29)
Accounting for private benefits	0.21*	(0.12)	0.39***	(0.08)	-0.03	(0.13)	0.03***	(0.01)	0.34**	(0.14)
Log(Restoration area target)	1.16^	(0.09)	1.19^^^	(0.05)	1.14^^	(0.06)	0.99^^	(0.00)	1.18^^^	(0.06)
Log(Area of native vegetation)	1.14***	(0.15)	0.36***	(0.08)	1.13***	(0.25)	-0.02	(0.02)	1.35***	(0.17)
Variance of intercept	1.22**	(0.50)	0.06**	(0.03)	0.69**	(0.28)	0.01*	(0.00)	0.26**	(0.11)
Number of observations	16,800		16,800		16,800		16,800		16,800	
AIC	78,778		44,391		61,007		31,178		81,977	

Notes: *denotes significance at the 10% level, **denotes significance at the 5% level; and ***denotes significance at the 1% level; ^denotes significantly different from 1 at the 10% level, ^^denotes significantly different from 1 at the 5% level; and ^^denotes significantly different from 1 at the 1% level.

Robust standard errors in parenthesis.

Table 3 Results of estimating generalized linear mixed model of the impact of spatial targeting strategies on the change in number of breeding pairs, conditional on species and landscape characteristics.

Parameters	Parameters estimates	Robust standard error	Elasticities
Intercept	-0.73***	0.23	
log(MVP patch size)	-1.09***	0.05	-1.09
log(Area of native vegetation)	1.04***	0.23	1.04
log(Restoration area target)	1.01	0.04	1.01
Accounting for private benefits	0.44***	0.15	
Aggregation	1.78***	0.13	
Aggregation × log(MVP patch size)	0.25***	0.03	-0.84
Aggregation × log(Native vegetation)	-0.41***	0.13	0.63
Aggregation × log(Restoration area target)	0.05	0.06	1.06
Aggregation × Accounting for private benefits	-0.53***	0.14	
Connectivity	1.34***	0.10	
Connectivity × log(MVP patch size)	0.17***	0.02	-0.92
Connectivity × log(Native vegetation)	-0.24**	0.11	0.80
Connectivity × log(Restoration area target)	0.28^^	0.05	1.29
Connectivity × Accounting for private benefits	-0.25*	0.15	
Representativeness	0.57***	0.15	
Representativeness × log(MVP patch size)	0.05*	0.03	-1.04
Representativeness × log(Native vegetation)	-0.39**	0.15	0.65
Representativeness × log(Restoration area target)	0.13^^	0.04	1.14
Representativeness × Accounting for private benefits	-0.21	0.14	
Variance of intercept	0.13**	0.06	
Number of observations	84,000		
AIC	461,241		

Notes: *denotes significance at the 10% level, **denotes significance at the 5% level; and ***denotes significance at the 1% level; ^denotes significantly different from 1 at the 10% level, ^^denotes significantly different from 1 at the 5% level; and ^^denotes significantly different from 1 at the 1% level.

Figures

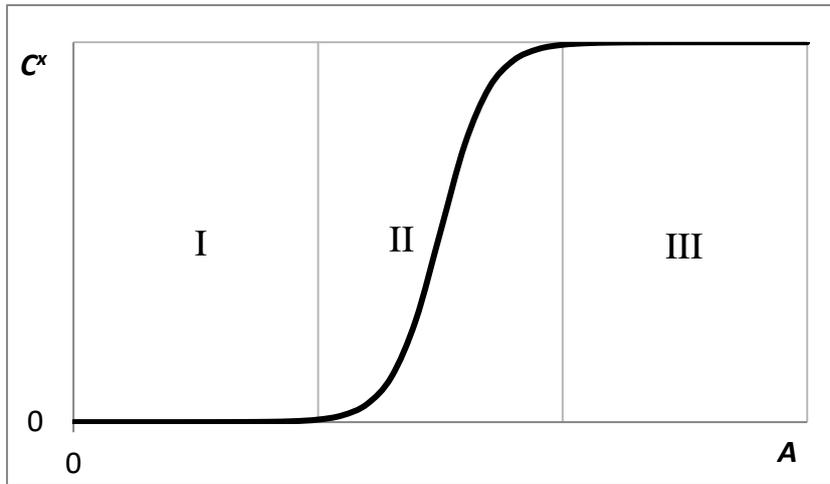


Figure 1. Carrying capacity function

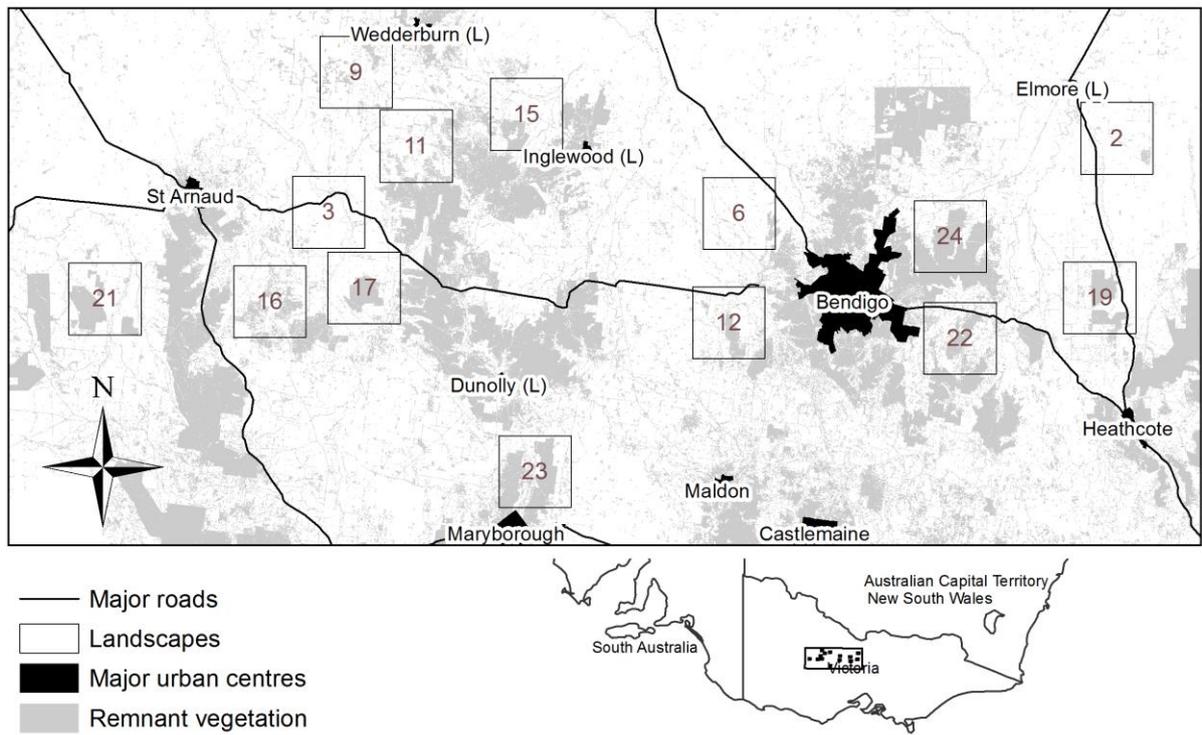


Figure 2. Study area within Victoria, Australia.

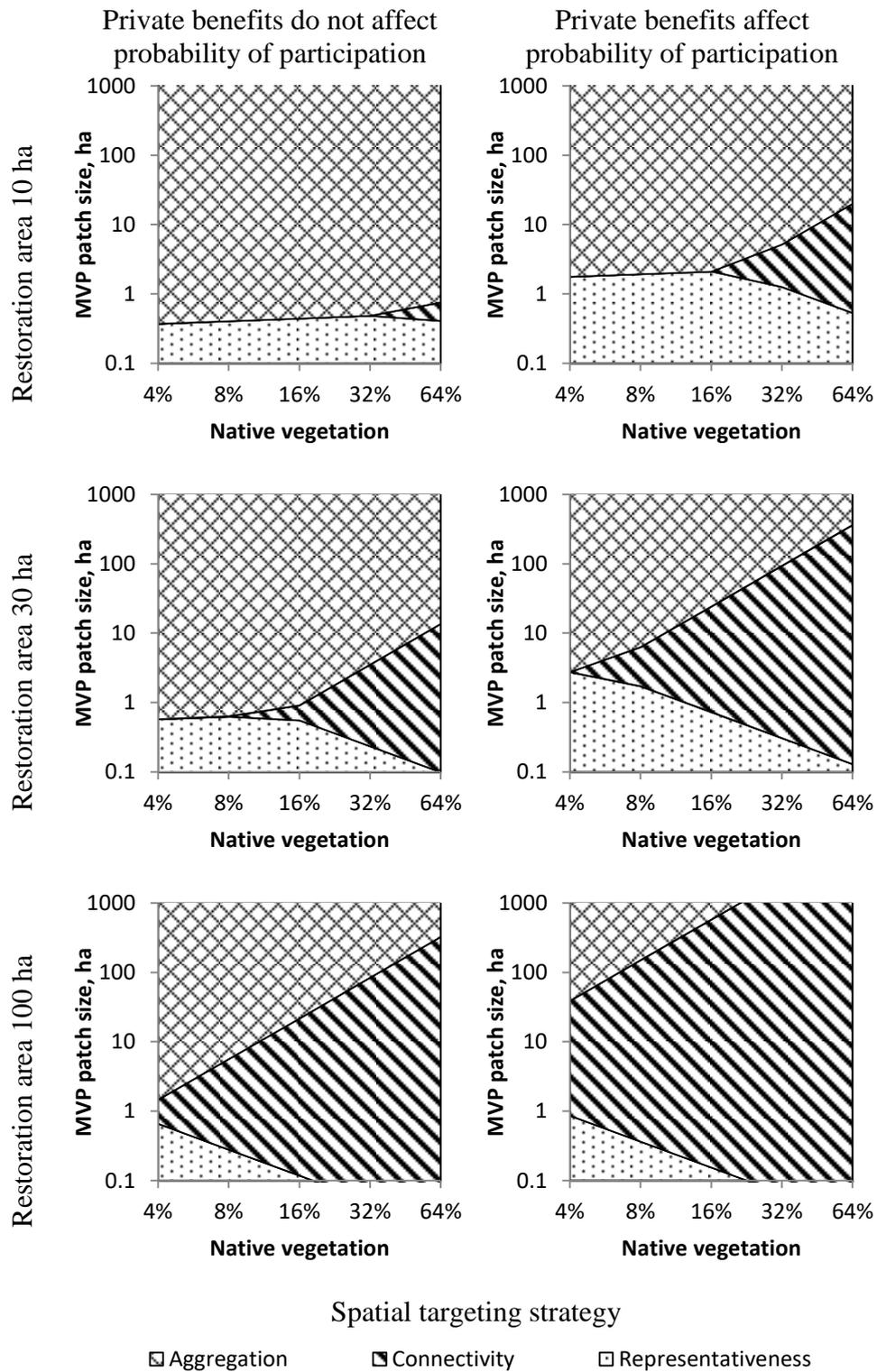


Figure 3. Optimal spatial targeting strategy of ecological restoration as a function of species characteristics, landscape characteristics, restoration area target, and assumption about impact of private benefit on participation in restoration. Optimal spatial targeting strategy is a strategy that results in greatest increase in number of breeding pairs.