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Conservation planning with dynamic threats: The role of spatial design and priority setting for species' persistence

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ABSTRACT

Conservation actions frequently need to be scheduled because both funding and implementation capacity are limited. Two approaches to scheduling are possible. Maximizing gain (MaxGain) which attempts to maximize representation with protected areas, or minimizing loss (MinLoss) which attempts to minimize total loss both inside and outside protected areas. Conservation planners also choose between setting priorities based solely on biodiversity pattern and considering surrogates for biodiversity processes such as connectivity. We address both biodiversity processes and habitat loss in a scheduling framework by comparing four different prioritization strategies defined by MaxGain and MinLoss applied to biodiversity patterns and processes to solve the dynamic area selection problem with variable area cost. We compared each strategy by estimating predicted species' occurrences within a landscape after 20 years of incremental reservation and loss of habitat. By incorporating species-specific responses to fragmentation, we found that you could improve the performance of conservation strategies. MinLoss was the best approach for conserving both biodiversity pattern and process. However, due to the spatial autocorrelation of habitat loss, reserves selected with this approach tended to become more isolated through time; losing up to 40% of occurrences of edge-sensitive species. Additionally, because of the positive correlation between threats and land cost, reserve networks designed with this approach contained smaller and fewer reserves compared with networks designed with a MaxGain approach. We suggest a possible way to account for the negative effect of fragmentation by considering both local and neighbourhood vulnerability to habitat loss.

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1. Introduction

Protected areas are the foundation of many conservation strategies and can be effective tools in maintaining biodiversity. However, the global network of protected areas still has extensive gaps in representing rare and endangered species (Rodrigues et al., 2004a). Of the 11,633 species of terrestrial vertebrates analysed by Rodrigues et al., 74% were poorly represented in protected areas. The picture was even darker for threatened and critically endangered species with 89% and 92% of these species analysed being poorly represented. An important reason for these gaps is that protected areas are often biased towards areas of low productivity and accessibility, also dubbed the “land nobody wants” (Pressey, 1994).

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To redress this bias, an approach to priority setting has been proposed that combines biodiversity value and vulnerability to threats (Myers et al., 2000; Pressey and Taffs, 2001; Rodrigues et al., 2004b). This approach (hereafter MinLoss) aims to minimize the expected loss of biodiversity and prioritize areas for conservation that are both important for biodiversity and likely to be lost without intervention. MinLoss considers areas that are not vulnerable to threats as protected *de facto*, therefore effectively contributing to the objective of minimizing biodiversity loss. In contrast, a more opportunistic approach, maximizing gain (hereafter MaxGain), prioritizes areas for conservation based only on biodiversity value and assumes that unreserved areas will not contribute to biodiversity persistence because they will eventually be lost. An implicit assumption of this approach is that threats to biodiversity are homogeneous and static. Threats to biodiversity, however, are spatially variable, and, in many cases, dynamic. Dealing with dynamic threats requires planners to first predict spatial and temporal changes in threats (Wilson et al., 2005) and then to devise responses (conservation actions). It is usually unrealistic to assume that conservation actions can be implemented all at once or that there are no

obstacles to implementation arising from limits on funds, availability, feasibility of interventions and so on (Meir et al., 2004). For this reason, managers are required to schedule conservation actions (Pressey and Taffs, 2001). Scheduling is the coordination of actions over time and space depending on the urgency for intervention, the spatial options for protecting features, the availability of funds, and other factors. Scheduling calls for the formulation of the dynamic area selection problem in which protection and loss are incremental, parallel processes (Costello and Polasky, 2004).

Comparisons of MaxGain and MinLoss in solving the dynamic area selection problem have shown that MinLoss loss generally outperforms MaxGain in retaining biodiversity features. One exception to this occurs when there is low spatial variability in vulnerability to threats, in this case the second assumption made by MaxGain is valid, i.e. vulnerability is homogeneous and the two approaches effectively converge. A second exception occurs when there is considerable uncertainty in future conservation funding or implementation opportunity (Costello and Polasky, 2004; McBride et al., 2007; Wilson et al., 2006).

Among the scientific and practical challenges to effective scheduling of limited conservation resources is the need to promote the persistence of biodiversity processes. Biodiversity processes, such as ecological and evolutionary dynamics are fundamental in maintaining and generating biodiversity (Balmford et al., 1998). Despite this, few studies have attempted to combine attention to biodiversity processes with dynamic threats (Pressey et al., 2007). Cabeza and Moilanen (2003) assessed an indicative reserve system based only on biodiversity pattern and the assumption of static threats. By accounting for population dynamics and habitat loss outside the reserves, they showed that some species would decline and disappear from the system. Cabeza (2003) and Van Teffelen et al. (2006) asserted that the impact of habitat loss and fragmentation on metapopulation dynamics might be reduced if reserve selection were based on species models that incorporated connectivity measures as predictor variables. Carroll et al. (2003) and Noss et al. (2002) integrated a spatially explicit population model and a reserve selection algorithm to identify priorities for mammalian carnivores in the Rocky Mountains. To measure priority for reservation, they expressed irreplaceability and vulnerability (sensu Margules and Pressey, 2000) respectively as the population growth rate and its expected decrease without conservation intervention. Williams et al. (2005) developed an approach to selecting reserves that accounted for range adjustments in response to climate change by designing a set of reserves that would provide connectivity over space and time for species with different dispersal abilities. Although connectivity or spatial population dynamics are receiving increasing attention in reserve design, we are aware of only two studies, that have considered both connectivity and threat within a scheduling approach (Harrison et al., 2008; Sabbadin et al., 2007). This is probably due to the complexity of the problem.

The few systematic conservation planning exercises that have addressed scheduling with respect to biodiversity processes and dynamic threats have failed to consider an important issue. They have not considered the variable cost of conservation action, assuming instead that costs were uniform. Conservation costs are rarely uniform across any region, and considering them can increase the cost-efficiency and feasibility of conservation (Naidoo et al., 2006). Moreover, land value is a major conservation cost and is often positively correlated with vulnerability to habitat loss because value is related to potential profits from extraction. Targeting vulnerable areas of low cost-efficiency can therefore preclude the protection of large, intact areas with higher cost-efficiency (Newburn et al., 2006; Spring et al., 2007). The implications of such choices only become obvious when variable costs are considered.

Here, for the first time, we address both biodiversity processes and dynamic threats by testing four different strategies defined

by maximizing gain and minimizing loss applied to both biodiversity patterns and processes (species-specific responses to habitat fragmentation) to solve the dynamic area selection problem with variable area cost. We use models of predicted probability of occurrence to approximate persistence, on the assumption that the predicted probability of occurrence of a species at time t is equivalent to the probability of persistence from now until time t . Probability of occurrence has been used previously as a surrogate for probability of persistence because both are dependent on the same factors related to habitat quality (Araujo and Williams, 2000). This surrogacy gains credibility when occupancy models incorporate neighbourhood covariates such as the proportion of suitable habitat in a defined radius. These models are also likely to relate to processes relevant to population viability such as edge avoidance, spatial population dynamics and lowered persistence of local populations in small habitat fragments (Araujo et al., 2002; Moilanen and Wintle, 2007). Species' persistence depends, of course, on extrinsic factors such as habitat loss (Araujo and Williams, 2000). We account for this by using a land-use change model to simulate loss of native vegetation. We use the results to answer the following questions:

- (1) Can information about species-specific fragmentation effects be used to schedule conservation actions and improve conservation outcomes?
- (2) Is minimizing loss better than maximizing gain when reservation cost and species-specific influences of fragmentation are incorporated into conservation planning?

2. Methods

2.1. Study region and species

The Lower Hunter Central Coast (LHCC) region in central-eastern New South Wales includes seven local government areas (Fig. 1a). These local governments have established a Regional Environmental Management Strategy to integrate biodiversity information and coordinate approaches to nature conservation, producing detailed vegetation and fauna survey and mapping (NSW National Parks and Wildlife Service, 2000; Wintle et al., 2004). For our analyses, we used a ~600-km² subregion of the LHCC (hereafter the planning region, Fig 1b). The planning region is representative of the larger region in terms of vulnerability to anthropogenic threats, habitat suitability for the target species, and land costs.

We selected three regionally important species with distribution models of high predictive power (see Wintle et al., 2005), differing responses to fragmentation (Moilanen and Wintle, 2007), and differing associations with land suitable for development. The squirrel glider (*Petaurus norfolcensis*) is an arboreal marsupial that feeds mostly on flowering *Acacia* and *Banksia* (Menkhorst and Knight, 2004). It occurs in vegetation types at risk from loss through urban and agricultural expansion in the lowlands of the study region. Its home range size is about 0.75–1.75 ha and its maximum juvenile dispersal is about 500 m (Quin, 1995). The yellow-bellied glider (*Petaurus australis*) is another arboreal marsupial occurring mainly in undisturbed patches of eucalypts and sap trees. Its home range size in a region with similar ecological characteristics varies between 46 and 59 ha (Goldingay and Kavanagh, 1993). In the study region, it is most abundant in higher-altitude forests that are less suitable for conversion to agriculture and urban development. The sooty owl (*Tyto tenebricosa*) tolerates some fragmentation and discontinuity in forest cover but relies on large tree hollows for nesting and preys on forest-dependent species, making it susceptible to declines in prey abundance after fragmentation (Kavanagh, 2002). Its home range size (200–800 ha) depends on habitat productivity (Kavanagh and Jackson, 1997). Its esti-

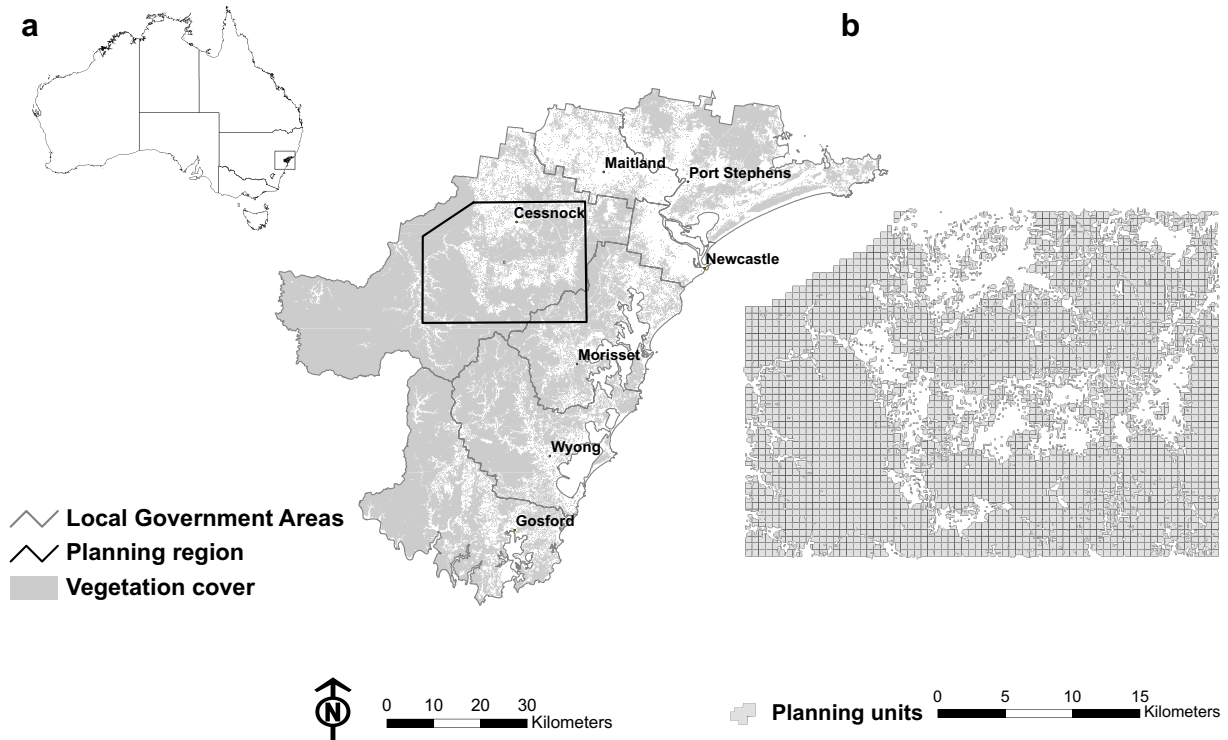


Fig. 1. The study region. (a) Overview of the Lower Hunter and Central Coast region, showing the boundaries of the smaller planning region. (b) The planning region; white areas are deforested and small irregular polygons are fragments that represent their own planning units.

mated juvenile dispersal is 10–20 km (NSW Department of Environment and Conservation, 2005). In the study region, it is most abundant on the south-eastern coastal uplands.

2.2. Planning units

We divided the region in 3698 planning units, which served as the primary units of assessment and comparison. Planning units ranged in size from 1 and 34 ha in size (Fig 1b), and where possible, were matched to the boundaries of existing forest fragments (Appendix A). This had several advantages: coupling ecological units with planning units; reducing spatial variance in cost and biodiversity benefit; and avoiding the costs of very large planning units exceeding annual constraints on budget.

2.3. Study design

Combining two approaches (maximizing gain and minimizing loss) with two types of species distribution models (local and neighbourhood, below), gave us four reserve selection strategies (Fig. 2a). We simulated each strategy under different scenarios defined by two rates of habitat loss and two rates of reservation (budgets available to managers for land acquisition), giving 16 scenarios (Fig. 2b).

We also simulated each strategy under the two extreme scenarios of loss and reservation (both high and both low) using planning unit area as a surrogate for cost to test the impact of using realistic cost data in dynamic conservation planning.

2.4. Simulation of reserve scheduling

In each year, we simulated annual, parallel loss and reservation of forest in the study region. Each annual cycle of the simulations consisted of the following steps:

1. Predict species' probability of occurrence.
2. Select planning units for protection. We allocated a fixed annual budget and selected planning units up to the limit of the budget with each reserve selection strategy.
3. Simulate habitat loss. At the beginning of the planning period, we assigned a vulnerability value to each planning unit V_p , which equalled its annual probability of being cleared, depending on its tenure and suitability for agricultural and urban development. When planning units lost their forest, they were removed from the simulations.
4. Update environmental predictors. At the end of each annual cycle, we updated the vegetation map and the input for species models for the next cycle.

For each simulation, we repeated these steps 20 times to simulate a 20-year planning process. We then projected habitat loss until year 40 or until there were no planning units available for reservation or development. While a 20-year planning period is more similar to the common horizon of conservation decision-making, we wanted to observe how strategies diverged in performance over time and what would happen if habitat loss continued after the implementation of the reserve network. The performance of each conservation strategy was the proportion of the initial expected occurrences of each species given by the neighbourhood model that were still extant after 20–40 years.

2.5. Species models

Presence and absence point records of the three species and the environmental layers used for model fitting and model projection at 1 ha resolution were made available by the University of Melbourne and the Lower Hunter Central Coast Regional Environmental Management Strategy. We used two different sets of species distribution models to measure the biodiversity benefit of conserving each planning unit. "Neighbourhood" models are described in

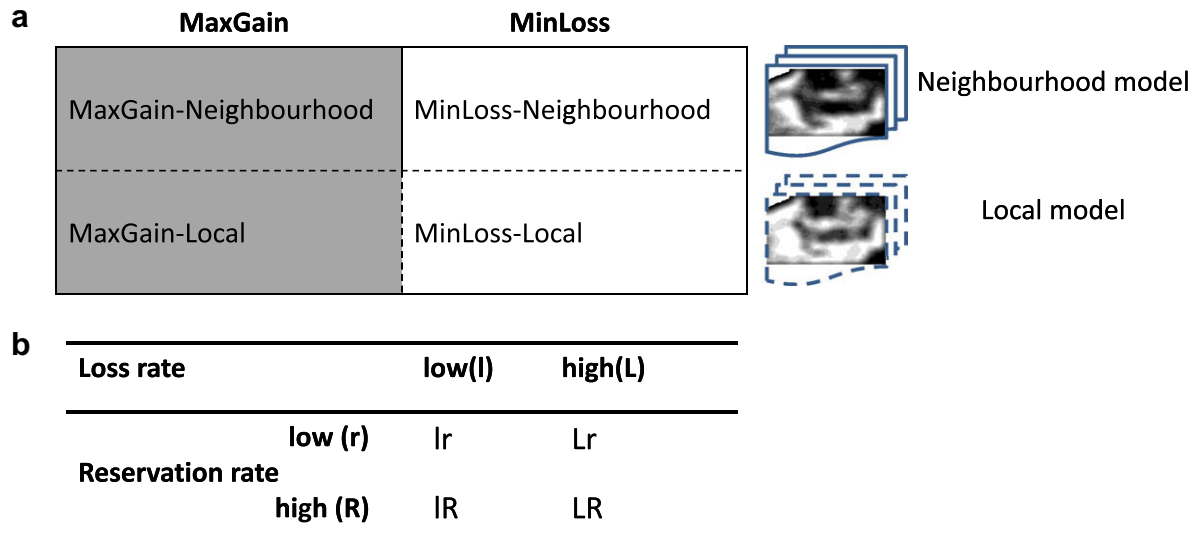


Fig. 2. Study design. (a) For each approach to priority setting (columns) and each approach to modelling species (rows) we defined a reserve selection strategy (cells). Dashed outlines indicate reserve selection based on local models. Solid lines indicate reserve selection based on neighbourhood models. Grey cells indicate maximum gain strategies and unshaded cells indicate minimum loss strategies. The MaxGain-local strategy maximizes the number of occurrences of species in reserves based on the predictions of the local model. The MinLoss-local strategy minimizes the loss of occurrences of species across the whole planning region as predicted by the local model. The MaxGain-neighbourhood strategy maximizes the number of occurrences of species in reserves as predicted by the neighbourhood model. The MinLoss-neighbourhood strategy minimizes the loss of occurrences of species across the whole planning region as predicted by the neighbourhood model. (b) We tested each strategy with four different scenarios defined by combinations of two rates of habitat loss and two rates of reservation.

Wintle et al. (2005). We use the term “neighbourhood” models because their predictor variables (Appendix B1) included contextual measures of habitat value, such as the proportion of unmodified forest within 2 km of a 1 ha cell, reflecting the spatial arrangement of forest patches and the edge effects caused by loss of adjacent patches. During the simulations, these models could therefore predict reductions in expected occupancy of cells because of clearing of nearby forest. Strictly speaking, with the neighbourhood models we modelled patterns of occupancy influenced by spatial population processes. We derived the set of “local” models ex novo. These include only local covariates in model fitting: attributes of individual 1 ha cells that are independent of neighbouring cells. The predictors included predominant vegetation type, temperature and rainfall. The local models predicted loss of species occurrences only because of forest clearing in individual cells. Despite their shortcomings (e.g. Van Teffelen et al., 2006) we used local models for two reasons. First, models that ignore spatial configuration of habitat are still commonly used for conservation planning. Second, we wanted to explore the interaction between model choice and scheduling approach (maximizing gain or minimizing loss). We fitted generalized linear models (McCullough and Nelder, 1989) and generalized additive models (Hastie and Tibshirani, 1990) with a binomial response in R (R Development Core Team, 2008). We reduced predictor variables with the Akaike Information Criterion (Akaike, 1974). For each species we chose the model with the highest area under the Receiving Operating Characteristic (ROC) curve (Hanley and McNeil, 1982). Formulae of best local and neighbourhood models and ROC values are in Appendix B2.

2.6. Land-use change model

We assumed that agricultural and urban development were the only sources of habitat loss and that all forest within a planning unit was lost if the planning unit was selected for development. For vulnerability to agricultural development, we used a map of land capability (Emery, 1988) that delineated four classes in our study region. Classes 4–2, (62.8% of the planning region), contained

private land with decreasing capability for intensive agriculture (respectively 1.7%, 32.3% and 28.8% of the planning region for classes 4–2). Class 1, (26% of the planning region), comprised unreserved public land, including production forest. We also included a class 0, (11.1% of the planning region), which consisted of reserves existing in 2007. We modelled vulnerability to urban development as inversely proportional to the distance from existing urban settlements and directly proportional to rates of growth of these areas (Appendix C). We reclassified the continuous urban vulnerability map into discrete classes to match those for agriculture. We then assigned each planning unit on private land the highest of either agricultural or urban vulnerability.

We modelled annual loss of forest as a series of independent probabilistic events. In each of the 20 annual cycles of the simulations, we removed all forest from a random sample of planning units in each vulnerability class. The size of the sample depended on the annual loss rate for the class. We simulated two rates of loss. The low rate involved annual loss of 2%, 1%, and 0.05% of the initial forest in classes 4, 3 and 2, respectively. These loss rates are consistent with recent land clearing rates in the study region (Pressey et al., 2004) and corresponded to annual losses of about 25, 250 and 115 ha, reflecting both different percentages and different initial areas of forest following more extensive historical deforestation in higher classes. The high rate of loss was five times higher in each class. When all vegetation in a vulnerability class had been lost or protected, we assumed that the loss rates in the other classes increased proportionally to maintain a constant rate of loss across the planning region.

2.7. Cost of reservation

Two different cost surfaces were considered. The first surface reflected some of the known spatial heterogeneity of land values in the region and consisted of the summed opportunity cost for agriculture and urbanization. We assumed that this was a surrogate of acquisition cost (see Naidoo and Adamowicz, 2006 and Appendix C for details). We intended the resulting land values, at

1 ha resolution, not to be exact acquisition costs, but rather to capture the relative spatial variations in cost. The cost of each planning unit was the sum of the estimated acquisition costs across the 1 ha cells it contained. In the second cost surface, we attributed to each planning unit a cost equal to its area. The purpose of this cost layer was to explore the quantitative effects of ignoring spatial variation in land value in reserve design.

2.8. Reserve selection strategies

We tested four different strategies for reserve selection (Fig. 2a), each with a different objective function to minimize subject to a budgetary constraint and each complementing the existing reserves in the study region. All variables and subscripts used in the following formulas are in Table 1. The objective functions contained two arguments:

- the planning unit cost $\$_x$;
- the target penalty which was equal to the cost of raising a species up to its target representation/retention level.

Both arguments of the objective function are therefore expressed as costs. The first argument ensures that, everything else equal, the cheapest solution is preferred, the second argument ensures that, everything else equal, the solution that is closer to meeting a defined target for each species is preferred. We minimized each objective function with the Marxan software (Ball and Possingham, 2000). We used two different budgets: \$1 million and \$5 million (Australian) per year. These corresponded to low and high rates of reservation, respectively. When using area as a surrogate for cost the budgets were 88 and 341 ha per year. These measures were the average annual rate of protection across all scenarios and all replicates in the base simulations.

We varied the calculation of the targets and the target penalty to produce a maximum gain and a minimum loss approach, each applied with both local and neighbourhood occupancy models. For MaxGain strategies, we set for all species a target T equal to 100% of the expected occurrences (EO_s) in the landscape expressed as $EO_s = \sum_u \sum_{i \in I_u} p_{is}$. p_{is} is the probability of occurrence of species s in cell i belonging to planning unit u . This probability was generated with the neighbourhood or the local model depending on the strategy applied. For MinLoss the target was 100% of the expected

occurrences at risk (EOR_s) expressed as $EOR_s = \sum_u v_u \sum_{i \in I_u} p_{is}$. v_u is the vulnerability (probability of loss) of planning unit u .

A generalization of the objective function to be minimized for all strategies is:

$$\sum_s SPF_s CR_s H(g_s) \left(\frac{g_s}{t_s} \right) + \sum_u \$_u x_u \quad (1)$$

SPF_s is the species penalty factor, and is used in Marxan to weight the contribution of different species in the objective function. We applied a SPF of 1 for all species. CR_s is the cost of meeting the target for species s starting from no representation in the reserve network (details in Game and Grantham, 2008). The shortfall or gap in protection g_s for MaxGain is the unmet representation target calculated as $g_s = EO_s - \sum_{u=1}^N x_u EO_{su}$ where EO_{su} is the expected number of occurrences in planning unit u calculated as $EO_{su} = \sum_{i \in I_u} p_{is}$. For MinLoss the shortfall is $g_s = EOR_s - \sum_{u=1}^N v_u x_u EO_{su}$ and represents the difference between the expected number of occurrences at risk in the landscape and the potential loss of occurrences averted by the proposed reserve network. The Heaviside function, $H(g)$, is a step function taking the value of zero when $g = 0$ and 1 otherwise.

All else being equal, MinLoss gives higher priority to planning units in higher vulnerability classes. MaxGain strategies instead would base their priorities only on the return on investment (contribution to the representation targets divided by the cost) in protecting a planning unit.

While the hypothetical MinLoss managers had no prior knowledge of which specific planning units would be lost in the next step, we assumed that they had perfect knowledge of the probability of conversion of each planning unit. It is possible that incorporating uncertainty in vulnerability estimate could affect the results but we did not test this possibility here.

2.9. Evaluation of the performance of reserve selection strategies

We measured the performance of each selection strategy for each species as the total number of remaining occurrences predicted by the neighbourhood model across the study region at the end of the 20 years planning period. Each of the 16 simulations followed an independent trajectory of lost occurrences. Because our model of vegetation loss was probabilistic, different repetitions of the same simulation could result in different levels of species' persistence depending on which planning units were lost and reserved, obscuring the between-simulation variation that we wanted to measure. We therefore ran ten replicates for each simulation, which gave us a statistical power of 0.9 to detect a difference in mean performance of 2% between simulations for all species. For each combination of loss and reservation rates, we compared the distribution of persistence values among the four strategies. We calculated the relative improvement from a worse strategy to a better strategy as:

$$\Delta P = \frac{P_{\text{better}} - P_{\text{worse}}}{P_{\text{worse}}} \quad (2)$$

where P_{better} and P_{worse} are respectively the mean persistence achieved by the better and worse of the strategies in the pairwise comparison.

2.10. Measuring the effect of fragmentation

Habitat loss during the planning period had two components: direct loss (d), which occurred when vegetation was removed from the focal planning unit, and loss due to fragmentation (f), which occurred when neighbouring planning units lost their vegetation and reduced the expected occurrences of species in

Table 1
Explanation for symbols.

Symbol	Explanation
CR_s	Cost of meeting the target for species s starting from the zero representation
EO_{su}	Expected number of occurrences of species s in planning unit u
EO_s	Total expected number of occurrences of species s in the landscape (only MaxGain)
EOR_s	Total expected number of occurrences at risk of species s in the landscape (only MinLoss)
g	Is the gap between current representation/retention and the representation/retention target (shortfall)
i	Cell index
I_u	Index set of cells within planning unit u
p_{is}	Probability of occurrence of species s in cell i
N	Number of planning units in the region
$s = 1, \dots, S$	Species index
S	Number of species
SPF	Species penalty factor
t	Target: EO for MaxGain and EOR for MinLoss
$u = 11, \dots, N$	Planning unit index
v_u	Vulnerability (probability of loss) of planning unit u .
x_u	1 if planning unit u is reserved, 0 otherwise
$\$_u$	Cost of planning unit u

the focal planning unit. These two combined represent total loss of expected occurrences. We calculated the fraction of this total habitat loss resulting from each component for both loss rates. To do so, we first measured the absolute number of occurrences lost through fragmentation (f), which is the difference in expected number of occurrences given by the neighbourhood model between the beginning (prior to fragmentation) and end of the planning period for all planning units still vegetated. We then divided this amount by the total loss of occurrences, including those from planning units that were cleared during the planning period, to give the proportion of the total loss attributable to fragmentation $f/(f+d)$. For each species and each loss rate, we calculated this proportion for nine simulations. One simulation was without reservation (potentially a worst-case scenario) and the remaining ones combined the four reservation strategies and the two budgets. We recorded the mean, minimum and maximum proportion across the nine simulations. For each simulation, the proportion was the average across the 10 replicates. We also measured the post-selection loss of occurrences in reserves due to their isolation by fragmentation during the planning period. This measure differed from the previous one in evaluating the impact of fragmentation on species only in actual and simulated reserves. We applied this second analysis for the strategies that used a neighbourhood model.

3. Results

3.1. Correlation between vulnerability, species abundance and cost

Across all planning units, the combined abundance of all three species was strongly negatively correlated with vulnerability ($\rho = -0.58$ for the neighbourhood model, $\rho = -0.48$ for the local model; both $p < 0.001$). The neighbourhood model predicted that approximately 49% of the expected occurrences of yellow-bellied glider, 34% of those of the squirrel glider, and 76% of those of the sooty owl were in existing protected areas or on public land not vulnerable to clearing. Similar values came from the local model. These relationships meant that MaxGain and MinLoss strategies produced spatially different reserve networks. MaxGain strategies placed reserves mostly in unreserved public land where the highest number of occurrences could be sampled with minimum cost. In contrast, MinLoss strategies focused reservation on parts of the planning region that were more vulnerable but had fewer occurrences of each species.

The correlation between habitat suitability and land cost was species-specific. Squirrel glider occurrences tended to be in more expensive areas ($\rho = 0.19$, $p < 0.001$) then either the sooty owl ($\rho = -0.04$, $p < 0.05$) or yellow-bellied glider ($\rho = -0.06$, $p < 0.001$).

Across all planning units, vulnerability and cost per hectare were slightly correlated ($\rho = 0.12$, $p < 0.001$). Across private land, subject to habitat loss in our scenarios, the correlation was stronger ($\rho = 0.31$, $p < 0.001$). Therefore, the emphasis of the MinLoss strategies on averting loss rather than maximizing protection meant that they tended to reserve more expensive planning units, exacerbating the budget stress already inherent in the conservation planning problem.

3.2. Reserve selection strategies

3.2.1. Can information about species-specific fragmentation effects be used to schedule conservation actions and improve conservation outcomes?

Fragmentation was a strong component of the total loss of expected occurrences for the sooty owl and the yellow-bellied glider (Fig. 3a). In the low loss rate scenario, an average of 65% of the expected loss of yellow-bellied glider occurrences

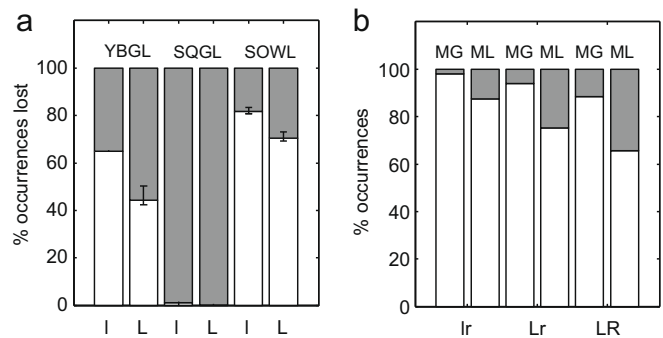


Fig. 3. (a) Percentages of occurrences lost in the landscape through the effects of fragmentation (unshaded portions of bars) and direct habitat loss (grey portions). I = low loss rate; L = high loss rate. YBGL = yellow-bellied glider; SQGL = squirrel glider; SOWL = sooty owl. Each bar shows the mean percentages across replicate simulations for combinations of reserve selection strategy and reservation and loss rate. Minimum and maximum proportions are shown with line-bar where extreme values differed by more than 2%. (b) Effect of habitat loss outside reserves on sooty owl occurrences inside the system of existing and simulated reserves. MG = MaxGain; ML = MinLoss; r = low reservation rate; R = high reservation rate. Both MaxGain and MinLoss were applied with the neighbourhood model. The grey portions of the bars are the percentages of the initial expected occurrences lost by isolation of reserves after their establishment. The unshaded portions of the bars are the percentages remaining in the reserves at the end of the planning period.

was attributable to fragmentation. This average percentage decreased to 46% with the high loss rate (minimum with MaxGain-local applied with high budget; maximum without reservation). For the sooty owl the averages for low and high loss rates were, respectively, 82% (minimum without reservation; maximum with MinLoss-neighbourhood applied with high budget) and 69% (minimum with MaxGain-neighbourhood applied with high budget; maximum with MinLoss-neighbourhood applied with high budget). The squirrel glider was barely affected by fragmentation.

We found no significant advantage in performance when using a MaxGain approach with a neighbourhood model compared to the same approach with a local model (Fig. 4).

When vulnerability was considered in the selection strategy (MinLoss), the choice of the appropriate model became more important. MinLoss-neighbourhood achieved better outcomes than MinLoss-local in scenarios with high loss and reservation rates. The relative improvement of the first on the latter were 9.2% for the yellow-bellied glider (515 expected occurrences), 3.5% for the squirrel glider (553 expected occurrences) and 5.3% for the sooty owl (193 expected occurrences). A complete evaluation of all strategies including extended analyses to year 40 of the simulations is in Appendix E.

3.2.2. Is minimizing loss better than maximizing gain when reservation cost and the species-specific influence of fragmentation are incorporated into conservation planning?

For this comparison, we focused on the strategies that applied a neighbourhood model. There were strong differences between MinLoss and MaxGain when both rates of loss and reservation were high (Fig. 4). In this comparison, the outcomes from MinLoss were 8.3% higher for the yellow-bellied glider (471 expected occurrences), 12.4% higher for the squirrel glider (1804 expected occurrences), and 5.0% higher for the sooty owl (183 expected occurrences). The difference between the performances of these two strategies increased with time for all three species, particularly after the end of the planning period when habitat loss was the only process operating in the region (Appendix E).

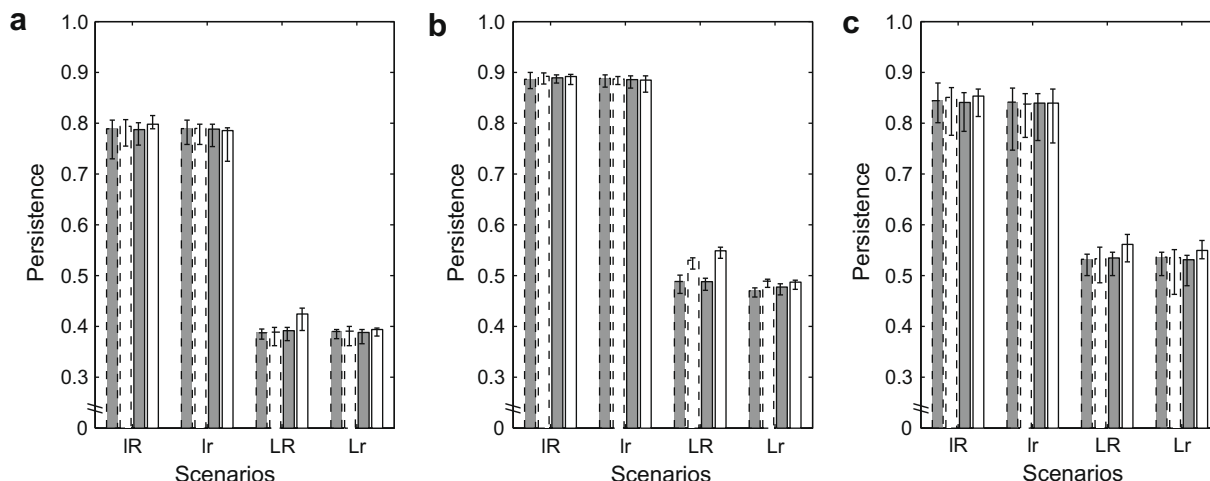


Fig. 4. Pairwise comparisons of reserve selection strategies in our base scenarios. The y-axes show the proportion of occurrences persisting at the end of the planning period (year 20) as predicted by neighbourhood models ("persistence"). Dashed outlines indicate reserve selection based on local models. Solid lines indicate reserve selection based on neighbourhood models. Grey bars indicate maximum gain strategies. Unshaded bars indicate minimum loss strategies. (a) Yellow-bellied glider, (b) squirrel glider, (c) sooty owl. l = low loss rate; L = high loss rate; r = low reservation rate; R = high reservation rate. For each strategy, the 90% confidence interval of the persistence values is also shown.

While a MinLoss approach resulted in higher levels of extant occurrences across the planning region, this net advantage was smaller than it might have been. Areas selected by MinLoss experienced greater subsequent losses of occurrences due to habitat fragmentation than those selected with the MaxGain approach. Post-selection loss of expected occurrences of the sooty owl was more evident with both high loss and high reservation rates, when it reached almost 40% of initial expected occurrences (Fig. 3b). Results were similar for the yellow-bellied glider but not for the squirrel glider which was insensitive to isolation of reserves.

When applying area as a surrogate for cost the improvement in performance of MinLoss over MaxGain increased, both when applying neighbourhood and local distribution models (Fig. 5). In particular, with the neighbourhood model and high rates of loss and reservation the difference increased by 15.3% for the yellow-bellied glider, by 12.6% for the squirrel glider and by 20.2% for the sooty owl compared to using our estimates of acquisition costs.

4. Discussion

We simulated the effect of incremental, interacting reservation and land conversion for 20 years for three species with a variety of reserve selection strategies and differing rates of reservation and loss of forest. Unlike previous studies, we considered the effect of fragmentation on the predicted occurrence of the target species by including neighbourhood context measures as predictors in the species distribution models. Also unlike previous studies, we considered realistic spatial variation in costs of reservation and compared our results with planning unit area as a surrogate for cost.

Our findings indicate that fragmentation is important in explaining loss of occurrences of two species, the sooty owl and the yellow-bellied glider. The squirrel glider was barely affected by fragmentation (Fig. 3a). Not surprisingly, the reserve selection strategy that minimized loss and considered the effects of fragmentation was better at promoting species persistence (Fig. 4). However, the neighbourhood model generally gave no consistent improvement over the local model when the approach

was maximizing gain (Fig. 4). This counterintuitive result was due to the local model predicting occupancy values that were less negatively correlated to vulnerability than the neighbourhood model. The MaxGain-local strategy therefore, incidentally, tended to focus more reservation on vulnerable areas than MaxGain-neighbourhood. The greater ability of MaxGain-local to mitigate direct habitat loss generally counterbalanced the superiority of MaxGain-neighbourhood in maximizing expected occurrences in reserves. This result reflects the idiosyncratic nature of our occupancy patterns. Its generality is difficult to judge and it does not justify the use of a simplistic model. Instead, the results overall reinforce the importance of incorporating data on vulnerability directly into priority setting and complementing these with the best available data on biodiversity.

Previous studies have argued that maximizing gain is less efficient than minimizing loss because it over-allocates budgets to secure areas and under-allocates them to areas more likely to be lost (Costello and Polasky, 2004; Drechsler, 2005; O'Hanley et al., 2007; Pressey et al., 2004; Strange et al., 2006; Wilson et al., 2006). Our simulations support the same conclusion (Fig. 4 and Appendix E). While generally these previous studies did not observe a difference between the two approaches larger than 5%, in our case MinLoss outperformed MaxGain by up to 12.4%. This is probably due to the larger size of our problem (~4000 planning units), and to a longer planning period. Large problems increase the number of possible solutions and therefore the potential difference between better and worse strategies. The differences in performance among reserve selection strategies tended to increase over time (Appendix E). In fact, during the planning period, MaxGain accumulated 'suboptimal'¹ decisions, progressively widening its inferiority to the MinLoss approach. This kind of trend was also noted by Pressey et al. (2004) and Moilanen and Cabeza (2007). With short planning periods the two approaches perform similarly. However minimizing loss could be a risky approach if the habitat loss continues without further investment in conservation. In these conditions, part of the high-value habitat left unprotected by MinLoss because of low vul-

¹ Suboptimal is quoted because neither of the algorithms provides a guaranteed optimal solution to the problem.

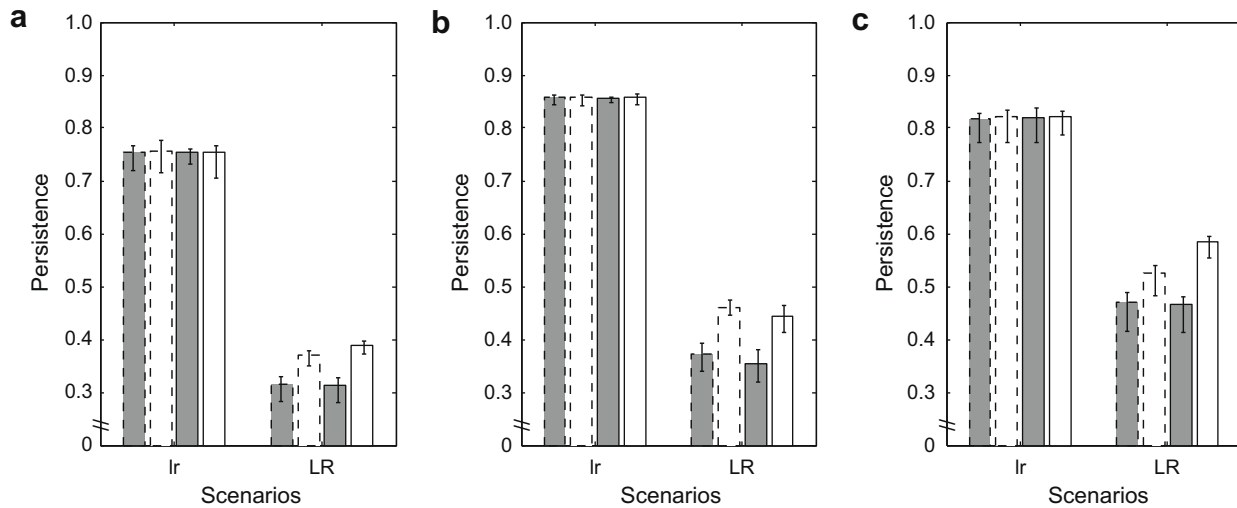


Fig. 5. Pairwise comparisons of reserve selection strategies using area as a surrogate for cost. Symbols and colour-coding are the same as in Fig. 4. The y-axes show the proportion of occurrences persisting at the end of the planning period (year 20) as predicted by neighbourhood models (“persistence”). Dashed outlines indicate reserve selection based on local models. Solid lines indicate reserve selection based on neighbourhood models. Grey bars indicate maximum gain strategies. Unshaded bars indicate minimum loss strategies. (a) Yellow-bellied glider, (b) squirrel glider, (c) sooty owl. l = low loss rate; L = high loss rate; r = low reservation rate; R = high reservation rate. For each strategy, the 90% confidence interval of the persistence values is also shown.

nerability can be lost afterwards, thus making the approach less effective. MaxGain is a more precautionary approach in this instance, because it secures areas of high biodiversity value in the short time allowed for protection. An algorithm has been proposed that is almost as good as MinLoss in terms of retention but is better in ensuring high representation, thus making it more resilient to further loss beyond the planning period (Moilanen and Cabeza, 2007).

On the other hand, MinLoss performed worse than we might have expected. We offer three explanations for this. First, vulnerability and cost were slightly correlated. Prioritizing vulnerable areas therefore translated into reserving smaller and fewer reserves than when vulnerability was ignored. Our finding that the difference in performance between MinLoss and MaxGain increased when using planning unit area as a surrogate for cost supports this hypothesis. Previous studies that ignored variable costs might have failed to accurately identify this trade-off.

A second explanation is related to the species used in the study. The sooty owl and the yellow-bellied glider tended to occur in extensive, intact forest with low suitability for development and were already largely protected. Therefore, expanding protected areas in the lowlands subject to habitat loss added only marginally to the persistence of these species.

The last explanation relates to the spatial autocorrelation of vulnerability. In our simulations, the pattern of vulnerability values tended to be clustered. Therefore, areas with high vulnerability values were likely to be surrounded by other areas with high vulnerability values. As a result, the neighbourhoods of areas reserved by the MinLoss approach tended to become more fragmented through time, reducing the 20-year outcomes of reserved areas for the yellow-bellied glider and the sooty owl (Fig. 3b). The extinction of local populations inside reserves after their isolation is well documented elsewhere and can be caused by stochastic events affecting small populations, breakdown of ecological processes, edge effects, or interactions between these (Newmark, 1996; Woodroffe and Ginsberg, 1998). Overall, our results strengthen the case for MinLoss strategies that consider neighbourhood processes in scheduling, while also indicating the potential value of a more sophisticated approach than the

one used in our study. This improved approach would also consider the vulnerability of areas in the neighbourhood of areas being considered for reservation (below).

Our analyses can be improved in several ways. We accounted for a contagion effect in deriving the initial probability of conversion to urban areas but did not have similar information for agricultural suitability. We therefore assumed that successive losses of vegetation were spatially independent.

We placed no spatial constraints on the displacement of land clearing by reservation, assuming only that it was moved elsewhere within vulnerability classes, whereas reservation can also attract or inhibit nearby development pressure. Our intent here was to test different scheduling strategies in a more realistic scenario that accounts for species dynamics and heterogeneous land cost. This is a fundamental first step towards forecasting the effect of conservation policies on biodiversity persistence and allowed us to observe novel and unexpected behaviours of two common reserve selection approaches. Building an accurate model of urban and agricultural development for the Hunter valley was beyond the scope of this research; moreover, a more sophisticated model of land-use change, incorporating the potential dynamic interactions between reservation and development pressure would not necessarily yield different results. The dynamics of costs (Armsworth et al., 2006), are also part of this more complex picture that we will explore in future research.

Prior to this study, the impact of ongoing habitat loss outside previously established reserves had not been explicitly identified in a scheduling framework. Because habitat loss is typically spatially auto-correlated (Overmars et al., 2003), strategies that consider habitat loss in priority setting are more likely to encounter the adverse impacts of fragmentation and isolation of reserves. These strategies are likely to benefit from considering the vulnerability of areas in the neighbourhoods of focal areas as well as that of the areas themselves. Our findings here have directed our future work toward accounting for neighbourhoods of focal areas in two ways: first by considering habitat configuration at the time of selection (in this study) and, second, by also anticipating the isolation of areas after they have been selected for conservation investment.

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Appendix A

A.1. Planning unit design

We attempted to match, as far as possible, the boundaries of planning units with those of discrete patches of forest to couple management and ecological units. We also tried to limit the variance in size of the planning units so that very large planning units would not dominate investments in terms of high biodiversity benefit and very small planning units would not dominate investments in terms of low cost. We also wanted to avoid having planning units that were too expensive to purchase with an annual budget. We first excluded all areas without forest because all three of our species were restricted to forest. Second, we transformed all vegetation fragments smaller than 25 ha into individual planning units. Third, we overlaid a 25 ha (500 m x 500 m) square grid layer on the larger polygons of forest to set the maximum size of planning units initially at 25 ha. We then clipped the 25 ha square grids to the external boundaries of the study region and to the external boundaries of fragments so that the configurations of fragments were retained. This clipping procedure created a large number of very small sliver polygons around the external edges of fragments and around the internal edges of the planning region. To reduce this number, we merged all planning units smaller than 3 ha with

the neighbouring planning unit having the largest shared boundary if they had one. The largest of our final planning units (34 ha) constituted a 25 grid combined with three adjacent units slightly smaller than 3 ha.

Appendix B

See Tables B1 and B2.

Appendix C

C.1. Habitat loss model

We calculated the average rate of increase of urban populations with the most recent data available on each major urban centre in the study region (2001–2004, Australian Bureau of Statistics, 2006). We assumed that the population density stayed constant during our 20-year planning period. Therefore, the extent of each urban settlement increased at the same rate as its population. We also assumed that the growth rate from 2001 to 2004 continued over our 20-year simulations. The annual radius of expansion was that of a circle equal in size to the urban settlement at the start of the land use simulations multiplied by its annual rate of expansion. Settlements adjacent to Lake Macquarie and the Pacific Ocean are constrained from expanding eastward so we doubled their westward rates of expansion to compensate. To derive a continuous probability surface for urban development (“vulnerability”), we used a dispersal kernel with the formula:

$$P = \exp(-\alpha \cdot d) \quad (C1)$$

where d is the distance between a cell and a settlement. The parameter α was a characteristic specific to each urban settlement related to its rate of expansion. We calculated α by assigning a probability of 0.5 to a distance equivalent to the estimated average annual distance of expansion for each settlement and solved Eq. (1) for α . When a cell was within the expansion radius of more than one

Table B1

Abbreviated names and definitions of the final predictor variables in the “local” and “neighbourhood” habitat models.

Predictor	Description	Local	Neighbourhood
Rugg500	Topographic ruggedness: standard deviation in elevation within a 500 m radius		✓
Ter1000	Relative terrain position within a 1000 m radius		✓
Rain	Mean annual rainfall derived from ANUCLIM	✓	✓
Temp	Mean annual temperature derived from ANUCLIM	✓	✓
Dry2000	The percentage of cells in a 2000 m radius containing dry forest		✓
Percnonfor2 k	The percentage of cells in a 2000 m radius classified as cleared of native vegetation		✓
Unmod	Factorial variable: 1 if the vegetation is unmodified, 0 otherwise	✓	
Unmod500	The percentage of cells in a 500 m radius containing unmodified forest		✓
Unmod2000	The percentage of cells in a 2000 m radius containing unmodified forest		✓
Ybglexp	Factorial variable: 1 if the cell is suitable for the yellow-bellied glider, 0 otherwise	✓	
Ybglexp2000	The percentage of cells in a 2000 m radius containing suitable yellow-bellied glider habitat		✓
Sowlexp	Factorial variable: 1 if the cell is suitable for the sooty owl, 0 otherwise	✓	
Sowlexp2000	The percentage of cells in a 2000 m radius containing suitable sooty owl habitat		✓
Sqglexp	Factorial variable: 1 if the cell is suitable for the squirrel glider, 0 otherwise	✓	
Sqglexp500	The percentage of cells in a 500 m radius containing suitable squirrel glider habitat		✓

Table B2

Final Local and Neighbourhood models and bootstrapped estimates of predictive discrimination given by the area under the Receiving Operating Characteristic Curve.

Species	Model type	Preferred model	Model type	ROC area
Yellow-bellied glider	Local	$sp \sim s(\text{temp}, 2) + s(\text{rain}, 2) + \text{unmod} + \text{ybglexp}$	GAM	0.74
Yellow-bellied glider	Neighbourhood	$sp \sim s(\text{temp}, 2) + s(\text{rain}, 2) + \text{unmod2000} + s(\text{ybglexp2000}, 3)$	GAM	0.76
Sooty owl	Local	$sp \sim \text{sowlexp} \times \text{rain} + \text{undmod} \times \text{rain}$	GLM	0.74
Sooty owl	Neighbourhood	$sp \sim s(\text{rain}, 2) + \text{rugg500} + s(\text{sowlexp2000}, 3) + s(\text{ter1000}, 2) + \text{unmod2000} \text{ cl}$	GAM	0.86
Squirrel glider	Local	$sp \sim \text{sqglexp} \times \text{unmod}$	GLM	0.78
Squirrel glider	Neighbourhood	$sp \sim s(\text{rugg500}, 3) + \text{sqglexp500} + s(\text{unmod500} \text{ cl}, 2)$	GAM	0.80

Table E
Fifth, 50th and 95th percentile of persistence values (proportion of occurrences still extant at a given time) for all species and all strategies at year 10, 20, 30, 40. For the simulation that terminated before year 30 or 40, the year is indicated in parentheses. PA and PR are the abbreviations for Pattern and Process. MG and ML are the abbreviations for MaxGain and MinLoss. The letter “l” and “r” follow the same coding of Fig. 4.

<i>Yellow-bellied glider</i>				
10	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.887,0.894,0.898	0.887,0.896,0.901	0.887,0.894,0.907	0.889,0.897,0.904
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.885,0.894,0.905	0.881,0.894,0.899	0.882,0.889,0.900	0.877,0.887,0.895
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.584,0.599,0.609	0.591,0.598,0.604	0.592,0.601,0.609	0.591,0.601,0.627
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.591,0.603,0.618	0.590,0.603,0.610	0.593,0.603,0.617	0.589,0.602,0.608
	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.769,0.790,0.797	0.781,0.793,0.807	0.779,0.785,0.801	0.802,0.809,0.815
20	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.782,0.787,0.806	0.778,0.790,0.798	0.776,0.789,0.798	0.758,0.775,0.791
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.385,0.387,0.395	0.380,0.388,0.398	0.385,0.391,0.398	0.414,0.426,0.436
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.385,0.390,0.394	0.381,0.392,0.400	0.380,0.389,0.394	0.389,0.395,0.397
	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.678,0.692,0.707	0.683,0.694,0.709	0.696,0.700,0.715	0.685,0.710,0.714
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.665,0.683,0.709	0.665,0.672,0.676	0.676,0.692,0.701	0.662,0.675,0.696
30	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	NA	NA	NA	NA
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	NA	NA	NA	NA
	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.607,0.614,0.629	0.608,0.616,0.626	0.616,0.625,0.642	0.619,0.638,0.647
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.595,0.608,0.629	0.584,0.596,0.602	0.607,0.619,0.633	0.591,0.600,0.617
	PA-MG-LR (27th year)	PA-ML-LR (25–26th year)	PR-MG-LR (27th year)	PR-ML-LR (24–25th year)
	0.296,0.296,0.298	0.303,0.308,0.312	0.299,0.301,0.305	0.362,0.376,0.382
PA-MG-Lr (27–28th year)	PA-ML-Lr (27th year)	PR-MG-Lr (27th year)	PR-ML-Lr (27th year)	
0.293,0.293,0.294	0.293,0.294,0.296	0.292,0.292,0.293	0.301,0.304,0.305	
<i>Squirrel glider</i>				
10	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.943,0.945,0.948	0.944,0.947,0.952	0.944,0.948,0.949	0.944,0.947,0.950
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.942,0.946,0.952	0.943,0.946,0.948	0.942,0.945,0.949	0.940,0.943,0.950
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.740,0.744,0.750	0.748,0.754,0.760	0.741,0.747,0.755	0.750,0.753,0.758
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.739,0.740,0.749	0.739,0.747,0.756	0.738,0.744,0.753	0.742,0.746,0.750
	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.881,0.887,0.891	0.888,0.892,0.899	0.887,0.889,0.895	0.886,0.892,0.896
20	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.883,0.887,0.895	0.884,0.886,0.892	0.881,0.885,0.893	0.877,0.885,0.893
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.483,0.488,0.501	0.524,0.530,0.535	0.481,0.486,0.491	0.545,0.548,0.556
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.467,0.469,0.476	0.485,0.489,0.493	0.473,0.477,0.484	0.482,0.488,0.491
	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.820,0.825,0.837	0.831,0.836,0.843	0.826,0.830,0.840	0.819,0.833,0.837
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.817,0.824,0.836	0.814,0.824,0.832	0.817,0.824,0.834	0.816,0.823,0.829
30	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	NA	NA	NA	NA
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	NA	NA	NA	NA
	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.763,0.768,0.778	0.776,0.784,0.789	0.768,0.774,0.782	0.764,0.781,0.785
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.760,0.768,0.773	0.761,0.768,0.774	0.756,0.766,0.780	0.760,0.765,0.774
	PA-MG-LR (27th year)	PA-ML-LR(25–26th year)	PR-MG-LR (27th year)	PR-ML-LR (24–25th year)
	0.367,0.370,0.385	0.434,0.438,0.441	0.364,0.367,0.371	0.457,0.460,0.465
PA-MG-Lr (27–28th year)	PA-ML-Lr (27th year)	PR-MG-Lr (27th year)	PR-ML-Lr (27th year)	
0.351,0.362,0.364	0.363,0.364,0.365	0.351,0.352,0.353	0.364,0.364,0.366	
<i>Sooty owl</i>				
10	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.906,0.921,0.931	0.915,0.921,0.930	0.907,0.921,0.944	0.908,0.918,0.936
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.894,0.908,0.929	0.884,0.919,0.932	0.905, 0.912,0.930	0.900,0.919,0.935
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	0.673,0.703,0.725	0.696,0.717,0.723	0.688,0.708,0.722	0.692,0.707,0.727
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.689,0.716,0.727	0.695,0.707,0.717	0.684,0.700,0.728	0.695,0.702,0.717

Table E (continued)

20	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.830,0.843,0.856	0.823,0.854,0.870	0.822,0.839,0.860	0.840,0.852,0.867
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.808,0.849,0.869	0.815,0.840,0.858	0.812,0.846,0.858	0.814,0.836,0.867
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
30	0.521,0.532,0.542	0.521,0.533,0.556	0.525,0.534,0.546	0.544,0.563,0.571
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
	0.523,0.536,0.546	0.507,0.536,0.551	0.510,0.534,0.540	0.531,0.540,0.549
	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.771,0.781,0.793	0.755,0.785,0.800	0.761,0.781,0.805	0.779,0.793,0.811
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.724,0.769,0.788	0.753,0.773,0.783	0.745,0.771,0.792	0.748,0.761,0.788
	PA-MG-LR	PA-ML-LR	PR-MG-LR	PR-ML-LR
	NA	NA	NA	NA
	PA-MG-Lr	PA-ML-Lr	PR-MG-Lr	PR-ML-Lr
Last	NA	NA	NA	NA
	PA-MG-IR	PA-ML-IR	PR-MG-IR	PR-ML-IR
	0.714,0.728,0.736	0.709,0.726,0.748	0.701,0.730,0.736	0.730,0.740,0.759
	PA-MG-lr	PA-ML-lr	PR-MG-lr	PR-ML-lr
	0.678,0.710,0.735	0.692,0.712,0.738	0.698,0.713,0.749	0.688,0.710,0.738
	PA-MG-LR (27th year)	PA-ML-LR (25–26th year)	PR-MG-LR (27th year)	PR-ML-LR (24–25th year)
	0.430,0.431,0.433	0.438,0.447,0.454	0.430,0.433,0.436	0.518,0.537,0.546
	PA-MG-Lr (27–28th year)	PA-ML-Lr (27th year)	PR-MG-Lr (27th year)	PR-ML-Lr (27th year)
0.426,0.427,0.430	0.426,0.429,0.433	0.425,0.425,0.426	0.438,0.445,0.449	

settlement its probability of conversion was the maximum possible given by equation C1 for all the settlements of interest.

We reclassified the continuous urban vulnerability map into four classes. We did this by applying cut-off values at 1, 2 and 3 standard deviations of urban vulnerability. We subsequently eliminated the first class (values from 0 to 1 standard deviation), because it consisted of areas far from existing urban settlements and with probabilities of conversion that were approximately zero. This class was redundant given that no area in private land was considered to have a null probability of conversion to agriculture.

For each 1 ha cell of native vegetation in private land, we assigned the highest value from the maps of agricultural and urban vulnerability. For planning units that covered more than one vulnerability class, we allocated vulnerability values to planning units as the rounded average vulnerability class of the cells it contained. We used average rather than maximum values within planning units to avoid overestimating probability of loss of vegetation in planning units containing 1 ha cells with variable vulnerabilities.

Appendix D

D.1. Planning unit cost

We assumed that the sale value of a planning unit (its acquisition cost) was equal to the discounted flow of net revenue that the planning unit is expected to generate into the future (its opportunity cost). We estimated the cost using the formula proposed by Naidoo and Adamowicz (2006):

$$EV = \sum_{k=1}^K \sum_{c=1}^C P_{ck} R_k \quad (D1)$$

where EV is the estimated land value equal to the sum across all the k possible land uses and all the 1 ha cells c within the planning unit of the return R_k associated with land use k multiplied by the probability of conversion to that particular land use P_k . The rationale for the use of the probability of conversion in the formula is that land values are modelled as the expected value of land arising from all possible uses k , where the expectation is taken over the probability that the land is converted to use k . In our case, we considered land uses related to urban and agricultural activities. The average values of land associated with each activity were available at the resolution of local government areas (LGAs) from the Australian Bureau of Agricultural and Resource Economics (ABARE, 2000).

We estimated urban value by calculating the mean value across all urban land uses (defined here as Business, Industrial and Residential) weighted by their proportional extent in the LGA. Because the two LGAs intersected by our planning region (Cessnock and Lake Macquarie) had different land values for both urban and agricultural uses, we applied a smoothing technique to avoid an abrupt difference in land values at the boundary between the LGAs. We did this for urban land value by placing a point in the centre of each urban settlement within each LGA and using an inverse distance weighted interpolation to generate a cost surface for the entire planning region. For agricultural value the interpolation was based on points placed in the centre of each LGA.

We calculated the acquisition cost surface by adding the urban and agricultural values together.

Appendix E

See Table E.

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