



Incorporating dynamic distributions into spatial prioritization

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ABSTRACT

Aim Species' distributions are generally treated as static for the purposes of prioritization, but many species such as migrants and nomads have distributions that shift over time. Decisions about priority actions for such species must account for this temporal variation, making planning for their conservation a complex problem. Here, we explore how dynamic distributions can be incorporated into a spatial prioritization, and suggest approaches for prioritizing conservation action when knowledge of species' movements is uncertain.

Location Australian rangelands, including the arid and semi-arid zones of central Australia and adjoining monsoonal tropics, although methods are applicable for any dynamic biodiversity feature.

Methods We used the decision-support software MARXAN to explore the impact of temporal dynamics on spatial conservation planning for a suite of 42 highly mobile birds across the study region. We explored scenarios comparing a static representation of species' distributions with four methods of integrating temporal dynamics: (1) accounting for temporal variability in distribution across months and years, (2) considering only monthly variability in distribution, (3) considering only annual variability in distribution and (4) considering only minimal distributions during spatial bottlenecks, ignoring distributions at other times.

Results Incorporating the temporal dynamics of species into spatial prioritization substantially changes the spatial pattern of conservation investment, increasing the overall area needed to be placed under conservation measures to achieve a specific target level of species protection. Targeting bottlenecks, locations critical to each species when its distribution is at a minimum, prioritizes a very different suite of sites to those chosen using the traditional approach of static distribution maps based on occurrences pooled across time.

Main conclusions Our results highlight the need to consider dynamic movements in the conservation planning process to ensure that mobile species are adequately protected. A static approach to conservation planning may misdirect resources and lead to inadequate conservation for mobile species.

Keywords

arid zone, dynamic distributions, migration, nomadic, protected areas, spatial prioritization, systematic conservation planning.

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INTRODUCTION

Spatial prioritization is one of the backbones of systematic conservation planning, and is a process whereby conservation actions are matched to locations based on their feasibility, conservation benefit and cost (Moilanen *et al.*, 2009a).

Conservation planners have rarely incorporated animal movements into prioritizations, instead focusing on more readily available information such as costs (Naidoo *et al.*, 2006), feasibility (Knight *et al.*, 2011; Tulloch *et al.*, 2014), uncertainty in data (Carvalho *et al.*, 2011; Tulloch *et al.*, 2013), future threats (Game *et al.*, 2008) and multiple

options for conservation action (Reyers *et al.*, 2012). However, increasing emphasis on the importance of incorporating spatial and temporal dynamics into the planning process (Grantham *et al.*, 2008; Lourival *et al.*, 2011) has led to attention being focused on this issue (Game *et al.*, 2013; Runge *et al.*, 2014) and there has been recent progress in understanding how to incorporate species with relatively simple and predictable movement patterns into spatial conservation planning (Martin *et al.*, 2007; Klaassen *et al.*, 2008; Moilanen *et al.*, 2008; Linke *et al.*, 2011; Iwamura *et al.*, 2013, 2014; Kool *et al.*, 2013).

However, many species show less predictable patterns of movement. For example, the irregular movements of nomadic and irruptive species (e.g. Flock Bronzewing *Phaps histrionica*; Dostine *et al.*, 2014 and Dickcissel *Spiza americana*; Bateman *et al.*, 2015) make their conservation a particular challenge due to uncertainty in exactly which parts of their geographic range are most important for persistence, and at what times they are occupied (Runge *et al.*, 2015). As a consequence, their distributions are generally treated as static, with little or no reference to their need for protection in particular parts of their life cycle or across resource hotspots (Rodrigues *et al.*, 2004; Gilmore *et al.*, 2007; Beresford *et al.*, 2011; Watson *et al.*, 2011; Venter *et al.*, 2014). Critical sites may be overlooked, leading to irreversible population declines or extinction (Reid & Fleming, 1992; Woinarski *et al.*, 1992). Understanding and incorporating spatial and temporal dynamics can be significant for any attempts to conserve mobile species including migrants and nomads (Runge *et al.*, 2014).

We are aware of only one attempt to consider the dynamics of nomadic species in a spatial prioritization scheme. In an elegant analysis, Fahse *et al.* (1998) examined alternative configurations of a simulated protected area system for a suite of nomadic larks in the Nama-Karoo, South Africa, using a spatio-temporal model to estimate the survival of flocks given known ecological relationships with seasonal rainfall patterns (Fahse *et al.*, 1998). They found that these nomadic birds were best protected by a series of sites spread across the study region, spatially focused on areas of high resource availability. Their study sought to inform the debate about optimal protected area size rather than a systematic conservation plan, and therefore did not incorporate cost or other feasibility metrics. However, this remains the only example where distributional dynamics have been incorporated into a prioritization for nomadic species.

Without guidelines for best practice approaches for incorporating spatial and temporal dynamics of species with variable distributions into systematic conservation planning, decision-makers run the risk of prioritizing the wrong areas, wasting funding and losing donor confidence. Conservation planning problems are typically formulated as either 'minimum set' (meet conservation targets using minimal resources i.e. area, money) or 'maximum coverage' (maximize conservation benefits given a fixed amount of resources; Possingham

et al., 2006; Moilanen *et al.*, 2009b). Regardless of the approach, using a distribution map that pools the occurrences of nomadic species would focus the result on the cheapest places regardless of whether or not those places are occupied more often than others, and risks overlooking key sites used by nomads if they are relatively expensive or used only during times of resource scarcity. A dynamic approach allows planners to incorporate places that are important at only certain points in time (e.g. when ephemeral resources are available in that area), with less risk of protecting areas of consistently low value for nomads.

There are several possible approaches to prioritizing conservation actions in the light of spatio-temporal dynamics in nomadic species distributions. However, the nature of movements of nomadic birds is poorly known (Chan, 2001; Dean, 2004; Burbidge & Fuller, 2007) and can differ across regions (Wyndham, 1982; Ziembicki & Woinarski, 2007). As a consequence, it remains difficult to determine the most effective conservation strategy for highly dynamic species. One approach may be to prioritize refugia or bottlenecks, places to which species contract during times of limited habitat suitability across the wider landscape. If such refugia exist, they may be crucial to long-term persistence (Reid & Fleming, 1992; Morton *et al.*, 1995; Bateman *et al.*, 2015). Currently, very little is known about the consistency of refugial sites over long time frames (Manning *et al.*, 2007) and their role in population persistence is not fully understood (Bennetts & Kitchens, 2000; Tischler *et al.*, 2013). Conservation of refugia may only guarantee a species survival during a small part of its lifetime. In some species, it may be more important to protect a good sample of suitable habitat across space and time (Dickman *et al.*, 1995; Stojanovic *et al.*, 2015). It is unclear how those differing approaches will affect population persistence, given the lack of ecological knowledge on many nomadic species. A bet-hedging approach may be to undertake conservation actions in refugia (where known) in combination with broader landscape management.

Here, we present an approach for incorporating spatio-temporal dynamics into a spatial prioritization for mobile species, using a case study of data-poor nomadic birds in the rangelands of Australia. Our objective was to compare the minimum set of areas identified for protected area designation (though the results are also applicable to any ecologically favourable management involving loss of agricultural profitability) under five scenarios of species representation that varied according to plausible beliefs about where and when the most important places for maintaining nomadic populations occur. This approach could inform conservation planning for any suite of species with dynamic distributions across time, from short-term migratory movements to long-term distributional changes driven by climate change. We then examine the impact of different temporal choices of distributional information on the configuration and cost of spatial priorities and suggest how that information might be used to guide both conservation and ecological research.

METHODS

The study region

We explore a conservation network for a suite of nomadic birds found within the rangelands of Australia, including the arid and semi-arid zones of central Australia, and adjoining monsoonal tropics. The rangelands of Australia occupy an area of over 6.2 million km² and large areas of the region are grazed, predominantly for cattle and sheep production, with smaller regions of cropping and irrigated agriculture (State of the Environment 2011 Committee, 2011). The study region was divided into grid cells of 10 × 10 km for analysis, resulting in 66,179 planning units.

Spatially explicit cost data are a key component of conservation planning, often driving the location of priority areas (Carwardine *et al.*, 2008). We estimated conservation feasibility using data on agricultural profit at full equity for the period 2005–2006 (Marinoni *et al.*, 2012). These data were calculated in a period of widespread drought, and to avoid underestimating landholder values, negative profitability values were set to zero. We adjusted for inflation to December 2013 (Australian Bureau of Statistics, 2013) and multiplied the average profitability per hectare in each planning unit by the area of that planning unit. We determined the net present value of foregone annual profitability as per Carwardine *et al.* (2008) in Australian dollars. A transaction cost (the cost associated with negotiating and managing land use) of \$10,000 was applied to each planning unit where agricultural activity occurred within that planning unit. Valuation has yet to be mapped for parts of the region, including indigenous lands and regions where no or very low intensity agricultural activity currently occurs. Conservation actions in such places will still incur costs, and there is still very little guidance about how to aggregate costs when land valuation is not linked to monetary value or is borne by different stakeholders (Ban & Klein, 2009). We assigned unvalued locations a transaction cost of \$5000 per planning unit, so they would not be automatically protected. The simplified transaction cost data used in this study only approximate actual reserve establishment and management costs, which will likely be heterogeneous over time and space, and dependent on a range of factors including the type of conservation project undertaken, the size and context of the planning unit, and the level of trust and confidence between parties (Garrick *et al.*, 2013; Pannell *et al.*, 2013). While we focus on protected area designation, the conservation feasibility metric used here, agricultural profitability, provides a surrogate estimate for a diversity of actions, from adopting lower stocking rates to setting aside wetlands and remnant woodlands facilitated by agreements with landholders or by designation of formal protected areas. The prioritization method used is sensitive to the relative values of planning units, rather than their absolute values.

Conservation features and targets

We derived distribution maps for a phylogenetically diverse but non-comprehensive subset of bird species thought to be nomadic and predominantly occurring in the rangelands of Australia (42 species; Appendix S1) from the study by Runge *et al.* (2015). Nomadic species range over large areas, and may show different movement patterns under different environmental conditions (Dean, 2004), limiting the ability of field experts to reliably classify species as nomadic. While recognizing that classification of movement patterns in the study region is subject to ongoing discussion, we include species where nomadism is indicated in part or all of their range according to the *Handbook of Australian, New Zealand and Antarctic Birds* (HANZAB; Marchant & Higgins, 1993; Higgins & Davies, 1996; Higgins, 1999; Higgins *et al.*, 2001; Higgins & Peter, 2002; Higgins *et al.*, 2006a,b) and a key reference where classification was based on other than HANZAB (Ziembicki & Woinarski, 2007). Though many water birds in the region are also highly nomadic (Kingsford *et al.*, 2010), they were excluded from the analysis as they present different conservation challenges to nomadic land birds. We use IOC nomenclature for all species. The aim of this study is to outline and test a new approach for spatial prioritization of dynamic species. We use a subset of the species found within the region to illustrate this approach, and our findings should not be taken as a prescriptive conservation plan for the region.

We represented species' distributions by building monthly time-sliced habitat suitability maps for the period June 2000 to March 2011, constructed by matching occurrence data with environmental conditions at the time of each observation (130 maps per species; for full details see Appendix S1 and Runge *et al.*, 2015). The study period covers two high rainfall events and an extended period of drought. We created a single model of each species occurrence in relation to environmental conditions, based on all occurrences in the study region for that species across time, and then projected this global model across the monthly environmental conditions in the study region. Some of the species modelled may occur outside the boundaries of the study region. Changes in detectability could occur over time, potentially affecting the comparability among time slices in model output. While comparable estimates of detectability over time do not yet exist for the study region, we sought to minimize these effects by only using standardized searches of 2 hectare plots over 20 minutes, in which detectability has been shown to be high (Possingham 2004).

We accounted for coastal and spring bias in bird survey effort by drawing 10,000 background data points from a random sample of Atlas surveys (Phillips *et al.*, 2009). We reclassified the MAXENT logistic probability into predictions of absence and probability of presence (hereafter referred to as habitat suitability) using equal sensitivity and specificity threshold values (Liu *et al.*, 2005). These maps provide quantitative estimates of monthly habitat suitability for each

species, at 0.05° resolution, clipped to exclude regions where the species is unlikely to occur. The maps were resampled to 10 × 10 km resolution by calculating the product of the area of the planning unit in km² and the area-weighted mean habitat suitability of the distribution map cells (0.05°) that overlapped the planning unit (10 × 10 km), to give the conservation value of each species–month combination in each planning unit. These maps were aggregated into conservation features, with each conservation feature being a map of the species distribution averaged across the time period described in each of the scenarios below.

We examined how spatial prioritization varied under five scenarios. Each scenario represented a different planning goal for an objective of finding the minimum set of reserves:

1. Static scenario representing a goal of maintaining complementary and representative coverage of the distribution averaged across time for all species. This scenario was based on species distributions pooled across all 130 time slices, yielding one conservation feature per species (42 conservation features in total).

2. Time-sliced scenario representing a goal of reflecting the temporal variation in use of planning units. This was based on species-estimated distributions in January, April, July and October of each year in the study period with the distribution for each species during each of those month–year combinations being input as a separate conservation feature (43 conservation features per species, 1806 conservation features in total). We excluded the other months from this analysis to ensure that the prioritization problem remained computationally tractable, while still representing seasonal habitat use.

3. Annual scenario representing a goal of accounting for interannual variability in target species distributions. This was based on the average habitat suitability for each of the 12 years in the study period (12 conservation features per species, 504 conservation features in total).

4. Monthly scenario representing a goal of accounting for monthly variability in target species distributions. The monthly scenario was based on estimated species distributions which had been averaged across all occurrences of each month in the study period (12 conservation features per species, 504 conservation features in total).

5. Bottleneck scenario representing a goal of protecting each species' distribution when its geographic range is at its minimum. This was based on the mapped species distributions in the month of the minimum geographic range extent across the time series for each species, and yielded one conservation feature per species, ignoring their distributions at other times (42 conservation features in total). We defined refugia as the absolute minimum distribution across the time period, though refugia could alternately be defined as distributions that drop below a threshold range size, allowing comparison of refugial stability across time.

The mathematical problem formulation for the five scenarios is included in Appendix S2.

To explore priority sites for the expansion of the current Australian protected area network, we additionally ran each

of the above scenarios with planning units that are already covered by protected areas locked into the final prioritization. Planning units were defined as protected where at least 50% of their area was covered by a protected area listed in the Collaborative Australian Protected Areas Database as IUCN management category I–IV (CAPAD; Australian Government Department of the Environment and Water Resources, 2012). We also calculated how the temporal distribution of nomadic species is covered by existing protected areas (Appendix S4). Geospatial analyses were conducted in PYTHON 2.6.5 (<https://www.python.org/>) and ARCGIS 10.0 (<http://www.esri.com/>).

The area prioritized under each scenario is a function of the geographic size of each conservation feature, and the bottleneck scenario will have the smallest spatial footprint. We acknowledge concerns regarding the setting of arbitrary representation targets (Carwardine *et al.*, 2009), and welcome research into more realistic targets (Addison *et al.*, 2015). In the absence of data to inform target selection and for the purposes of a comparative analysis, we set representation targets at 30% for each conservation feature, that is, aiming to protect 30% of each species' distribution according to the scenarios above.

Prioritizing habitats for nomads

We identified potential priority regions for conservation action using the conservation planning software MARXAN version 2.43 (Ball *et al.*, 2009). MARXAN uses a simulated annealing algorithm to select areas that minimize the cost of the final set of planning units while meeting representation targets for conservation features such as species distributions (the objective function). We performed 100 runs for each scenario and set the boundary length modifier (BLM) to zero assuming all species can reach available habitat through stepping stones rather than continuous corridors. We ran the prioritization under five scenarios, and identified the optimal spatial distribution of the protected area designation for each scenario, that is the set of planning units that met the representation target while minimizing cost. We also calculated selection frequency, the number of times a planning unit was selected across the 100 runs. We compared the spatial concordance of the resulting prioritizations by calculating Bray–Curtis dissimilarity in R version 3.0.0 (<http://www.r-project.org/>).

RESULTS

The conservation planning scenarios that accounted for the movements of nomadic birds prioritized more area than the static scenario, with priority areas located in different places compared with a simple static approach that ignores species' changing distributions over time (Table 1). The 'time-sliced' scenario required the greatest area for protection, with a higher cost than other scenarios (\$177 million, 2.02 million km²). It also showed only limited spatial congruence with

Table 1 Cost and area prioritized under each of the five scenarios.

| Scenario | Number of conservation features | Area selected (million km ²) | Total cost (million \$) |
|---------------|---------------------------------|--|-------------------------|
| 1 Static | 42 | 1.89 | 130 |
| 2 Time-sliced | 1806 | 2.02 | 177 |
| 3 Annual | 504 | 1.96 | 142 |
| 4 Monthly | 504 | 1.94 | 138 |
| 5 Bottleneck | 42 | 1.59 | 104 |

the static scenario, with a Bray–Curtis dissimilarity of 21.7% (Table 2). As expected, total cost and reserve area were lowest under the bottleneck prioritization, which attempts to represent species distributions only when they are at their minimum (\$104 million, 1.59 million km²).

Priority locations for protection differed markedly among scenarios. The most similar solutions were the monthly and static (Bray–Curtis dissimilarity 12.6%) and the annual and monthly scenarios (Bray–Curtis dissimilarity 10.5%; Table 2). The spatial pattern of the bottleneck scenario was the most divergent from other scenarios (Bray–Curtis dissimilarities ranging from 30.9% to 34.7%). The time-sliced solution was more divergent from the static and bottleneck solutions (Bray–Curtis dissimilarity 21.7% and 34.7%, respectively) than from the monthly and annual scenarios (Bray–Curtis dissimilarity 18.0% and 16.5%, respectively), suggesting that temporal variation in the distribution of nomads is relatively well represented even by a relatively coarse annual representation of temporal distribution.

When spatial dynamics were incorporated into planning, the conservation planning goal had a large impact on both the cost and spatial pattern of the resulting conservation prioritization (Fig. 1). For example, sites prioritized across eastern Australia showed high selection frequency under every scenario, where high agricultural profitability across the region limits conservation action to the few remaining intact patches. However, the bottleneck scenario, which emphasized very different spatial priorities compared to the other scenarios, placed less emphasis on protection of sites in eastern Australia. During bottleneck times, highest species richness for the species analysed is concentrated in a band

Table 2 Comparison of spatial dissimilarity of the five scenarios, Bray–Curtis dissimilarity. 0 = identical, 100% = completely dissimilar.

| | Static (%) | Time-sliced (%) | Annual (%) | Monthly (%) |
|-------------|------------|-----------------|------------|-------------|
| Time-sliced | 21.7 | | | |
| Annual | 15.0 | 16.5 | | |
| Monthly | 10.2 | 18.0 | 12.6 | |
| Bottleneck | 30.9 | 34.7 | 31.7 | 31.3 |

across central northern Australia, with low richness across the eastern third of the continent (Fig. 2a). In contrast, overall species richness for the subset of species analysed (as represented by aggregated distributions across time) is spread widely across the central inland (Fig. 2b), though it is more consistently focused on sites in central and north-western deserts across time (Fig. 2c).

Because this study used a subset of the nomadic birds in study region, we evaluated the extent to which the number of species considered increases the overall area under conservation (Appendix S3). This analysis indicated that the overall area under conservation increases linearly with the addition of species, consistent with previous studies (Chittaro *et al.*, 2010).

DISCUSSION

Protecting mobile species requires that their movement dynamics be incorporated into systematic conservation tools (Runge *et al.*, 2014). Despite increasing awareness of the need for movement dynamics to be included in systematic planning and attempts to incorporate the dynamics of predictable migrations (Martin *et al.*, 2007; Iwamura *et al.*, 2014; Nicol *et al.*, 2015), it has proven more difficult to deal with nomadic species (Runge *et al.*, 2014).

The currently accepted approach for incorporating the distributions of most species into systematic conservation planning pools their spatial distribution across time, without considering the dynamics within that distribution (Gilmore *et al.*, 2007; Watson *et al.*, 2011; Venter *et al.*, 2014). Our results show that spatial prioritizations under such an approach differ substantially from those that incorporate movement dynamics, and risk leaving dynamic species unprotected at certain times. We discovered that incorporating the temporal dynamics of species distributions into spatial prioritization increases the area of land selected for conservation action and reduces the selection frequency of any one site. Patterns of expansion and contraction in dynamic species vary among years, and as a consequence, a broad range of sites need to be prioritized even though many sites will be at times unoccupied. The resulting spatial prioritization is affected by the time-scale across which distributions are summarized, and the different goals (i.e. planning to maintain habitat across time, or maintain bottleneck refugia, or maximize coverage of overall range) result in spatially divergent prioritization schemes (Fig. 1). Prioritizing bottlenecks, sites critical to the species when its distribution is at a minimum, is the cheapest and most spatially constrained solution, and for many nomadic species, this will be the time when conservation actions are most required (Runge *et al.*, 2015). The potential scale of misspending is large, ranging between 31 and 53% of total budget (\$40.6 m to \$68.9 m), with inefficient protection of 930,000 km² of the rangelands by ignoring species dynamics (Table 3), and this is likely to increase if more species are considered.

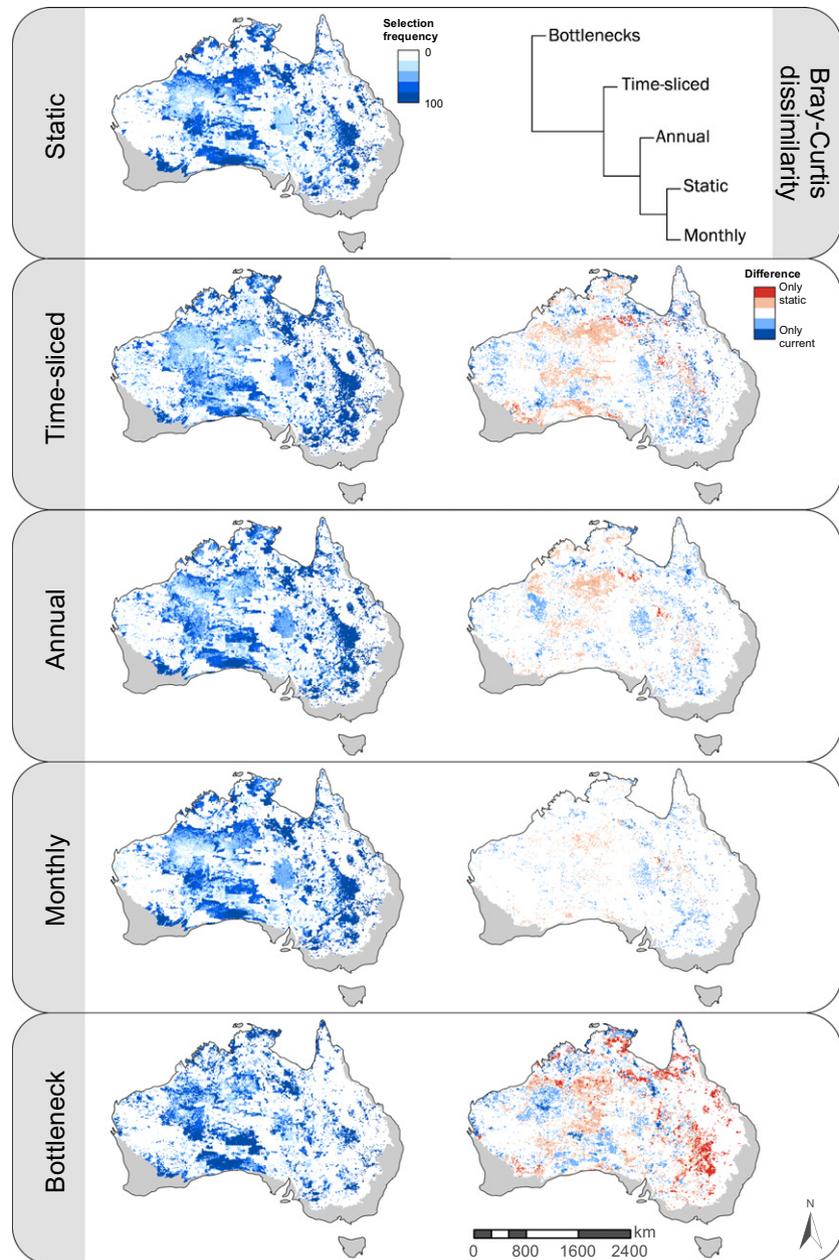


Figure 1 Selection frequencies and difference maps of spatial prioritization under five scenarios. Selection frequency (how often a planning unit (PU) is chosen across 100 runs) under scenario: (a) static, (b) time-sliced, (c) annual, (d) monthly and (e) bottleneck; Dark blue = PU chosen in 100 runs, white = PU never chosen; difference maps of static vs (f) time-sliced, (g) annual, (h) monthly and (i) bottleneck. Colours indicate the difference in selection frequency between the static scenario and the current scenario. Blue = PU chosen in current scenario, but not in static scenario; red = PU chosen more often in the static scenario. White = PU selected (or not selected) equally in both.

The relatively low agricultural value of much of the region means the cost of purchasing the land suggested for conservation action by our study is not prohibitive. However, the large area and isolation of the sites required for protection under each scenario (one-third of the landscape under the time-sliced scenario to one-quarter under the bottleneck scenario) means that conflict with land users combined with high cumulative management costs will soon limit the feasibility of a conservation approach based solely on protected area designation, consistent with previous studies on dynamic systems (Lourival *et al.*, 2011). A move away from reliance on static protected areas into large-scale integrated land management, where conservation actions and human land use are intertwined, will be crucial for the majority of nomadic species. Conservation actions outside of protected

areas could involve working with landholders to limit overgrazing of shrubs and native grasses, maintain vegetation along waterways or in ephemeral swamplands, or manage feral predators, although the different costs associated with these actions may change the location of some priority areas. Inclusion of the full suite of rangeland species, and more ecologically realistic conservation targets will only increase the amount of land required for conservation, lending further support to our call for landscape-scale conservation management.

While in some systems knowledge on species distributions may be available on a daily basis (Fink *et al.*, 2010), the temporal rate at which a distribution should be mapped will depend in part on the rate of change in the distribution, but also whether temporal resolution changes the management

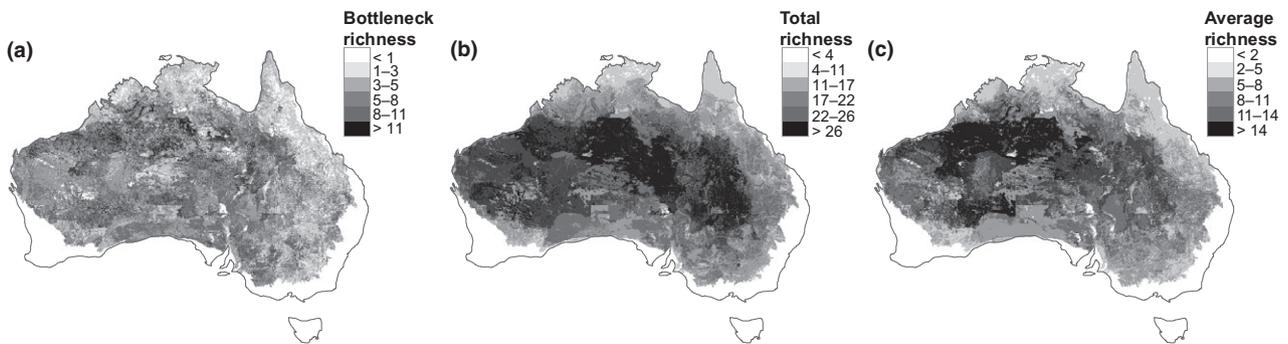


Figure 2 Maps of bird species richness for 42 nomadic species: (a) bottleneck richness, overlaying each species' minimal distribution; (b) total species richness, summing the number of species present at any time from 2000 to 2011; and (c) average species richness for the period 2000 to 2011.

Table 3 Comparison of underprotection and overprotection using static approach rather than a dynamic approach, and the potential cost of misspent funding using a static approach.

| Dynamic scenario | Area selected by dynamic scenario that was not selected in static scenario (million km ²) | Area selected by static scenario that was not selected by dynamic scenario (million km ²) | Cost of static area not represented in dynamic scenario (million \$) | Amount misspent as percentage of cost of static scenario (%) |
|------------------|---|---|--|--|
| 1 Time-sliced | 0.84 | 0.70 | 45.3 | 34.9 |
| 2 Annual | 0.73 | 0.65 | 42.9 | 33.1 |
| 3 Monthly | 0.67 | 0.61 | 40.6 | 31.3 |
| 4 Bottleneck | 0.63 | 0.93 | 68.9 | 53.1 |

actions or decreases management uncertainty. For instance, in Neotropical migrants a single seasonal time slice may be sufficient to capture species' breeding distributions. However, during migration when species can move large distances very quickly (DeLuca *et al.*, 2015), the temporal scale at which distributions should be sampled will depend on how rapidly conservation actions can be implemented. Actions implemented in real time such as stopping wind turbines will require daily knowledge on distributions, whereas aggregating distributions seasonally will be sufficient for actions with slow rates of implementation such as land protection. While our study was not designed to evaluate the value of temporal information for informing choice between management options, this is a key area for future research.

Generating time-sliced habitat suitability models is a time-consuming exercise, and relies on specialist skills and adequate data with which to build models. Our study benefited from eleven years of citizen science surveys across a generally data-poor region (Mac Nally *et al.*, 2004; Szabo *et al.*, 2007). Lack of long-term survey data would limit applicability of this approach for many non-avian species. Where budget, data or time constraints limit the generation and use of time-sliced habitat suitability models, estimates of spatial distribution can be generated through expert elicitation approaches such as Bayesian belief networks (Smith *et al.*, 2007; Murray *et al.*, 2009). Our results indicate that a prioritization based on the annual distribution of these birds is a good surrogate for one incorporating shorter time-scale dynamics Table 2.

Lack of ecological knowledge might often limit our understanding of whether managing species across time or during bottlenecks is the more suitable approach. This lack of certainty could result in significant misspending of limited conservation funding where conservation of nomadic species was the primary goal. However, a suite of 'no-regrets' sites in eastern Australia are consistently prioritized across all planning goals and resilient to differing hypotheses or approaches to dealing with nomadic behaviour (Fig. 3c; Carvalho *et al.*, 2011). Other sites are robust to uncertainty in the conservation goal in some but not all scenarios, so planners will need to decide which of the scenarios are more likely to represent the resource needs of species. The mechanisms driving the response of nomads to resource availability are most likely species- and threat dependent – some species might best be represented by a bottleneck planning approach, but other species with high interannual variability in distribution might be best represented by an interannual approach.

Ecological uncertainty is just one of the many uncertainties that make conservation decisions difficult, particularly when it comes to managing data-poor species. The prioritization approach illustrated here is based entirely on distributional information, and neglects the interactions of resource and site use across time, which may often have unexpected population consequences (Hostetler *et al.*, 2015). The modelled distributions are themselves subject to uncertainty, and the model variables may only approximate the complex drivers of resources such as flowering events (Runge *et al.*,

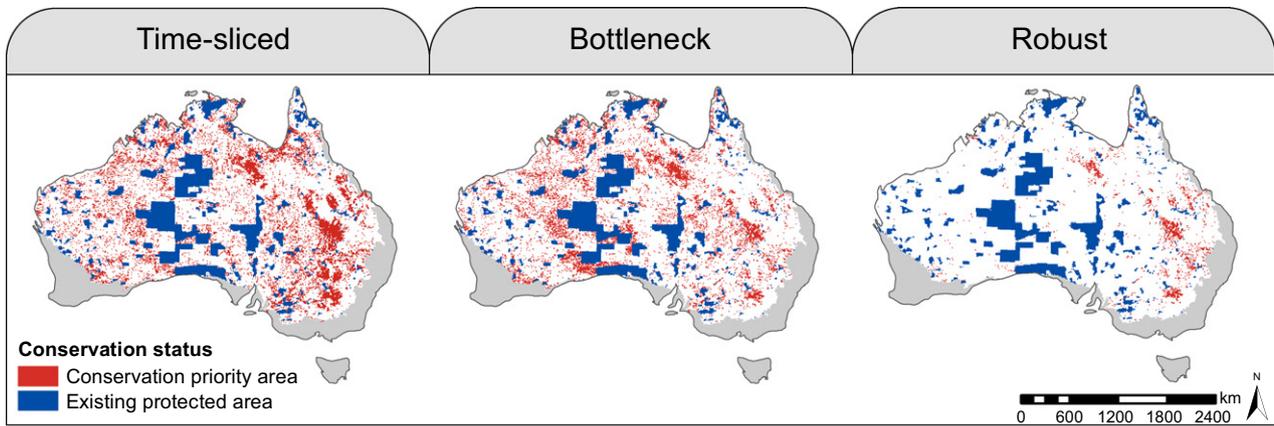


Figure 3 Priority areas for protected area expansion: (a) sites prioritized under time-sliced scenario, (b) sites prioritized under bottleneck scenario and (c) robust sites irreplaceable under all five scenarios.

2015). Strategies for buffering against uncertainty include setting high conservation targets (Steele, 2006), or increasing the size of protected areas (Tulloch *et al.*, 2013), and it is likely that explicitly accounting for uncertainty would further increase the area under conservation management in this study.

While we here consider only a static conservation network, dynamic conservation actions that track the movements and population dynamics of species across time could limit the area under conservation action at any one time and may be appropriate where threats are also dynamic (Bengtsson *et al.*, 2003; Costello & Polasky, 2004; Grantham *et al.*, 2008; Howell *et al.*, 2008; O’Keefe & DeCelles, 2013). Several options for dynamic or adaptive prioritization of conservation action across networks have been proposed (Chadès *et al.*, 2011; Golovin *et al.*, 2011; Grantham *et al.*, 2011; Levin *et al.*, 2013; Nicol *et al.*, 2015), and advances in computational methods in other fields may provide further options (Jafari & Hearne, 2013; Minas *et al.*, 2014; Mortazavi-Naeini *et al.*, 2014). The success of such an approach will rely on a management framework that allows for timely identification of sites and rapid implementation of conservation action at those sites (Martin *et al.*, 2012).

The simple approach outlined here can be applied to other mobile species including regular migrants or wide ranging species such as large carnivores, and is most useful when species have irregular movement patterns that are not readily predicted and limit use of more sophisticated approaches (e.g. Nicol *et al.*, 2015), such as seabirds or facultative migrants (Stojanovic *et al.*, 2015). This approach can be also adapted to include connectivity. There has been much recent research on incorporating connectivity into conservation planning, and current approaches rely on setting either species-specific dispersal distances (Moilanen *et al.*, 2005), or assigning values to the connections between planning units (Beger *et al.*, 2010; Pouzols & Moilanen, 2014). In this study, we explored changes in priority areas based on temporal changes in habitat suitability for nomadic species, without

imposing additional assumptions about connectivity requirements based on very little empirical data. Some species might depend heavily on adequate connectivity across time and space, especially those with limited or constrained dispersal capabilities (e.g. ground-dwelling mammals that require corridors for movement, or species in marine environments constrained by currents and other environmental factors). For such species, the approach outlined here could be adapted to incorporate connectivity by estimating the strength of connectivity among planning units (e.g. Kool *et al.*, 2013). This would also allow connectivity between non-contiguous planning units to influence the prioritization, for example species that can travel long distances, using sites as ‘stepping stones’ rather than requiring continuous connectivity.

In this study, we considered only a single conservation goal at a time, that is protect bottleneck habitat or protect a proportion of species’ entire distribution across time. In many migratory species, separate threats act on different parts of the annual cycle, and their efficient conservation will require prioritization of conservation actions across multiple goals (for instance, protecting breeding populations from invasive predators while maintaining sufficient habitat along the migration route). Conservation scientists are only just beginning to explore how to achieve multiple goals for managing species (e.g. through multiple-use zoning using MARXAN with zones; Klein *et al.*, 2009), but prioritizing multiple goals across space and time will require significant advances in optimization techniques due to the size of the decision space (Cattarino *et al.*, 2015; Chadès *et al.*, 2015).

CONCLUSIONS

The success of conservation planning for dynamic species will depend on identifying actions that maintain viable populations across both space and time and discovering ways to integrate those actions into human land use. By incorporating time-sliced distributions of each single species as multiple

conservation features in the spatial prioritization problem, we present a simple approach for accounting for temporal and spatial dynamics in spatial prioritization schemes for highly mobile species. We have shown that dynamic distributions strongly influence the optimal spatial configuration of conservation actions. Our results highlight that movements of species are often far from simple, and conservation of dynamic species depends on accounting for these complex patterns.

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SUPPORTING INFORMATION

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

Appendix S1 Methods for species distribution modelling of bird distributions

Appendix S2 Mathematical formulation of MARXAN with temporal dynamics

Appendix S3 Sensitivity analysis exploring effect of number of species on overall area under conservation

Appendix S4 Protected area coverage of nomadic species across time

BIOSKETCH

The Environmental Decisions Group (<http://www.edg.org.au/>) is a network of conservation researchers working on the science of effective decision-making to better conserve biodiversity. The EDG includes a variety of Australian and international research centres, hubs and teams, all focused on Environmental Decisions Science.

C.A.R., A.I.T.T., R.A.F., H.P.P. and V.J.D.T. conceived the ideas; C.A.R. analysed the data and led the writing; all authors contributed to final manuscript.

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