A Bayesian model of metapopulation viability, with application to an endangered amphibian

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Abstract

Aim: Population viability analysis (PVA) is used to quantify the risks faced by species under alternative management regimes. Bayesian PVAs allow uncertainty in the parameters of the underlying population model to be easily propagated through to the predictions. We developed a Bayesian stochastic patch occupancy model (SPOM), and used this model to assess the viability of a metapopulation of the growling grass frog (*Litoria raniformis*) under different urbanisation scenarios.

Location: Melbourne, Victoria, Australia.

Methods: We fitted a Bayesian model that accounted for imperfect detection to a multi-season occupancy dataset for *L. raniformis* collected across northern Melbourne. The probability of extinction was modelled as a function of effective wetland area, aquatic vegetation cover and connectivity, using logistic regression. The probability of colonisation was modelled as a function of connectivity alone. We then simulated the dynamics of a metapopulation of *L. raniformis* subject to differing levels of urbanisation and compensatory wetland creation. Uncertainty was propagated by conducting simulations for 5000 estimates of the parameters of the models for extinction and colonisation.

Results: There was considerable uncertainty in both the probability of quasi-extinction and the minimum number of occupied wetlands under most urbanisation scenarios. Uncertainty in the change of quasi-extinction risk and the minimum metapopulation size increased with increasing habitat loss. For our focal metapopulation, the analysis revealed that investment in six or more wetlands may be required to offset the impacts of urbanisation.

Main conclusions: Bayesian approaches to PVA allow parametric uncertainty to be propagated and considered in management decisions. They also provide means of identifying parameters that represent critical uncertainties, and, through the use of informative priors, can easily assimilate new data to reduce parametric uncertainty. These advantages, and the ready availability of software to run Bayesian analyses, will ensure that Bayesian approaches are used increasingly for PVAs.

Introduction

Even the simplest conservation decisions may entail considerable uncertainty. The complexity of ecological processes and their inherently stochastic nature ensures that the response of populations or communities to particular management actions cannot be assessed in a purely mechanistic framework (Williams *et al.*, 2002). Instead, conservation biologists turn to probabilistic approaches to explore the risks associated with particular management decisions. They seek to estimate the probability that an adverse event will occur in the future under a particular management scenario, given a mathematical model of the system, and known or plausible sources of stochasticity (Burgman *et al.*, 1993). In many cases, the uncertainty captured by this approach relates only to the stochasticity of the modelled dynamics, but incorporating uncertainty in the model itself is also important. Doing so allows known uncertainty around the estimated risk to be considered in management decisions, and highlights areas where better knowledge of the system is required to reduce that uncertainty (Burgman, 2005).

Population viability analysis (PVA) remains an important form of risk analysis for the management of threatened species. PVA is the quantitative evaluation of factors that influence population growth and persistence for single species (Boyce, 1992; Lindenmayer *et al.*, 1995; McCarthy & Possingham, in press). Early incarnations were focussed on single populations, and sought to estimate the probability of extinction for small populations subject to environmental, demographic and genetic stochasticity (Soulé, 1987; Beissinger, 2002). Contemporary PVAs are designed for more complicated problems, and incorporate more complicated dynamics. Because many threatened species display some population sub-division, and because habitat fragmentation is near ubiquitous as a threatening process, PVAs that incorporate multiple interacting populations (metapopulations) have now largely replaced PVAs focussed on a single population (Morris & Doak, 2002). These models allow migration between the component populations, and may also incorporate such things as spatially-variable demographic parameters, habitat dynamics, and spatially-correlated disturbance regimes (McCarthy, 2009). The application of these models is now less concerned with the outright risk of extinction, and instead focuses on comparative risks. Given a set of options for future management, analysts seek to quantify and compare the relative risk of extinction under each (e.g., Lindenmayer & Possingham, 1996; Akçakaya & Raphael, 1998; Drechsler *et al.*, 2003). Alternatively, they may seek to optimise viability subject to budget constraints. In these situations, the candidate set of management options is not predefined; rather the analyst is charged with identifying the combination of management actions that minimizes the probability of extinction for a set budget (e.g., Moilanen & Cabeza, 2002).

While the use of PVA to predict the relative risk of extinction should be more robust to uncertainty than predictions of outright extinction risk (McCarthy *et al.*, 2003), propagating uncertainty through to the model predictions remains desirable for such analyses (Morris & Doak, 2002). Numerous uncertainties may influence a given PVA, but parametric uncertainty is ubiquitous. Parametric uncertainty arises from sampling variation, observer bias, and sampling error in empirically derived population models, and through differences of opinion for models parameterised using expert knowledge (McGowan *et al.*, 2011). Despite its ubiquity, accounting for parametric uncertainty in PVAs has proven technically challenging, and somewhat contentious (Wade, 2002). Bayesian approaches are becoming an increasingly popular means of performing PVAs as a result, because they allow straightforward propagation of parametric uncertainty through to model predictions (Ludwig, 1996; Wade, 2002; McCarthy, 2007). Bayesian statistical methods represent uncertainty in model parameters by using probability distributions, with the width of a parameter's distribution representing the imprecision of the associated estimate (McCarthy, 2007). Importantly, Bayesian methods recognise that information about a parameter accumulates over time. The prior distribution represents what is known about a parameter before considering the latest set of data. The information in the data about the parameters is combined with the prior using Bayes' rule, generating the posterior distribution (McCarthy, 2007). Propagating parametric uncertainty in Bayesian PVA is simply a matter of simulating the dynamics of the focal population/s for combinations of parameter values drawn from their joint posterior distributions, thereby providing a distribution for the chosen viability metric that represents uncertainty due to imprecision in the parameters, as well as that due to stochasticity of the modelled dynamics.

In the metapopulation literature, Bayesian approaches to PVA have primarily been pursued in the context of stochastic patch occupancy models, or SPOMs. These models are designed for the situation in which population extinction is commonplace, and persistence of the metapopulation relies upon a balance between the rate of population extinction and the rate of colonisation of vacant habitat patches (Sjögren-Gulve & Hanski, 2000; Hanski, 2002). Rather than attempting to model the internal demographic processes of the constituent populations, SPOMs describe the stochastic changes in population occurrence arising from population extinction and colonisation (Sjögren-Gulve & Hanski, 2000; Hanski, 2002). The most well known and widely applied SPOM is the incidence function model (IFM) pioneered by Hanski (1994). Hanski's model incorporates the key effects of patch area and isolation on the probabilities of extinction and colonisation (see Hanski, 1999), and was the first to allow simulation of the dynamics of real metapopulations subject to habitat loss, degradation and fragmentation. Bayesian formulations of the IFM have been offered by O'Hara *et al.* (2002), ter Braak & Etienne (2003), Harrison *et al.* (2011) and Risk *et al.* (2011).

Nevertheless, the application of the IFM to conservation planning has been criticized. The reasons are various, ranging from arguments against the generality of the patch area and isolation paradigm (Pellet *et al.*, 2007), to technical concerns such as the need to assume stationarity of extinction and colonisation rates when estimating the parameters of the model using occupancy data (Thomas, 1994). While these concerns are by no means fatal to the IFM, they do point to a need for alternative approaches when the shortcomings of the IFM are not trivial. One option is to model the probabilities of population extinction and colonisation directly (Sjögren-Gulve & Ray, 1996; Sjögren-Gulve & Hanski, 2000; Morris & Doak, 2002). The idea is simple – given an adequate sample of extinction and colonisation events, one may build regression models of relationships between the probabilities of extinction and colonisation and particular patch- and landscape-level variables thought to influence these processes. Arbitrarily complex linear and non-linear relationships can be incorporated, providing considerable flexibility for model development. As demonstrated by Sjögren-Gulve & Ray (1996), the resulting regression models for the probabilities of population extinction and colonisation can be used to simulate the dynamics of real metapopulations in the same way as the IFM, and therefore offer the same opportunities to predict the viability of real metapopulations subject to habitat change (see also Sjögren-Gulve & Hanski, 2000; Morris & Doak, 2002).

Here we present a Bayesian version of the regression approach introduced by Sjögren-Gulve & Ray (1996), and use it to assess the viability of a metapopulation of an endangered frog from southern Australia. This is, to our knowledge, the first time a Bayesian formulation of Sjögren-Gulve & Ray's approach to metapopulation viability analysis has been presented. We demonstrate how the Bayesian formulation allows parametric uncertainty to be easily propagated through to predictions of metapopulation viability under differing scenarios of habitat loss and creation.

Methods

The approach

Before proceeding to the technical aspects of our approach, we first briefly expand on the theoretical basis of SPOMs. Classical metapopulation theory assumes networks of spatially discrete populations connected by infrequent dispersal. Within these networks, populations are prone to extinction given sensitivity to demographic, genetic and environmental stochasticity, but these extinctions may be offset by colonisation of vacant habitat patches. Population extinction and colonisation are thus random events, but the probabilities of extinction and colonisation vary among patches and over time. The probability of extinction is modeled as a function of population size and, in some cases, immigration rate (the ‘rescue effect’ *sensu* Brown & Kodric-Brown, 1977). The probability of colonisation is modeled as a function of the number of immigrants. Spatially-realistic SPOMs are based on the premise that particular patch- and landscape-scale variables may be used as surrogates for population size and immigration rate (Hanski, 1994; Sjögren-Gulve & Ray, 1996). The most basic of these relationships are encapsulated by the IFM: population size scales with patch area, and immigration rate depends on the number, proximity and size of neighboring populations (‘isolation’, or, conversely, ‘connectivity’). However, additional variables are likely to be important determinants of population size and immigration rate in some circumstances. When patch quality is highly variable, even small patches may have high carrying capacities (Fleishman *et al.*, 2002). Similarly, the surrounding landscape could be more or less permeable to migrants, in which case the number of immigrants arriving at a patch will only partly reflect its proximity to neighbouring populations (Wiens, 1997).

As above, the approach of Sjögren-Gulve & Ray (1996) is predicated on the use of regression models to describe relationships between the probabilities of extinction and colonisation and patch- and landscape-scale variables thought to influence population size and immigration rate. Applying the logit link, the probability of extinction (ε) for population *i* at time *t* is modelled as:

$$\mathrm{logit}\left(\varepsilon_{i,t}\right) = \alpha_{\varepsilon} + \beta_{\varepsilon 1}\left(X_{1,i,t\text{-}1}\right) + \beta_{\varepsilon 2}\left(X_{2,i,t\text{-}1}\right) + \ldots + \beta_{\varepsilon N}\left(X_{N,i,t\text{-}1}\right), \qquad \text{(Eq. 1)}$$

where α_{ε} is the intercept term, $X_{1,i,t-1}$, $X_{2,i,t-1}$, and $X_{N,i,t-1}$ are values for the relevant patch- and landscape-scale variables at the preceding time-step, and $\beta_{\varepsilon 1,}$ $\beta_{\varepsilon 2,}$ and $\beta_{\varepsilon N}$ are regression coefficients. Likewise, the probability of colonisation (γ) for patch *i* at time *t* is modelled as:

$$\operatorname{logit}\left(\gamma_{i,t}\right) = \alpha_{\gamma} + \beta_{\gamma 1}\left(Z_{1,i,t-1}\right) + \beta_{\gamma 2}\left(Z_{2,i,t-1}\right) + \ldots + \beta_{\gamma N}\left(Z_{N,i,t-1}\right). \qquad \text{(Eq. 2)}$$

Sjögren-Gulve & Ray (1996) describe how the parameters of Eq. 1 and Eq. 2 may be estimated using maximum likelihood when data on occupancy turnover between two time-steps are available. However, as Sjögren-Gulve & Ray acknowledge, their approach assumes that the focal species is detected without error; an assumption that may be problematic for many species (Tyre *et al.*, 2003; MacKenzie *et al.*, 2006). Recent advances in occupancy modelling circumvent this problem. Mackenzie *et al.* (2003) provided an approach in which maximum likelihood estimates of the probabilities of extinction and colonisation may be derived from multi-year occupancy datasets, whilst accounting for imperfect detection. Although the data requirements are slightly different (repeat survey data within years being required to jointly estimate the probability of detection), the approach of Mackenzie *et al.* (2003) is similar to that of Sjögren-Gulve & Ray (1996), because the probabilities of extinction and colonisation may be modelled as functions of covariates using the logit link function.

Royle & Kéry (2007) provided a Bayesian state-space formulation of the dynamic occupancy model of Mackenzie *et al.* (2003) which allows the posterior distribution of the parameters of equations 1 and 2 to be derived using Markov chain Monte Carlo (MCMC) sampling. Royle & Kéry (2007) implemented their method using *WinBUGS* (Lunn *et al.*, 2000), but it is also directly transferable to *OpenBUGS* (the open-source version of *WinBUGS*; Thomas *et al.*, 2006) and may also be implemented in *JAGS* (an alternative program for fitting Bayesian models using MCMC sampling; Plummer, 2003) with only minor alteration.

Once estimates of the parameters of equations 1 and 2 have been derived using MCMC sampling, they can be inserted into the standard equation for changes in patch occupancy to define a SPOM. The standard equation is (MacKenzie *et al.*, 2003):

$$O_{i,\,t+1} = o_{i,t}\ \left(1 - \varepsilon_{i,t}\right) + \left(1 - o_{i,t}\right)\gamma_{i,t}, \qquad \text{(Eq. 3)}$$

where $O_{i,t+1}$ is the probability of occupancy of patch *i* at time *t*+1, $o_{i,t}$ is the occupancy status of patch *i* at time *t* (1 if occupied, 0 otherwise), and $\varepsilon_{i,t}$ and $\gamma_{i,t}$ are the probabilities of extinction and colonisation for patch *i* at time *t*, as defined by equations 1 and 2. Thus, the probability of occupancy at time *t*+1 is equal to the probability of colonisation ($\gamma_{i,t}$) if the patch was unoccupied at the previous time step, and is equal to the probability of persistence ($1 - \varepsilon_{i,t}$) if the patch was occupied. Using the resulting model to simulate the dynamics of the metapopulation over a chosen time period is straightforward. For one time step to the next, the process is as follows: (i) estimate the probability of occupancy for each patch at the second time-step ($O_{i,t+1}$), according to the occupancy status in the first time step ($o_{i,t}$) and the probabilities of population extinction ($\varepsilon_{i,t}$) and colonisation ($\gamma_{i,t}$); (ii) set occupancy of each patch at the second time-step as the outcome of a Bernoulli trial with probability $O_{i,t+1}$, and; (iii) record the occupancy status of each patch at the second time-step. In order to incorporate parametric uncertainty, these simulations are simply repeated for each of the sample of parameter values derived from the MCMC algorithm.

By running many simulations for each parameter combination and recording the number of occupied patches through time for each simulation, one can estimate of the probability of extinction or quasi-extinction for the metapopulation through time (Hanski, 2002). For each parameter combination, the probability of extinction is simply the proportion of simulations in which the metapopulation reached zero occupied patches. Similarly, the probability of quasi-extinction is estimated as the proportion of simulations in which the metapopulation declined below some threshold patch occupancy (e.g., < 5 occupied patches). Of course, alternate measures of metapopulation viability could also be derived from the simulations, such as the expected minimum number of occupied patches. This measure is equivalent to the expected minimum population size in demographic PVAs, and gives a better indication of the propensity for decline when the risk of extinction is small (McCarthy & Thompson, 2001). Regardless of the metric used, uncertainty may be presented as the full distribution of estimates across the parameter combinations, or through a summary of this distribution, such as the mean and 95% credible interval.

Case study

The growling grass frog (*Litoria raniformis*) is an endangered frog that occurs throughout south-eastern Australia (Pyke, 2002). In the vicinity of Melbourne, the capital city of Victoria, urban expansion is a key threat to this species. Numerous remnant populations occur in areas slated for urban growth, and associated wetland loss, degradation and fragmentation may place metapopulations of *L. raniformis* at considerable risk of extinction (Heard *et al.*, 2012a, b). Developing a model of the extinction and colonisation dynamics of *L. raniformis* has subsequently been identified as a priority for understanding the species' conservation requirements (Heard *et al.*, 2012b).

We built a Bayesian regression-based SPOM for *L. raniformis* using occupancy data from 167 wetlands monitored across northern Melbourne between the 2001/2002 and 2006/2007 breeding seasons (Heard *et al.*, 2012b). Wetlands included slow-flowing pools along streams, swamps, ponds, farm dams and quarry pits. All wetlands were surveyed on between one and four occasions in the first and last years of the study (with the exception of four wetlands that were destroyed before the final year), and a subset surveyed on up to 10 occasions in the intervening years. A total of 1380 surveys were completed.

We began by identifying patch- and landscape-scale variables that influence the extinction and colonisation dynamics of *L. raniformis*. For the purposes of this paper, we focussed on a model in which the probability of extinction was a function of effective wetland area, aquatic vegetation cover and connectivity, and the probability of colonisation was a function of connectivity alone. Effective area (A_{eff}) was defined as:

$$A_{eff_i} = \frac{\log(A_i) \times H_i}{H_{max}} , \qquad \text{Eq. 4}$$

where A_i is the surface area of wetland *i*, H_i is the hydroperiod of wetland *i* measured on an ordinal scale between 1 (temporarily fills only during high rainfall periods) and 4 (permanently inundated, regardless of rainfall variability), and H_{max} is the maximum hydroperiod score (4). Adjusting wetland area for hydroperiod accounted for the fact that wetland carrying capacity should be closely tied to fluctuations in water-level for *L. raniformis*, due to its highly aquatic nature (Heard *et al.*, 2008; Heard *et al.*, 2012b). Aquatic vegetation cover is considered a key microhabitat for both larval and adult *L. raniformis,* and therefore represents a key patch quality variable for the species (Hamer & Organ, 2008; Heard *et al.*, 2008; Wassens *et al.*, 2010). Aquatic vegetation cover for each wetland (V_i) was defined as the mean cover of emergent, submergent and floating aquatic vegetation. After Heard *et al.* (2012b), connectivity of each wetland in each year ($S_{i,t}$) was defined as:

$$S_{i,t} = \sum w_{i,j} \times o_{j,t} , \qquad \text{Eq. 5}$$

where $w_{i,j}$ is a weighting function, and $o_{j,t}$ is the occupancy status of each neighbour *j* in year *t* (one if the wetland is occupied, zero if not). For years 2–6, calculation of connectivity was complicated by the fact that some wetlands were not surveyed in those years, whilst others had been destroyed. When occupancy data were not available for a wetland in a given year, the outcome of the nearest preceding survey for that wetland was used instead. Wetlands that had been destroyed were simply removed from connectivity calculations for the years following their destruction. The weighting function, $w_{i,j}$, defines a negative power relationship between the probability of dispersal from wetland *i* to *j* and the Euclidean distance between their centres ($d_{i,j}$, at 10 m increments). This function, derived by Heard *et al.* (2012b) using mark-recapture data, was:

$$w_{i,j} = 0.10026 \ d_{i,j}{}^{-0.719877} \ . \qquad \text{(Eq. 6).}$$

Connectivity ($S_{i,t}$) was log-transformed for further analyses.

Using the approach of Royle & Kéry (2007), we fitted a dynamic occupancy model to these data in which the logits of the probabilities of extinction and colonisation were modelled as additive, linear functions of the above variables. The logit of the probability of detection was set as an additive, linear function of survey effort (person minutes), date (days since October 1) and time of day (day or night) following Heard *et al.* (2012b). Vague, normally-distributed priors (N[0, 0.001]) were used for all model parameters. Convergence was assessed by visually inspecting the histories of two Markov chains with over-dispersed initial values. Convergence was achieved within 25,000 MCMC samples. We extracted the subsequent 5000 estimates of the parameters of the model. Model fitting was completed with *OpenBUGS* v. 3.0.3, called from *R* v. 2.12.0 (R Development Core Team, 2012) using the add-in package *BRugs* v. 0.5-3 (Ligges, 2008). Code for running the analysis is provided in Appendix S1 of the Supporting Information. Table S1 gives summary statistics for the posterior distributions of the model parameters, and Fig. S1 shows the fitted relationships.

The parameter estimates were used to assess the viability of a metapopulation of *L. raniformis* located in Donnybrook, on Melbourne's northern fringe. This metapopulation occupies a reasonably discrete cluster of 30 wetlands, including pools along the Merri and Kalkallo Creeks, and farm dams within 500 m of these creeks (Fig. 1). Many of these wetlands were included in the broader study of Heard *et al.* (2012b), meaning that estimates of A_{eff} and V were already available. Estimates of A_{eff}

and V for wetlands that were not surveyed by Heard *et al.* (2012b) were acquired in a subsequent study (Heard & McCarthy, 2012). The only other information required to simulate the dynamics of the metapopulation were the coordinates of wetland centres and the initial occupancy status of each wetland. For simplicity, we assumed all wetlands were occupied at the initial time-step.

The dynamics of the Donnybrook metapopulation were simulated for a period of 30 years under three broad scenarios. The first (referred to hereafter as 'current conditions') entailed no change in wetland number or condition over this period (Fig. 1). In the second scenario, we deleted dams in accordance with urban growth plans for Donnybrook (DPCD, 2009). These plans involve the maintenance of riparian reserves for conservation purposes and for public parkland, although the size of these reserves is yet to be finalised. We trialled riparian reserves ranging from 500 m either side of both creeks, to 100 m either side, at 100 m increments (Fig. 1). In the final scenario, we assessed the ability of replacement wetlands to offset the losses expected under a 200 m riparian reserve scenario. One to four pairs of wetlands were placed in the riparian reserve, next to central, high-quality patches (Fig. 1). Each new wetland was set to have the same features: A = 1250 sq. m, H = 3, V = 60%. These schemes sought to create clusters of populations which would display high probabilities of occupancy through time. We assumed that the dynamics of *L. raniformis* within created wetlands could be adequately described by our model, as the majority of lentic wetlands monitored in the previous occupancy study were artificial (farm dams, ponds and quarries).

For each of these scenarios, we ran 500 simulations for each of the 5000 combinations of the model parameter estimates. For each simulation run for each combination of parameter estimates, we recorded the minimum number of occupied wetlands across the 30 year time period. The mean minimum number of occupied wetlands (*minocc*) was calculated by averaging over the 500 simulations for each scenario and parameter estimate combination. We defined the metapopulation as having gone quasi-extinct during a simulation run if fewer than three wetlands were occupied at any time-step. The probability of quasi-extinction (*qe*) for each scenario and parameter estimate combination was then simply the proportion of the 500 simulations in which quasi-extinction occurred. Change in the probability of quasi-extinction (Δ*qe*) and mean minimum number of occupied wetlands (Δ*minocc*) was calculated for each scenario and parameter estimate as:

$$\Delta qe_i = qe_i - qe_c, \qquad \text{(Eq. 7)}$$

and

$$\Delta minocc_i = minocc_i - minocc_c, \qquad \text{(Eq. 8)}$$

where qe_i is the probability of quasi-extinction for scenario *i*, qe_c is the probability of quasi-extinction assuming no change from current conditions, $minocc_i$ is the mean minimum number of occupied wetlands for scenario *i*, and $minocc_c$ is the mean minimum number of occupied wetlands assuming no change from current conditions. Simulations were run in *R*, using code provided in Appendix S2.

Results

There was considerable uncertainty in the estimates of the minimum number of occupied wetlands (*minocc*) for the Donnybrook metapopulation of *L. raniformis* given either the maintenance of current conditions or the maintenance of a 500 m riparian reserve (Fig. 2). The 95% CI for *minocc* was ~3–18 for both scenarios. Uncertainty in this metric declined with increasing levels of urbanisation due to the reduced size of the metapopulation. Importantly, both the mean estimate and upper 95% CI of *minocc* fell substantially between the 500 m to 400 m reserve scenarios (Fig. 2); a result of the fact that the 400 m reserve entails the loss of three large farm dams (see Fig. 1). There was also little difference between the 300 m to 100 m reserve scenarios for *minocc* (Fig. 2), as most dams lost across these scenarios were small, shallow and lacked aquatic vegetation. Mean estimates suggest that the probability of quasi-extinction (*qe*, defined as less than three occupied wetlands) would be < 0.2 for this metapopulation over 30 years under all scenarios (Fig. 2). However, the uncertainty in these estimates was very large for the 400 m to 100 m reserve scenarios; the 95% CI being at least 0–0.7 in each case. As with *minocc, qe* increased between the 500 m and 400 m reserves, and stabilised thereafter.

Change in both the minimum number of occupied wetlands (Δ*minocc*) and the probability of quasi-extinction (Δ*qe*) was negligible for the 500 m riparian reserve scenario (mean estimates = -0.674 and 0.003 respectively; Fig. 3). The rate of change in Δ*minocc* was greatest between the 500 m to 400 m reserve scenarios, reflecting the stabilisation of *minocc* for the narrower reserves (Fig. 3). However, uncertainty in Δ*minocc* displayed the opposite trend to *minocc*, with wider 95% CIs for the narrower reserves. While estimates of Δ*minocc* show that the metapopulation will decline with increasing habitat loss, the 95% CI for Δ*qe* overlapped zero for all reserve scenarios (Fig. 3). Hence, in each case, there was a small chance that the probability of quasi-extinction would not change from current conditions. Uncertainty in Δ*qe* increased with decreasing reserve sizes, in accord with Δ*minocc* (Fig. 3).

Estimates of Δ*minocc* and Δ*qe* for the Donnybrook metapopulation given the creation of new wetlands are depicted in Fig. 4. Recall that a 200 m riparian reserve is assumed in each case. Mean estimates of Δ*minocc* suggest that the creation of six to eight new wetlands is required to offset the loss of wetlands outside of the 200 m reserve. However, the lower bound of the 95% CI for Δ*minocc* was -1.9 with the creation of six new wetlands, suggesting that the metapopulation could still decline under this scenario. Only with the creation of eight wetlands was the lower bound of the 95% CI for Δ*minocc* above zero (0.36). Estimates of Δ*qe* present a slightly different picture of the response of this metapopulation to wetland creation (Fig. 4). In all cases, the mean estimates of Δ*qe* were close to zero (-0.018–0.024), suggesting little change in metapopulation viability from current conditions. However, there was a rapid transition in the distribution of estimates of Δqe from the first scenario (two new wetlands) to the third (six new wetlands). Under the first scenario, an increase in the probability of quasi-extinction was predicted for almost all parameter combinations (95% CI of Δqe = -0.002–0.264). The reverse was true when six new wetlands were added (95% CI of Δqe = -0.230–0). This rapid transition in Δqe stemmed from the strategic placement of the new wetlands, and the low threshold for quasi-extinction. By locating the new wetlands in pairs close to high-quality patches, clusters of persistent populations were created. With three such clusters (six new wetlands), there was a sharp drop in the chance of falling below the quasi-extinction threshold of three extant populations.

Discussion

Bayesian models allow straightforward propagation of parametric uncertainty through to predictions derived from these models. Previous studies have shown how Bayesian PVA models may be used to derive probability distributions for the chance of extinction or the expected minimum (meta)population size (Ludwig, 1996; Wade, 2002; ter Braak & Etienne, 2003; McCarthy, 2007). Here we have shown that uncertainty in the relative increase or decrease in these measures under alternate management scenarios is also easily calculated using Bayesian models. This is important for decision-making because the magnitude of uncertainty can influence the perceived impacts of management, and the relative performance of different options. For example, in our case study, the mean estimates of the minimum number of wetlands occupied by *L. raniformis* ($\Delta minocc$) and the probability of quasi-extinction (Δqe) did not change markedly between the 300 m, 200 m and 100 m riparian reserve scenarios (because the wetlands lost under these scenarios were small and of relatively poor quality). As these scenarios would differ markedly in their cost to implement, it may be concluded that benefits conferred by the larger reserves are not economically justified. However, our analysis also demonstrates that there is considerable and increasing uncertainty about the change in both Δ*minocc* and Δ*qe* as the reserve size narrows, with large decreases in metapopulation viability being plausible (Fig. 3). Documenting this uncertainty allows managers to account for it in their decisions. A risk-tolerant manager might be prepared to choose narrower reserves based on the central tendency, whereas a risk-averse manager striving for negligible impacts might impose a large riparian reserve (e.g., 500 m; Fig. 3) or demand considerable offsetting works (e.g., six to eight new wetlands; Fig. 4).

Of course, it is preferable to subject these sorts of decision-making processes to analyses in which the objectives are explicit, and uncertainty is directly integrated. Although we have not illustrated it here, Bayesian PVA models may be coupled with formal decision analyses (Possingham *et al.*, 2002; Wade, 2002; Drechsler & Burgman, 2004). For example, Drechsler *et al.* (2003) coupled a Bayesian incidence function model with a multi-criteria decision analysis to rank a set of patch retention scenarios for a metapopulation of the Glanville Fritillary Butterfly (*Melitaea cinxia*). The optimal strategy in their analysis was simply the one that showed the lowest probability of metapopulation extinction across the greatest number of parameter combinations. Alternatively, managers might seek to identify the strategy that minimizes the chance of breaching a particular threshold for the probability of quasi-extinction (e.g., > 10%), or for the number of occupied patches (e.g., < 5). In this case, the objective is not simply to identify the strategy that minimizes the risk of decline, but rather to set some standard for the trajectory of the metapopulation, and identify the strategy that minimizes the chance of breaching that standard (a form of satisficing; Simon, 1982; Burgman, 2005; McCarthy *et al.*, 2010). The task for the analyst is then to calculate the chance of breaching the threshold for the probability of quasi-extinction or number of occupied patches under each possible management option. In a Bayesian analysis, these probabilities may be calculated as the proportion of the posterior distribution of the viability metric that breaches the chosen threshold.

While the above analyses are useful for identifying the best strategy when there is a single decision to be made, management of metapopulations can involve recurrent decisions about how to manage the constituent populations. Stochastic dynamic programming (SDP) is ideally suited for these situations (Possingham, 1996; Westphal *et al.*, 2003). Nevertheless, current examples of SDP do not include uncertainty in the parameters of the underlying metapopulation model. Including parametric uncertainty produces an optimization problem in which the parameter estimates, the management actions and the response of the metapopulation to those actions are all variable. While including each of these sources of uncertainty in SDP would be a valuable advance, it may prove technically challenging, or even impossible, due to the size and complexity of the optimization problem.

As well as propagating parametric uncertainty through to predictions and the resulting decision-making process, Bayesian approaches to PVA are also useful for identifying parameters that represent critical uncertainties of the underlying model. Critical uncertainties are not just highly uncertain components of the system being modelled. They are uncertainties which, if resolved, can change management decisions (Rumpff *et al.*, 2011; Runge, 2011). One option for identifying parameters that represent critical uncertainties in a Bayesian PVA is to perform analyses akin to traditional sensitivity analyses. Simulations could be run for multiple combinations of parameters drawn from their joint posterior distributions, and the management scenario which is optimal for each draw identified from the simulations. The change in the optimal scenario across the posterior distribution of each parameter could then be quantified, and used as measure of the influence of uncertainty in each parameter on management decisions. When only two management scenarios are considered, the influence of parameter uncertainty on the optimal scenario could assessed using logistic regression, with the response variable being which management strategy is optimal (McCarthy *et al.*, 1995).

Bayesian methods also provide a clear path to increasing the precision of parameters that represent critical uncertainties. Because they incorporate existing knowledge by specifying a prior distribution, Bayesian approaches explicitly recognise that information about a parameter accumulates over time (McCarthy, 2007). In the context of PVA, one can envision building an initial model using vague priors and available data (as we have done here), and then periodically updating the model as monitoring data accumulate, using the posterior from the previous model as the prior in the new one. When both management and monitoring are directed at reducing uncertainty about key parameters, this should help resolve critical uncertainties. For example, in our case study, it was apparent that the relationship between connectivity and the probability of colonisation for *L. raniformis* was highly uncertain at the upper levels of connectivity, because wetlands with high connectivity were rarely unoccupied (see Fig. S1). Should an interrogation of the model reveal that this uncertainty influences the optimal management strategy, one could ensure that at least some created wetlands are placed very close to currently occupied wetlands. Subsequent monitoring of metapopulations manipulated in this way will deliver data about the rate of colonisation of highly connected wetlands, which, when combined with existing information, will reduce uncertainty about this relationship, and reduce management indecision.

This study focused on a regression-based stochastic patch occupancy model (SPOM) following Sjögren-Gulve & Ray (1996). The regression-based approach has advantages over alternatives when data are available to model extinction and colonisation probabilities directly (Sjögren-Gulve & Hanski, 2000; Morris & Doak, 2002). Model structure is highly flexible, meaning that the inclusion of patch quality variables (in particular) is easily accomplished. There is also no need to assume stationarity of extinction and colonisation rates to parameterize the model using occupancy data. As well as providing a Bayesian implementation, we have shown that the approach of Sjögren-Gulve & Ray (1996) may also be extended to account for imperfect detection, given recent advances in occupancy modeling (Mackenzie *et al.* 2003, 2006; Royle & Kéry 2007). This is important, because failing to account for false absences may bias estimates of the parameters of SPOMs, and undermine their predictive power (Moilanen, 2002). Nevertheless, we did not fully account for imperfect detection in our case study. For the purposes of calculating connectivity ($S_{i,t}$), we assumed that the occupancy status of each wetland by *L. raniformis* was determined perfectly in years for which survey data were available, and that occupancy status had not changed from previous years when survey data were unavailable. These assumptions were tolerable in this study, with cumulative probabilities of detection averaging > 0.8 when survey data were available, and missing data being largely restricted to sites whose occupancy status was unlikely to have changed through time. Nevertheless, allowing for imperfect detection and changes in occupancy status when calculating $S_{i,t}$ will be appealing in many situations. Both can be accommodated in Bayesian occupancy models (Royle & Dorazio, 2008; Bled *et al.*, 2011; Risk *et al.*, 2011), because the occupancy status of each patch at each time-step is simulated for each iteration of the MCMC algorithm, enabling stochastic realizations of $S_{i,t}$ to be calculated (see Appendix S1). However, this comes at considerable computational cost when the number of patches is large. The decision to include stochastic realizations of $S_{i,t}$ in the model therefore requires consideration of the likely scale of bias induced by its exclusion, and the computational costs of including it.

Bayesian approaches to PVA explicitly incorporate and propagate uncertainty in models of population processes, allowing informed decision-making and identification of critical uncertainties in the underlying model. For these reasons, and because of the ready availability of software to fit Bayesian models, we expect interest in Bayesian approaches to PVA to continue to rise. When focused on the comparative risks associated with alternate management options, and particularly when coupled with formal decision analyses that identify the optimal approach given a particular objective, these analyses have the potential to provide valuable direction to the management of threatened species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 {Code for fitting the occupancy turnover model and extracting parameter estimates}

Appendix S2 {Code for simulating the dynamics of the Donnybrook metapopulation}

Figure S1 {Relationships between the probability of extinction and effective wetland area, aquatic vegetation cover and connectivity, and between the probability of colonisation and connectivity}

Table S1 {Posteriors of the coefficients of the regression models for extinction and colonisation}

Captions to Figures

Fig. 1. The Donnybrook metapopulation of *Litoria raniformis* under alternate management scenarios. The top panel displays the distribution of wetlands (grey circles) under current conditions, where ‘wetlands’ include pools along the Merri and Kalkallo Creeks (represented by the black trace) and adjacent farm dams. As an example of different urbanisation scenarios considered, the middle panel displays the distribution of wetlands given urbanisation (shading) of all land beyond a 400 m reserve either side of each stream. The bottom panel displays the distribution of wetlands given a 200 m riparian reserve and the construction of eight new wetlands (black circles). Numbering of the new wetlands is the modelled sequence. Co-ordinates follow the Australian Map Grid system (with WGS 1994). Wetland sizes are scaled to their effective areas, but their shapes are stylised.

Fig. 2. The minimum number of occupied wetlands (*minocc*) and the probability of quasi-extinction (*qe*) for the Donnybrook metapopulation of *Litoria raniformis* over 30 years under five urbanisation scenarios. The scenarios represent maintenance of current conditions (CC) or five possible riparian reserve scenarios given urbanisation. These scenarios entail reservation of all land within 500 m of both streams in the area (‘500 m’), reservation of all land within 400 m of both streams (‘400 m’), and so on down to 100 m either side of both streams. Points represent the mean estimates, and vertical lines represent the 95% credible intervals.

Fig. 3. Change in both the minimum number of occupied wetlands (Δ*minocc*) and the probability of quasi-extinction (Δ*qe*) for the Donnybrook metapopulation of *Litoria raniformis* over 30 years under five urbanisation scenarios. The scenarios represent possible widths of a riparian reserve system, as in Fig. 1. A score of zero on the y-axis represents no change in *qe* or *minocc* from current conditions. Points represent the mean estimates, and vertical lines represent the 95% credible intervals.

Fig. 4. Change in the minimum number of occupied wetlands (Δ*minocc*) and the probability of quasi-extinction (Δ*qe*) for the Donnybrook metapopulation of *Litoria raniformis* over 30 years, given reservation of all land within 200 m of both streams in this area, and the creation of either two, four, six or eight new wetlands. A score of zero on the y-axis represents no change in *qe* or *minocc* from current conditions. Points represent the mean estimates, and vertical lines represent the 95% credible intervals.

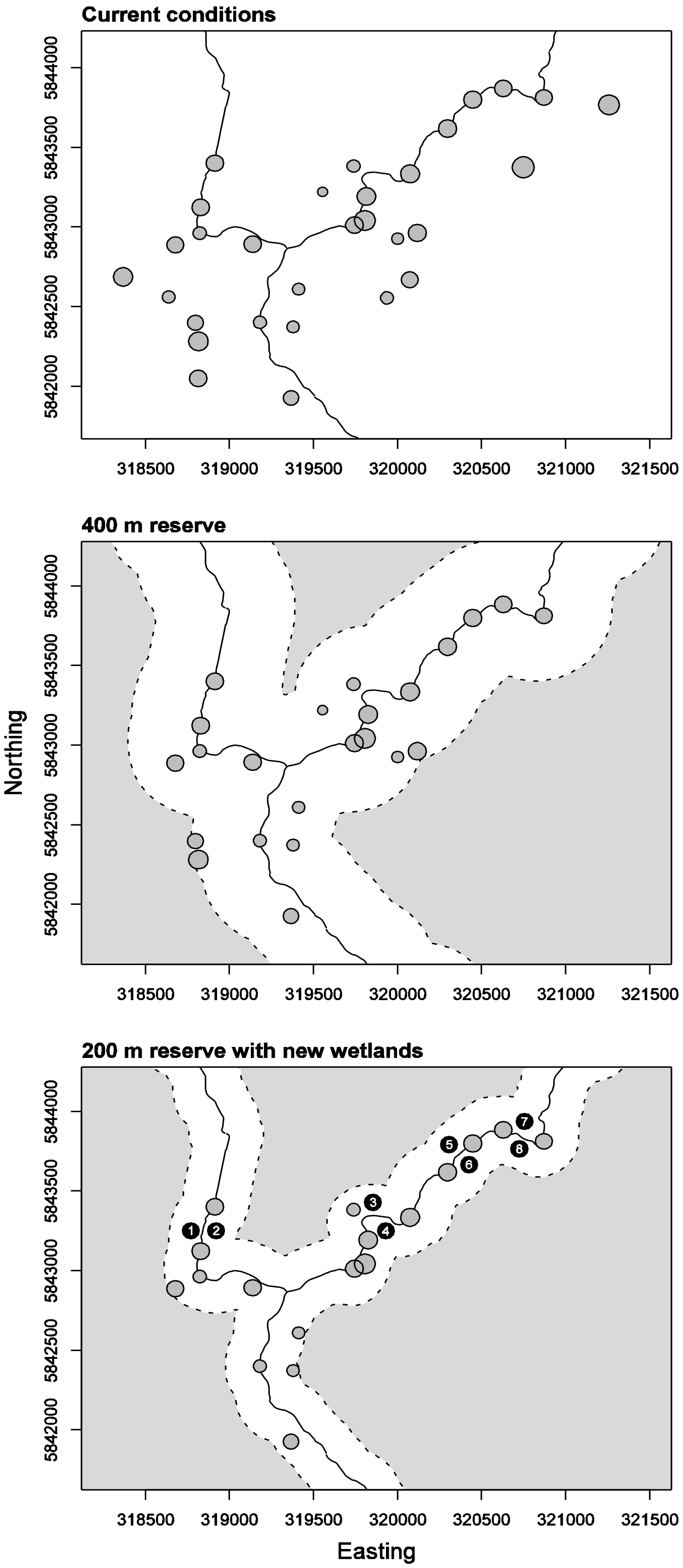
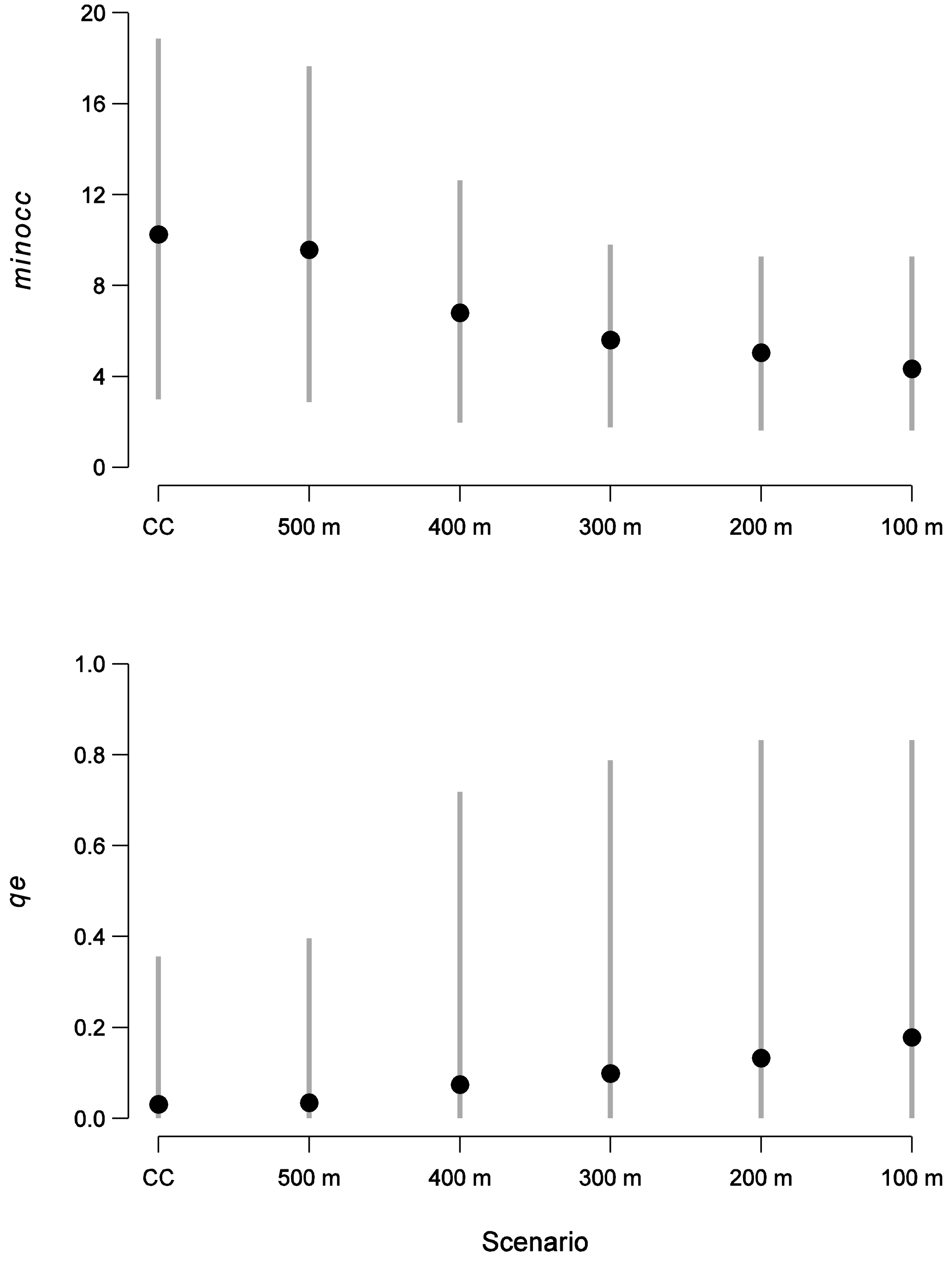

Current conditions
400 m reserve
200 m reserve with new wetlands
Northing
Easting
5842000
5842500
5843000
5843500
5844000
318500
319000
319500
320000
320500
321000
321500
1
2
3
4
5
6
7
8

Fig. 1



20
16
12
8
4
0
minocc
CC
500 m
400 m
300 m
200 m
100 m
1.0
0.8
0.6
0.4
0.2
0.0
qe
CC
500 m
400 m
300 m
200 m
100 m
Scenario

Fig. 2

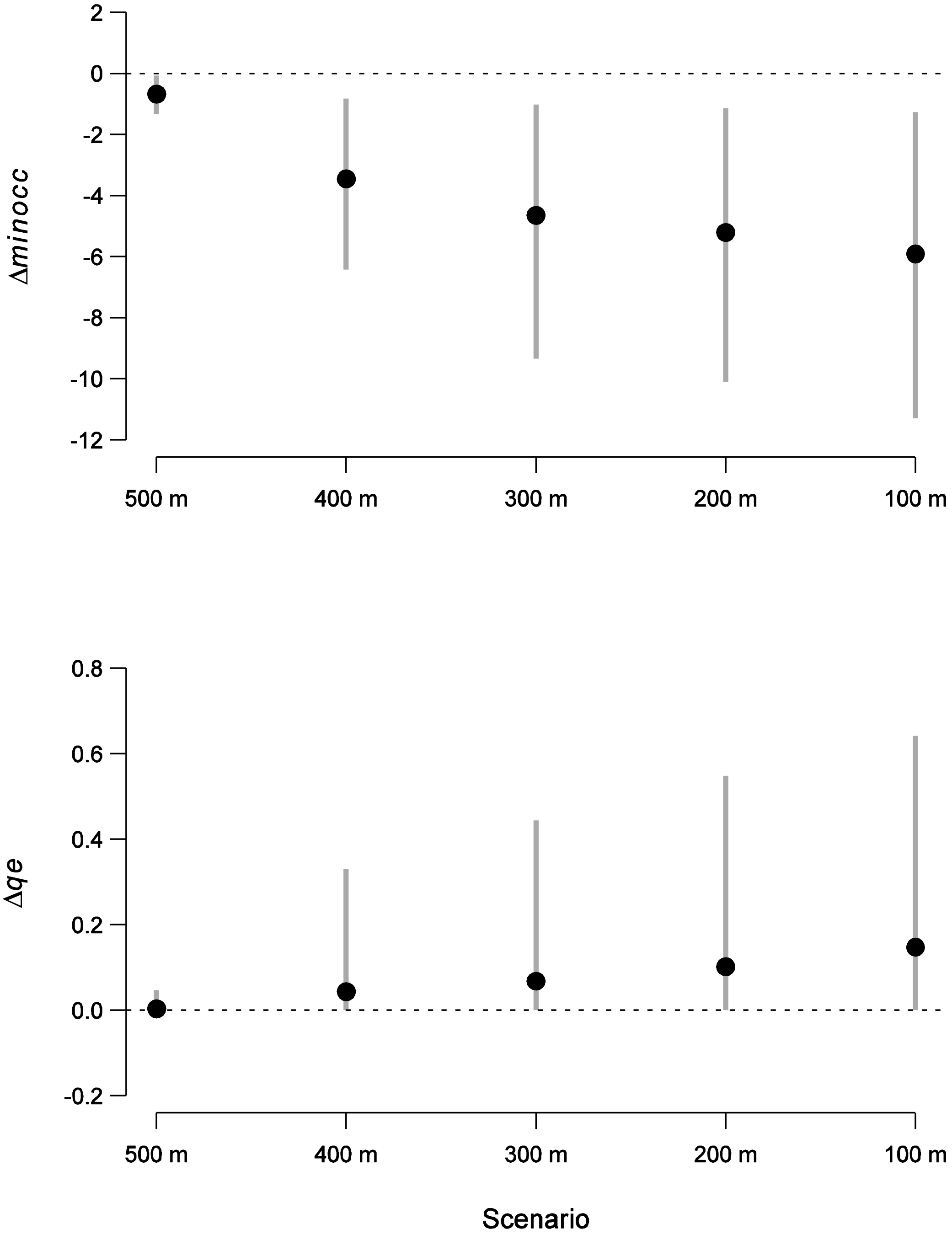

Δ*minocc*
2
0
-2
-4
-6
-8
-10
-12
500 m
400 m
300 m
200 m
100 m
Δ*qe*
0.8
0.6
0.4
0.2
0.0
-0.2
500 m
400 m
300 m
200 m
100 m
Scenario

Fig. 3

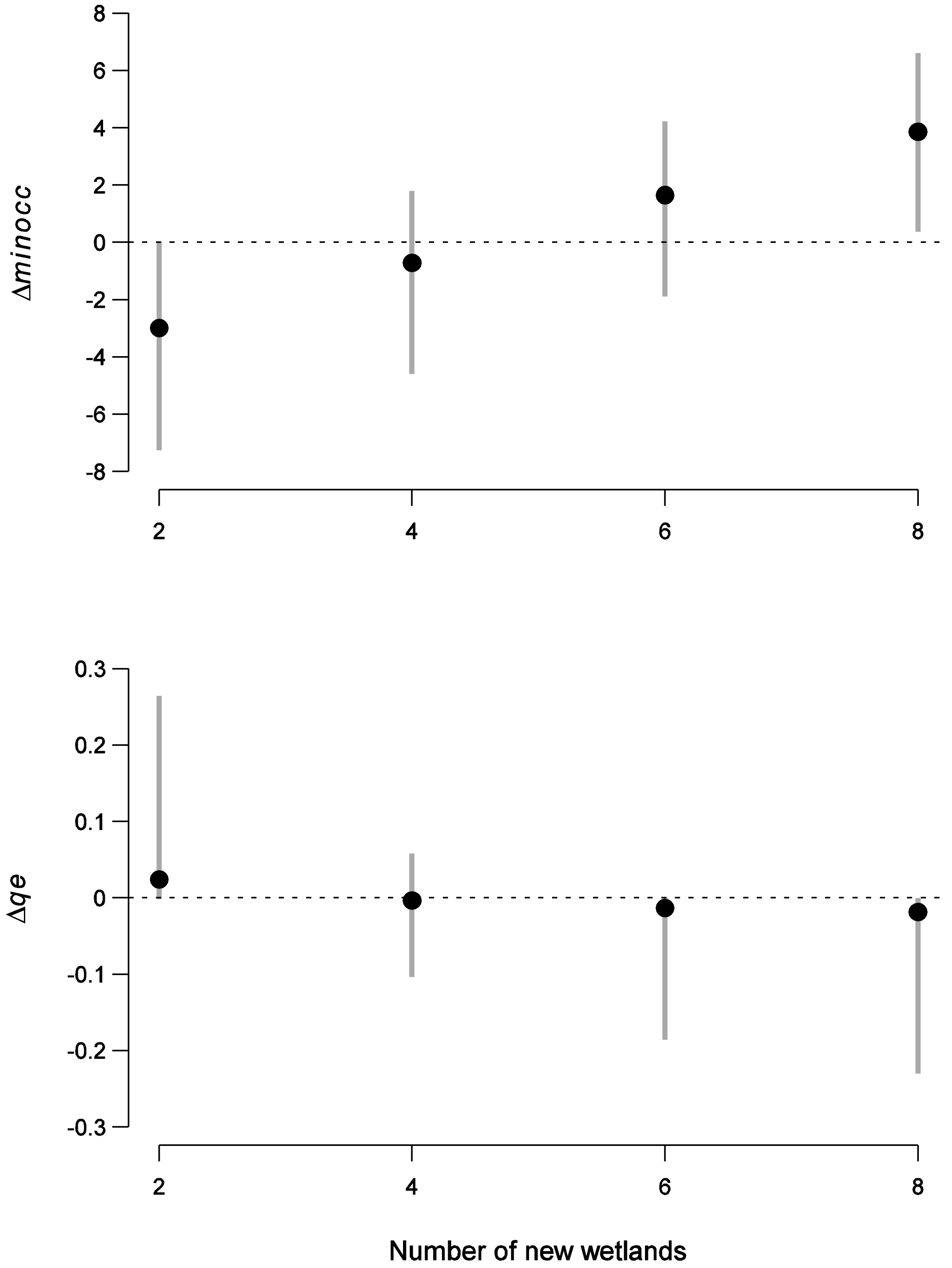

8
6
4
2
0
-2
-4
-6
-8
Δminocc
2
4
6
8
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
Δqe
2
4
6
8
Number of new wetlands

Fig. 4