

Conservation under uncertainty: optimal network protection strategies for worst-case disturbance events

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Summary

1. Conservation goals are ideally set after a thorough understanding of potential threats; however, predicting future spatial patterns of threats, such as disturbance, remains challenging. Here, we develop a novel extension of network fortification–interdiction models (NFIM) that deals with uncertainty in future spatial patterns of disturbance by optimally selecting sites that will best mitigate a worst-case scenario for a given magnitude of disturbance.

2. This approach uses information on between-patch movement probabilities and patch-specific survival, which can be estimated from mark–recapture data, to optimize life expectancy. Optimization occurs in three interrelated stages: protection, followed by disturbance and then assessment.

3. We applied the modelling approach to two mark–recapture data sets: roseate terns *Sterna dougallii* in the north-eastern United States and the Everglade snail kite *Rostrhamus sociabilis plumbeus* in Florida. We contrasted the results to a more conventional approach of protecting sites that maximize connectivity (by minimizing the distances among protected sites) and a bi-objective model that maximizes connectivity and the number of individuals under protection.

4. Protecting sites that best mitigate future worst-case disturbance scenarios consistently resulted in higher predicted life expectancies than protecting patches that minimize dispersal distance. Predicted life expectancy was similar between NFIM and the bi-objective model for the small roseate tern network, yet the NFIM predicted higher life expectancy than any of the scenarios in the bi-objective model in the snail kite network.

5. *Synthesis and applications.* This application of interdiction models prescribed a combination of patches for protection that results in the least possible decrease in life expectancy. Our analyses of the snail kite and roseate tern networks suggest that managing to protect these prescribed patches by the network fortification–interdiction models (i.e. protecting against the worst-case disturbance scenario) is more beneficial than managing patches that minimize dispersal distance or maximize the number of individuals under protection if the conservation goal is to ensure the long-term persistence of a species.

Key-words: conservation planning, disturbance, life expectancy, movement, network fortification–interdiction, optimization, spatial networks, spatial prioritization, survival

Introduction

There is an urgent need for conservation strategies that can help ameliorate the expected impacts of large-scale

biodiversity threats, such as human-induced habitat loss and global climate change (Sala *et al.* 2000). Yet, much uncertainty exists about future threats and their ecological consequences owing to a lack of complete knowledge about how these threats will affect ecological processes driving biodiversity patterns. Failing to account for these

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uncertainties may result in the suboptimal allocation of limited resources and inadequate conservation and management actions (Regan *et al.* 2005).

Managing networks of protected areas is a common conservation strategy to ensure the long-term persistence of biodiversity (Margules & Pressey 2000). Often, these networks are designed under a systematic conservation planning framework that employs mathematical models to determine an optimal set of geographical regions to protect for a given conservation objective and budget (Cabeza & Moilanen 2001). Recently, the focus of these optimization models has shifted from pattern-based objectives, such as the maximization of species representation (e.g. O'Hanley, Church & Gilless 2007a,b), to process-based objectives that drive long-term species persistence and ecosystem functioning, including demographic processes (Klein *et al.* 2009). The preservation of demographic processes allows for a more biologically meaningful assessment of threats while making fewer assumptions about species–habitat associations (Klein *et al.* 2009).

In spatially structured populations, local demographic processes are coupled by movement. The importance of facilitating movement has been acknowledged in spatial prioritization by applying models (Moilanen, Leathwick & Elith 2007; Moilanen, Wilson & Possingham 2009) that prioritize actions to protect sites that minimize dispersal distance (e.g. Ball, Possingham & Watts 2009). The rationale behind this idea is that sites that are closer to each other have higher colonization and re-colonization rates, and lower extinction rates due to rescue effects, ultimately leading to greater long-term viability (Hill, Hastings & Botsford 2002; Doerr, Barrett & Doerr 2011). Therefore, minimizing dispersal distance is often viewed as a precautionary way of dealing with uncertain future patterns of disturbance (Doerr, Barrett & Doerr 2011).

Epistemic uncertainty, related to lack of knowledge or data, can arise from multiple sources including limited biodiversity data and lack of a thorough understanding of potential threats (Regan, Colyvan & Burgman 2002; Pressey *et al.* 2007). Uncertainty analysis methods, such as sensitivity analysis and information-gap approaches, are promising ways to address epistemic uncertainties arising from limited biodiversity data (Regan *et al.* 2005; Moilanen *et al.* 2006b; Kujala, Burgman & Moilanen 2013). Yet, accounting for uncertainty arising from limited understanding of threats remains a major challenge.

There is high uncertainty associated with predicting the spatial location of future disturbances because proximate threats, such as land-use change and over-harvesting, have their roots in complex political and socio-economical processes (ultimate threats) that result in complex spatial patterns of disturbance (Pressey *et al.* 2007). In addition, spatially structured populations are vulnerable to natural disasters, which may also cause spatially complex patterns of disturbance that are difficult to predict. How can conservation strategies prioritize actions to protect areas that

will best maintain demographic processes given high uncertainty in future spatial disturbance patterns?

Network fortification–interdiction models (NFIM) are applied in military applications and are gaining relevance in conservation planning due to their ability to incorporate uncertainty in future threats. For example, O'Hanley, Church & Gilless (2007a) used these type of models to incorporate uncertainty in reserve designs that minimize patterns of species loss by selecting low-risk and high-value sites. Here, we describe a novel application of NFIMs that selects an optimal set of sites to protect that will best mitigate a worst-case disturbance scenario for life expectancy. Allocating limited resources to protect against a worst-case scenario follows the precautionary principle in conservation biology (Cooney & Dickson 2005) and may be more meaningful than protecting against an uncertain average scenario of environmental change. It is increasingly apparent that extreme events of weather and climate have more profound effects on populations rather than average changes (e.g. Reichert *et al.* 2012). This approach complements existing tools such as Marxan that optimize species representation (e.g. Ball, Possingham & Watts 2009). This approach optimizes a life expectancy measure that is highly related to the persistence of spatially structured populations, and incorporates uncertainty in future spatial patterns of disturbance.

We introduce the modelling framework and apply it to two empirical systems, roseate tern *Sterna dougallii* colonies in the eastern United States and the Everglade snail kite *Rostrhamus sociabilis plumbeus*, to illustrate its application and highlight the assumptions, sensitivity and potential extensions for a variety of conservation problems. We compare this approach to a prioritization approach that minimizes dispersal distance, which is commonly employed to accommodate future uncertainties in spatial patterns of disturbance (Doerr, Barrett & Doerr 2011). We also make a further comparison with a bi-objective model that minimizes dispersal distance while maximizing the number of individuals under protection.

Materials and methods

NETWORK FORTIFICATION–INTERDICTION MODEL

Ecological spatial networks consist of nodes that represent discrete spatial locations such as forest patches, grasslands, ponds, or animal colonies, and links (or arcs) that describe the flow of individuals between node pairs, typically the presence of potential movement or probability of movement between nodes (Fletcher *et al.* 2011). Arcs and nodes may be vulnerable to disturbances as a consequence of human activities or natural disasters. These disturbances may decrease habitat quality, resulting in decreases in survival rates and changes in movement patterns (e.g. Phillips & Allredge 2000; Bélisle, Desrochers & Fortin 2001).

Network fortification–interdiction models are applied in military and anti-terrorism scenarios to assess network vulnerabilities and plan protective measures when uncertainty about potential threats is high (Brown *et al.* 2006; Smith 2010). In ecological

spatial networks, these vulnerabilities refer to regions that, if disturbed, will cause the most harm to the biological processes driving biodiversity patterns. The goal of NFIM is to select an optimal set of sites that, if protected (i.e. fortification), would minimize the worst disturbance that can happen to the demographic processes of interest (i.e. interdiction). These models are applicable to conservation scenarios in which a decision-maker is concerned with designing a robust network of protected areas that will best maintain the biological processes of interest after any possible spatial combination of disturbances.

The modelling approach consists of three interrelated stages: a protection, disturbance and assessment stage. Solving the optimization problem requires the protection stage to occur first, which involves the protection of a limited set of patches in anticipation of future disturbances. Next, the disturbance stage takes place, in which a subset of unprotected patches is disturbed in a manner that minimizes life expectancy. Finally, the third stage assesses life expectancy, given the set of disturbed patches. Hence, the third stage depends on the selected disturbance actions in the second stage, which depends on protection decisions made in the first stage (noting that protected patches cannot be disturbed). For clarity, below we first describe the assessment stage, then the disturbance stage and finally the protection stage.

Assessment stage: estimating life expectancy

The assessment stage estimates life expectancy (objective to optimize) using patch-specific survival, site fidelity, and between-patch transition probabilities estimated from mark-recapture data (e.g. Hestbeck, Nichols & Malecki 1991). This measure describes the amount of time (i.e. number of time steps) an individual remains alive in the network. Long-term population persistence can be influenced by a variety of vital rates depending on the species; however, many sensitivity analyses suggest that population growth is generally sensitive to adult survival because of the high variability related to other vital rates such as fecundity (Pfister 1998). Site fidelity is positively correlated with population persistence in predictable environments when individuals decide to remain due to favourable conditions (Schmidt 2004). In contrast, movement may be advantageous when conditions in a patch are less favourable, increasing long-term persistence for moderate levels of spatial variation (Hill, Hastings & Botsford 2002). Therefore, our measure of life expectancy is an appropriate conservation objective to optimize due to its ability to summarize three meaningful demographic processes: survival, site fidelity and movement, which are closely related to long-term population persistence.

Life expectancy is commonly quantified in demographic population models by using a stage- or age-based transition matrix that describes the probabilities of surviving and moving between stages (e.g. Tuljapurkar & Horvitz 2006). Here we developed a new spatial application in which the transition matrix describes three potential transitions: dying, surviving and staying in the same patch, or surviving and moving to a different patch. The transition matrix used to estimate life expectancy represents a reducible Markov chain because it has an absorbing state corresponding to mortality (Ross 2006). To describe this Markov chain, we consider a landscape composed of discrete patches denoted by $\mathcal{N} = \{1, \dots, |\mathcal{N}|\}$. Each patch is characterized by patch-specific survival S_i (before moving). To account for between-patch survival and between-patch movements, the Markov chain contains $|\mathcal{N}| + 1$ states, where the additional state is an absorbing state d

(i.e. all sites plus death) that describes mortality; hence, $\mathcal{M} = \mathcal{N} \cup \{d\}$ denotes the set of all Markov states. The transition matrix associated with this Markov chain is represented by \mathbf{Q} , comprised of elements q_{ij} that describe the probability that an organism transitions from state i to state j (in one step), for all $i, j \in \mathcal{M}$. Mortality (i.e. moving to state d) is represented by the transition $q_{id} = 1 - S_i, \forall i \in \mathcal{N}$. Disturbance to any patch will change these transition probabilities (as described below).

Let \mathbf{n} be a $|\mathcal{N}|$ -dimensional column vector whose i th element, n_i , describes abundance in patch i and let \mathbf{A} be the submatrix of \mathbf{Q} obtained by removing the row and column of \mathbf{Q} corresponding to state d (Ross 2006). Life expectancy z is calculated as:

$$z = \mathbf{n}^T (\mathbf{I} - \mathbf{A})^{-1} \mathbf{1}, \quad \text{eqn 1}$$

where \mathbf{I} is the $|\mathcal{N}| \times |\mathcal{N}|$ identity matrix and $\mathbf{1}$ is the $|\mathcal{N}|$ -dimensional column vector of all ones. See Appendix S1 (Supporting information) for additional mathematical details of the assessment stage. This measure of life expectancy uses the distributions of patch-specific abundances to inform the initial conditions in the Markov chain, but these abundances are not updated after disturbance. Life expectancy increases when patches associated with high survival have also high abundances, because more individuals are subject to the favourable conditions in that patch. In contrast, life expectancy decreases if patches with low survival have higher abundances (e.g. an ecological trap), because more individuals are subjected to the unfavourable conditions in these patches. When patch-specific abundance information is unavailable, we can weight all patches equally.

Disturbance stage: worst-case scenario

In this stage, the model selects a limited number of unprotected patches to disturb, with the objective of minimizing life expectancy (i.e. worst-case scenario). Disturbance actions may vary depending on the system and may include habitat alteration, introduction of exotic species, over-harvesting, pollution, diseases, parasitism or any action that decreases habitat quality for which we can develop protective measures (Sutherland 1998; Johnson 2007). Disturbance actions can decrease patch quality, affecting demographic processes in multiple ways. For instance, decreasing patch-specific survival is one of the most common demographic consequences of decreasing patch quality (Phillips & Aldredge 2000; Griffen & Drake 2008). Also, in many species, organisms respond by avoiding these disturbed areas (Gilliam & Fraser 2001; Dodd, Ozgul & Oli 2006). These demographic consequences of disturbance are captured in the model by changing the transition probabilities in the Markov chain, resulting in a decrease in patch-specific survival, site fidelity and/or movement to disturbed patches. When a patch is disturbed, the mortality probability of an individual living in that patch increases by the same amount that the probability of surviving and staying or moving to another patch decreases.

In general, the updated transition probabilities as a function of disturbances are computed as:

$$q_{ij} = \begin{cases} \bar{q}_{ij}(1 - \alpha_{ij}y_j - \beta_{ij}y_i + \rho_{ij}y_i y_j) & \text{if } i, j \in \mathcal{N} \\ \bar{q}_{ij} + \sum_{k \in \mathcal{N}} \bar{q}_{ik}(\alpha_{ik}y_k + \beta_{ik}y_i - \rho_{ik}y_i y_k) & \text{if } i \in \mathcal{N} \text{ and } j = d \\ \bar{q}_{ij} & \text{if } i = d \text{ and } j \in \mathcal{M}, \end{cases} \quad \text{eqn 2}$$

where \bar{q}_{ij} represents the initial transition probabilities in the Markov chain between patches i and j as estimated from mark–recapture data and q_{ij} the updated transition probabilities after disturbance. Recall that patch i represents the focal patch, and patch j represents another state in the network to which individuals in i can transition (including all other patches and mortality state d). Also, individuals in j can contribute with immigrants to i . Binary variables y_i describe disturbance actions, where $y_i = 1$ if patch i is disturbed and 0 otherwise. Parameters α_{ij} and β_{ij} represent the magnitude of decrease in habitat quality (i.e. how \bar{q}_{ij} changes) given that patch j and/or i is disturbed, respectively. Parameter ρ_{ij} is used in two ways. First, ρ_{ij} is used as a correction term when both patches are disturbed (i.e. $y_i = 1$ and $y_j = 1$), to ensure that $q_{ij} \geq 0$. Secondly, if patch i is disturbed, the updated probability of staying in the same patch decreases proportionally to ρ_{ii} , because we set $\alpha_{ii} = \beta_{ii} = 0$ (see Appendix S2).

The optimization problem in this stage is constrained by four rules. First, no protected patch can be disturbed. Secondly, the number of patches that can be disturbed (i.e. disturbance budget) is no more than b . Thirdly, the life expectancy of an individual currently at patch i , denoted by h_i , is calculated according to the Markov chain. Fourthly, variables representing disturbances (i.e. y_i) are binary. Note that y_i is an indicator variable, while the magnitude of disturbance is captured by q_{ij} . The set of all disturbances that satisfy these constraints is denoted by $\mathcal{Y}(\mathbf{w})$, where \mathbf{w} is an $|\mathcal{N}|$ -dimensional vector whose i th element, w_i , describes the decision of whether or not to protect patch i . Observe that $\mathcal{Y}(\mathbf{w})$ is a function of \mathbf{w} , because no protected patch can be disturbed. The optimization model in this stage seeks to minimize life expectancy and can be written as:

$$\min_{\mathbf{y} \in \mathcal{Y}(\mathbf{w})} \sum_{i \in \mathcal{N}} n_i h_i, \quad \text{eqn 3}$$

where \mathbf{y} is an $|\mathcal{N}|$ -dimensional vector whose i th element corresponds to y_i . We select an optimal set of patches to disturb by means of the mixed-integer linear program which is detailed in Appendix S3.

Protection stage

The protection stage prescribes an optimal set of patches to protect that maximizes life expectancy, given that a worst-case disturbance of unprotected patches will occur. No more than u patches can be protected. Hence, this problem has a *max-min* objective: the protection stage maximizes the minimum life expectancy resulting from the disturbance stage. Protection measures include actions that prevent patch deterioration such as legislating against future development, reducing human use (e.g. limiting fishing or hunting), managing for fire, invasive species or controlling predator populations.

Protected patches cannot be disturbed (e.g. if patch i is protected, then $y_i = 0$); however, transition probabilities of protected patches may be indirectly affected through their interaction with disturbed patches. For instance, if both patches i and j are protected, transition probability q_{ij} will remain unchanged after disturbances occur in other patches. In contrast, if patch j is disturbed (but not patch i), then individuals living in i may tend to avoid patch j , resulting in a decrease in the probability of movement from i to j . This decrease in movement from patch i will result in an increase in mortality of the same magnitude as

the decrease in movement (Rose *et al.* 2001), because probabilities need to sum to unity.

The optimization problem in this stage can be written as:

$$\max_{\mathbf{w} \in \mathcal{W}} \min_{\mathbf{y} \in \mathcal{Y}(\mathbf{w})} \sum_{i \in \mathcal{N}} n_i h_i, \quad \text{eqn 4}$$

where \mathcal{W} is the set of all protection measures that satisfy the protection budget constraint and the binary restrictions on variables w_i , $\forall i \in \mathcal{N}$. See Appendix S4 for further details.

GENERAL MODEL ASSUMPTIONS

The model makes assumptions common to other models in population ecology. For instance, we consider survival rates estimated from mark–recapture as reflecting true survival, but these may be negatively biased due to the difficulty of discerning between mortality and permanent emigration (Gilroy *et al.* 2012). Also, we assume that individuals follow a random walk between patches, which is common to other modelling approaches that incorporate movement (e.g. McRae *et al.* 2008; Fernández-Chacón *et al.* 2013).

MODEL COMPARISONS

We compared the predicted life expectancy resulting from the NFIM with that predicted by two other models: one that minimizes dispersal distance, and a bi-objective model that minimizes dispersal distance and maximizes abundance under the same protection budget u . To select the set of patches that minimizes dispersal distance, we applied the integer program of Önal & Briers (2002) (See Appendix S5 for further details). The additional objective of maximizing abundance in the second model results in a Pareto optimal frontier (Chankong & Haimes 2008), which trades off the distances being minimized and the total abundance being maximized, instead of optimizing a single objective (see Appendix S5). We compared the prescribed life expectancy of the NFIM with the solution of the bi-objective model that resulted in the highest predicted life expectancy in the Pareto optimal frontier.

CASE STUDIES

We applied the NFIM framework to two mark–recapture data sets: adult roseate terns *S. dougallii* living in the north-eastern United States and adult Everglade snail kites *R. sociabilis plumbeus* (Reichert *et al.* 2012). The roseate tern data set is a small network (4 nodes and 20 potential transitions) that illustrates the NFIM in simple terms. The snail kite data set is a larger and more complex data set (19 nodes and 380 potential transitions) that allows us to explore a more realistic conservation example. Patch-specific survival, site fidelity and patch transition probabilities for both species were estimated using variations of the Arnason–Schwarz multistate model (Nichols & Kendall 1995).

Roseate terns

Roseate Tern colonies were located on Bird Island (BI) in Marion, Massachusetts, Great Gull Island in New York (GG), Falchner Island in Connecticut (FI) and Cedar Beach (CB) in Long

Island, New York (Fig. 1). A total of 2043 individual adults were captured from 1988 to 1990 in these sites using treadle traps and individually marked with colour bands (Spendlow *et al.* 1995). We used the 1988–1990 arithmetic mean of survival, transitions and colony size estimates.

The parameters that describe how disturbance affects transition probabilities (α_{ij} , β_{ij}) were not included in the original article. Therefore, we randomly generated these parameters once from a continuous uniform distribution with bounds 0 and 0.3, a range that represents the magnitude of changes in survival, site fidelity and movement after disturbance previously reported for similar species (e.g. Béchet *et al.* 2003; Calvert & Gauthier 2005), and $\rho_{ij} \in [\alpha_{ij} + \beta_{ij} - 1, \alpha_{ij} + \beta_{ij}]$. By keeping ρ_{ij} within these bounds, we ensure that $q_{ij} \geq 0$.

Everglade snail kites

The Everglade snail kite is a locally and critically endangered species in Florida, who depends on wetlands dominated by sparsely emergent vegetation. We used 17 years of band-resight data (1997–2013) and a multistate capture–mark–recapture model (Hestbeck, Nichols & Malecki 1991) to estimate annual transition probabilities ($n = 1180$ adults). We included nine lacustrine and 10 palustrine geographical states representing wetland patches throughout the snail kite’s range. We constrained survival to be constant because adult survival does not vary considerably through time (Martin, Kitchens & Hines 2007; Reichert *et al.* 2012) (see Appendix S6).

Droughts are a strong disturbance in the Everglades that negatively influences food availability resulting in decreased adult

snail kite survival (Mooij *et al.* 2002; Martin, Kitchens & Hines 2007). In contrast, lacustrine wetlands are more robust to prolonged dry conditions and may serve as refugia for snail kites (Martin, Kitchens & Hines 2007). Based on the results of previous studies, we expected that disturbance would have significant negative impacts on the survival probability (16% decline) of individuals within palustrine wetlands. The probability of surviving and staying in the same patch or moving decreases by the same magnitude (recall that all transitions need to sum to unity). Despite reports of snail kites moving to lakes during drought conditions (Martin *et al.* 2006), Martin, Kitchens & Hines (2007) did not find evidence for drought effects on movement. Therefore, we did not include a direct effect of drought on movement and disturbance only influences survival in the patch of origin i .

Scenarios

In the roseate terns network, we started by considering a protection budget of $u = 2$ and a disturbance budget of $b = 2$, while in the snail kite network $u = 4$ and $b = 5$ (i.e. all other patches unprotected). We also studied the sensitivity of predicted life expectancy by considering all remaining combinations of protection and disturbance budgets for both species. In the snail kite network, disturbance and protection will affect some of the 10 palustrine patches, because disturbance by drought has little effect on lacustrine wetlands.

To calculate between-patch Euclidean distances in the roseate tern network, we used the latitude and longitude coordinates reported for the centroid of the patches (Spendlow *et al.* 1995). In the snail kite network, we considered the centroid of the wetland patches. Our algorithms were implemented on a Windows 7

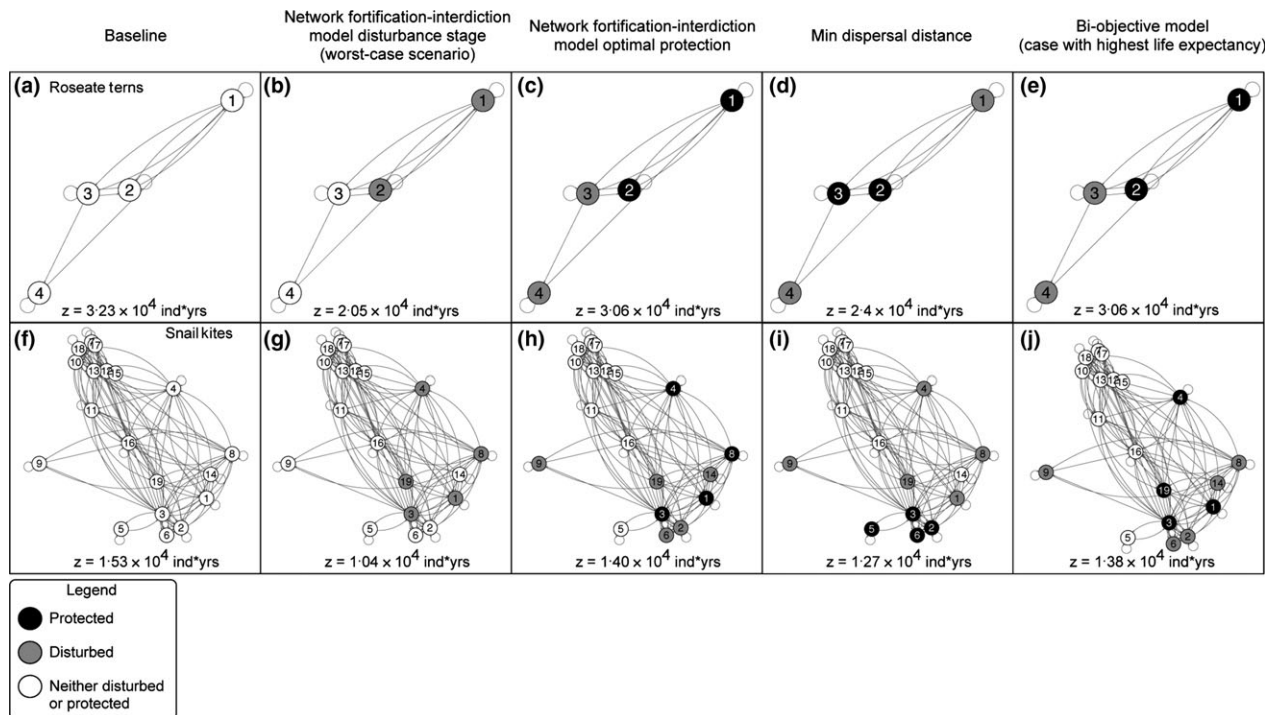


Fig. 1. The diagram compares predicted life expectancy when no patch is disturbed, after a worst-case disturbance, after the protection of the set prescribed by the network fortification -interdiction model (NFIM), after minimizing dispersal distance and after protecting the set prescribed by the bi-objective model. Note that the disturbance and protection budget (number of patches allowed to be disturbed and protected) were the same for all models ($u = b = 2$ for roseate terns and $b = 5$, $u = 4$ for snail kites). Also note that the bi-objective model resulted in multiple optimal solutions and this figure shows the solution that resulted in the highest life expectancy.

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64-bit desktop with an Intel Core 2 Quad Q9500 CPU (2.83 GHz) and 4 GB of RAM. All mathematical programs were solved using IBM CPLEX optimizer 12.3 (New York, NY, USA).

Results

Protecting the set of patches prescribed by the NFIM resulted in lower predicted reductions in life expectancies relative to baseline life expectancy (i.e. no disturbance or protection) than protecting the set patches that minimized dispersal distance in both species (Fig. 1). The NFIM predicted the same life expectancy as the bi-objective model in the roseate tern network; yet, the NFIM predicted lower reductions in life expectancy than the bi-objective model for snail kites. In the roseate terns network, the worst-case scenario is the disturbance to patches 1 and 2 (Fig. 1b), with a reduction in life expectancy of 37%. The prescribed protection set by the NFIM also includes patches 1 and 2 (Fig. 1c) with a resulting reduction in life expectancy of 5%. This reduction in life expectancy is smaller than the reduction attained by protecting the patches that minimize dispersal distance (patches 2 and 3 with a reduction of 24%) and the same as that predicted by the bi-objective model (Fig. 2a). In the snail kite network, the worst-case scenario is the disturbance to patches 1, 3, 4, 8 and 19 (Fig. 1g), which resulted in a reduction in life expectancy of 32%. The prescribed protection set by the NFIM included patches 1, 3, 4 and 8 with a predicted reduction in life expectancy of 8% (Fig. 1h). This reduction was lower than the reduction in life expectancy predicted by minimizing dispersal distance (patches 2, 3, 5 and 6), which resulted in a 17% reduction in life expectancy. The NFIM also predicted a lower decrease in life expectancy than the protection of patches 1, 3, 4 and 19 prescribed to be protected by the bi-objective model (10% reduction, Fig. 2b). The NFIM for rose-

ate terns and snail kites took 0.28 and 7.04 s to find an optimal solution, respectively. Each frontier in the bi-objective model took *c.* 0.32 s to find an optimal solution.

Not surprisingly, life expectancy increased with increasing protection budget and decreased with increasing disturbance budget (Fig. 3). The sensitivity analysis on *u* and *b* combinations provides insight into how predicted life expectancy changes with variation in these budgets. For instance, in the roseate terns network life expectancy decreased the most by increasing the disturbance budget from *u* = 1 to *u* = 2 (Fig. 3a). Similarly, life expectancy in snail kites decreased nonlinearly with increasing the number of patches allowed to be disturbed (Fig. 3b). In both species, life expectancy increased with increasing protection budget, but the marginal impact of additional protected patches decreased as the number of protected patches increased (Fig. 3). The shape of these curves is relevant when evaluating protection budgets. Sometimes, increasing the protection budget by as little as one patch might result in a significant increase in life expectancy (e.g. increasing from one to two patches in Fig. 3a).

Discussion

We developed a novel application of NFIM that accounts for uncertainty in future spatial patterns of disturbance by selecting an optimal set of sites to protect that will best mitigate a worst-case disturbance scenario for life expectancy. We showed that the prescribed protection solutions by the NFIM resulted in higher predicted life expectancies than protecting the sites that minimize dispersal distance and better than the bi-objective model at least in the larger network.

In the roseate tern network, optimal protection sets were composed of patches with high survival, site fidelity, immigration and emigration rates to patches with simi-

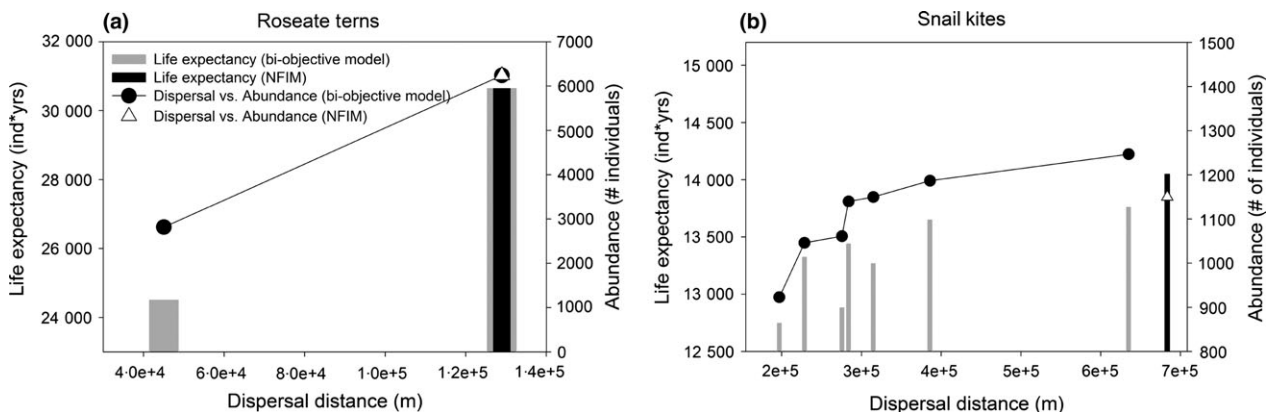


Fig. 2. The diagram compares life expectancy predicted by the network fortification -interdiction model (NFIM) and Pareto frontier plot showing predicted life expectancies of the bi-objective model. The bi-objective model minimizes dispersal distance and maximizes abundance for a disturbance budget of $b = 2$ and $u = 2$ in the roseate tern network, and $b = 5$ and $u = 4$ in the snail kite network. In the bi-objective model, there is no single optimal solution because there is a trade-off between attaining both objectives (i.e. the optimal solution can protect higher abundances at the expense of longer dispersal distances). The network fortification -interdiction model (NFIM) (represented by a triangle) predicted the same life expectancy as the maximum abundance scenario in the roseate tern example, but predicted higher life expectancy than any of the scenarios of the bi-objective model in the snail kite network.

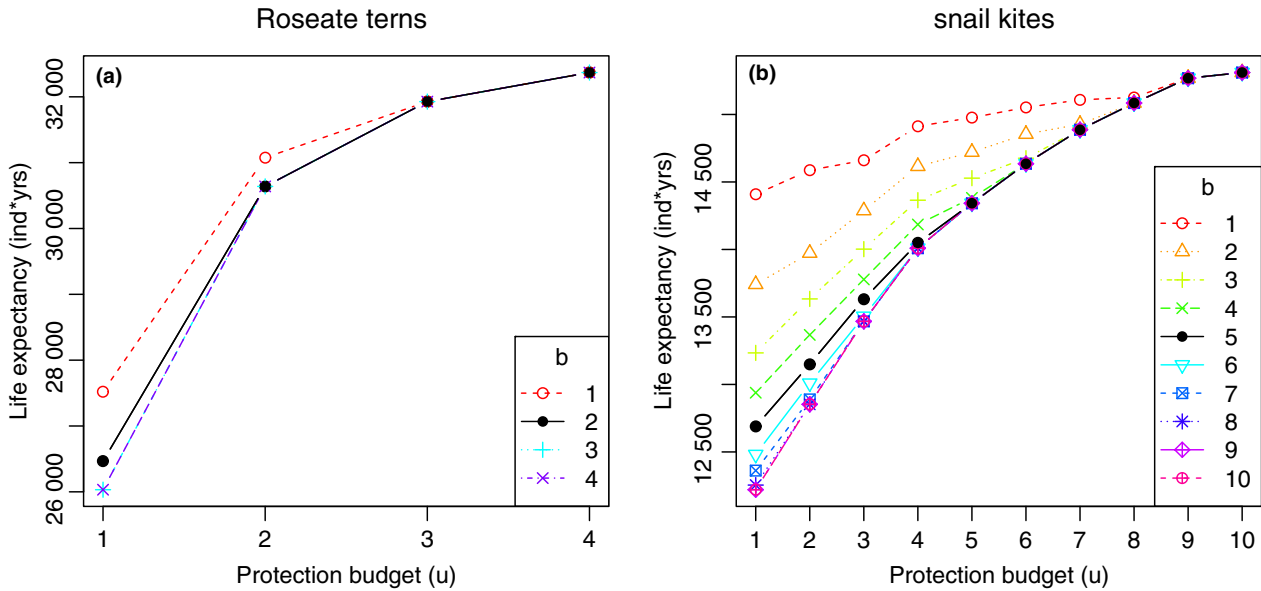


Fig. 3. Predicted life expectancy (z) with increasing protection (u) and disturbance (b) budgets for (a) roseate terns and (b) Everglade snail kites. Note that in panel (a), life expectancy for budgets $b = 3$ and $b = 4$ overlaps for all protection budgets. The black line with closed symbols represents the disturbance budget that we discuss as an example in this study.

larly favourable conditions. Understanding the specific patch characteristics that drive the inclusion of patches in the optimal protection set was feasible in this example because it was a small network (see Appendix S7). In general, this patch-level understanding becomes less feasible as the number of patches increases (as in the snail kite example) because the model considers the importance of a particular subset of nodes instead of nodes individually.

The bi-objective model outperformed the strategy of minimizing dispersal distance, because it incorporated abundance data. The bi-objective model performed similar to the NFIM in the roseate tern network because the two patches selected for protection had abundances orders of magnitude greater than the other patches. However, the bi-objective model underperformed in the snail kite network compared to the NFIM. The bi-objective model selected patch 19 as part of the protection set (instead of patch 8 selected by the NFIM) because it had the third highest abundance. However, this patch was also characterized by having low site fidelity and high emigration rates, which suggests that it might contribute little to life expectancy. The NFIM accounts for relationships between patches in the network, and how disturbance affects these relationships (see Appendix S7). Ultimately, disturbance and future threats rarely influence biodiversity one patch at a time (e.g. Seabloom, Dobson & Stoms 2002) and the NFIM framework better captures that unfortunate reality.

LIMITATIONS

Given that the NFIM optimizes life expectancy, its limitations are similar to those of population viability analysis, including a single-species focus and high data require-

ments (Akçakaya & Sjögren-Gulve 2000). Even though between-patch transition and survival estimates require much field effort (Calabrese & Fagan 2004), these data sets are becoming more common in conservation efforts, mostly due to recent advances in remote animal monitoring technology and large-scale sensor networks (Kool, Moilanen & Treml 2013). Parameter estimates that describe how survival, site fidelity and between-patch movements change when patches are disturbed (i.e. α , β and ρ) can also be estimated from the field or taken from the literature when available (e.g. Béchet *et al.* 2003), as in the snail kite example. If these estimates are not available, then the model can be used as a scenario-planning tool (Peterson, Cumming & Carpenter 2003).

When conservation goals are at the community or ecosystem level, the single-species limitation can be ameliorated by selecting a limited number of species that are representative of the ecological processes of interest or are particularly sensitive to the disturbance of interest (i.e. indicator species). Alternatively, the combination of worst-case disturbance protection and approaches that promote species representation may be useful in assessing the robustness of a protection solution. If both approaches prescribe a similar set of patches, then the solution can be considered robust, potentially yielding a reserve design that promotes meaningful demographic processes and species representation (Carroll *et al.* 2003).

Exact optimization techniques have traditionally been used in conservation prioritization (Cabeza & Moilanen 2001; Westphal *et al.* 2003). The advantage of mathematical programs is that they produce optimal solutions; however, they might be computationally demanding for larger networks. Heuristic approaches can be applied to this problem to produce near-optimal solutions in affordable

times, but no method of this type is yet available in the literature.

EXTENSIONS

The NFIM is a flexible framework that can be applied to a wide array of problems in conservation and management. The model could be formulated to assess vulnerabilities in the surrounding matrix by optimizing life expectancy given the protection or disturbance of links in the network instead of patches. This modification would potentially allow the identification of places in the matrix to perform restoration or build corridors that promote an increase in life expectancy (McRae *et al.* 2012).

Our modelling approach inherently assumes that the cost of protecting each patch will be the same. Variations in protection costs could easily be incorporated as a constraint in the protection model by specifying a monetary budget instead of a limit on the number of patches to protect. This incorporation would require the addition of the following constraint to the protection submodel:

$$\sum_{i \in \mathcal{N}} c_i w_i \leq u,$$

where c_i is the monetary cost of protecting patch i , w_i is a binary variable that describes if patch i is included in the protection set, and u is the protection budget. This protection budget can include the cost of acquiring or managing a particular set of patches.

Also, our model assumes that a protected patch cannot be disturbed. Yet, there is the possibility that management actions might not prevent disturbance entirely, but just decrease its potential impact. A natural model extension would thus allow protected patches to be disturbed, but with a lower impact on transition probabilities than in the case in which the patch is unprotected.

Even though the parameterization of the model we described optimizes life expectancy, alternative objective functions can be applied. For instance, minimizing biodiversity loss or loss of the proportion of area occupied after a worst-case disturbance could be an alternative objective. An application of such an approach found significant predicted reductions in biodiversity loss when protecting against a worst-case disturbance scenario compared to simply maximizing species representation (O'Hanley, Church & Gilles 2007a). This result suggests that interdiction models might be well suited for conservation planning due to their generality and robustness.

UNCERTAINTY AND WORST-CASE DISTURBANCE PROTECTION

Uncertainty is rarely incorporated into conservation planning (Pressey *et al.* 2007), yet information-gap approaches are gaining popularity to address uncertainty in model structure and parameters (Regan, Colyvan & Burgman

2002; Moilanen *et al.* 2006a). Information-gap approaches often favour the selection of patches that minimize dispersal distance when faced with high uncertainty on how future spatial patterns of disturbance will affect the dispersal behaviour of a species because there is more certainty about short-distance movements than long ones (Halpern *et al.* 2006).

The usefulness of minimizing dispersal distance as a conservation objective has been debated. Some studies argue for promoting movement by minimizing either the perimeter length of the network or the distance between patches. Minimizing these metrics allows individuals to respond to disturbance by moving to higher-quality sites (Gillson *et al.* 2013). Other studies show that minimizing dispersal distance may not necessarily promote persistence, because protecting patches that are closer together may leave higher-quality, but isolated, patches unprotected (Hodgson *et al.* 2011). Our results provide support for the latter. Life expectancy was higher in the prescribed optimal solution from the NFIM than minimizing dispersal distance. This application of network fortification - interdiction may be an appropriate way to resolve this debate because it follows a precautionary approach, but also optimizes life expectancy, which combines information on movement with demographically relevant measures such as site fidelity and survival (Ellis, Václavík & Meentemeyer 2010). Site prioritization for conservation should consider network fortification approaches, as their prescribed protection solutions result in higher predicted long-term persistence than minimizing dispersal distance or maximizing abundance.

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Data accessibility

The roseate tern data are available in the original paper (Spendlow *et al.* 1995). The snail kite data is available at Dryad repository at doi: 10.5061/dryad.30rf6 (Acevedo *et al.* 2015).

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Supporting Information

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

Appendix S1. Mathematical details of the assessment stage.

Appendix S2. Two-patch example that shows how disturbance and protection influences the transition probabilities.

Appendix S3. Mathematical details of the disturbance stage.

Appendix S4. Mathematical details of the protection stage.

Appendix S5. Mathematical details of models for comparison (minimizing dispersal distance and bi-objective model).

Appendix S6. Details on transition probability estimation for snail kites.

Appendix S7. Patch-specific characteristics.