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Title: Incorporating dynamic distributions into spatial prioritization

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1 **Aim**

2 Species' distributions are generally treated as static for the purposes of prioritization, but

3 many species such as migrants and nomads have distributions that shift over time. Decisions

4 about priority actions for such species must account for this temporal variation, making

5 planning for their conservation a complex problem. Here we explore how dynamic

6 distributions can be incorporated into a spatial prioritization, and suggest approaches for

7 prioritizing conservation action when knowledge of species' movements is uncertain.

8 **Location**

9 Australian rangelands, including the arid and semi-arid zones of central Australia and

10 adjoining monsoonal tropics, although methods are applicable for any dynamic biodiversity

11 feature.

12 **Methods**

13 We used the decision-support software MARXAN to explore the impact of temporal dynamics

14 on spatial conservation planning for a suite of 42 highly mobile birds across the study region.

15 We explored scenarios comparing a static representation of species' distributions with four

16 methods of integrating temporal dynamics (i) accounting for temporal variability in

17 distribution across months and years, (ii) considering only monthly variability in distribution

18 (iii) considering only annual variability in distribution and (iv) considering only minimal

19 distributions during spatial bottlenecks, ignoring distributions at other times.

20 **Results**

21 Incorporating the temporal dynamics of species into spatial prioritization substantially

22 changes the spatial pattern of conservation investment, increasing the overall area needed to

23 be placed under conservation measures to achieve a specific target level of species protection.

24 Targeting bottlenecks, locations critical to each species when its distribution is at a minimum,

25 prioritizes a very different suite of sites to those chosen using the traditional approach of

26 static distribution maps based on occurrences pooled across time.

27 **Main conclusions**

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

32 **Keywords**

33 Arid-zone, dynamic distributions, migration, nomadic, protected areas, spatial prioritization,
34 systematic conservation planning.

35 **(A) Introduction**

36 Spatial prioritization is one of the backbones of systematic conservation planning, and is a
37 process whereby conservation actions are matched to locations based on their feasibility,
38 conservation benefit and cost (Moilanen *et al*., 2009a). Conservation planners have rarely
39 incorporated animal movements into prioritizations, instead focusing on more readily
40 available information such as costs (Naidoo *et al.*, 2006), feasibility (Knight *et al.*, 2011;
41 Tulloch *et al.*, 2014), uncertainty in data (Carvalho *et al.*, 2011; Tulloch *et al.*, 2013), future
42 threats (Game *et al.*, 2008) and multiple options for conservation action (Reyers *et al.*, 2012).
43 However, increasing emphasis on the importance of incorporating spatial and temporal
44 dynamics into the planning process (Grantham *et al.*, 2008; Lourival *et al.*, 2011) has led to
45 attention being focused on this issue (Game *et al.*, 2013; Runge *et al.*, 2014) and there has
46 been recent progress in understanding how to incorporate species with relatively simple and
47 predictable movement patterns into spatial conservation planning (Martin *et al.*, 2007;
48 Klaassen *et al.*, 2008; Moilanen *et al.*, 2008; Linke *et al.*, 2011; Iwamura *et al.*, 2013; Kool *et*
49 *al.*, 2013; Iwamura *et al.*, 2014).

50 However, many species show less predictable patterns of movement. For example, the
51 irregular movements of nomadic and irruptive species (e.g. Flock Bronzewing *Phaps*
52 *histrionica;* Dostine *et al.,* 2014 and Dickcissel *Spiza americana;* Bateman *et al.,* 2015) make
53 their conservation a particular challenge due to uncertainty in exactly which parts of their
54 geographic range are most important for persistence, and at what times they are occupied
55 (Runge *et al.*, 2015). As a consequence, their distributions are generally treated as static, with
56 little or no reference to their need for protection in particular parts of their lifecycle or across
57 resource hotspots (Rodrigues *et al.*, 2004; Gilmore *et al.*, 2007; Beresford *et al.,* 2011;

58   Watson *et al.*, 2011; Venter *et al.*, 2014). Critical sites may be overlooked, leading to

59   irreversible population declines or extinction (Reid & Fleming, 1992; Woinarski *et al.*, 1992).

60   Understanding and incorporating spatial and temporal dynamics can be significant for any

61   attempts to conserve mobile species including migrants and nomads (Runge *et al.*, 2014).

62   We are aware of only one attempt to consider the dynamics of nomadic species in a spatial

63   prioritization scheme. In an elegant analysis, Fahse *et al.,* (1998) examined alternative

64   configurations of a simulated protected area system for a suite of nomadic larks in the Nama-

65   Karoo, South Africa using a spatio-temporal model to estimate the survival of flocks given

66   known ecological relationships with seasonal rainfall patterns (Fahse *et al.*, 1998). They

67   found that these nomadic birds were best protected by a series of sites spread across the study

68   region, spatially focused on areas of high resource availability. Their study sought to inform

69   the debate about optimal protected area size rather than a systematic conservation plan, and

70   therefore did not incorporate cost or other feasibility metrics. However, this remains the only

71   example where distributional dynamics have been incorporated into a prioritization for

72   nomadic species.

73   Without guidelines for best practice approaches for incorporating spatial and temporal

74   dynamics of species with variable distributions into systematic conservation planning,

75   decision-makers run the risk of prioritizing the wrong areas, wasting funding, and losing

76   donor confidence. Conservation planning problems are typically formulated as either

77   'minimum set' (meet conservation targets using minimal resources i.e. area, money) or

78   'maximum coverage' (maximize conservation benefits given a fixed amount of resources;

79   Possingham *et al.*, 2006; Moilanen *et al.*, 2009b). Regardless of the approach, using a

80   distribution map that pools the occurrences of nomadic species would focus the result on the

81   cheapest places regardless of whether or not those places are occupied more often than

82   others, and risks overlooking key sites used by nomads if they are relatively expensive or

83   used only during times of resource scarcity. A dynamic approach allows planners to

84   incorporate places that are important at only certain points in time (e.g. when ephemeral

85   resources are available in that area), with less risk of protecting areas of consistently low

86   value for nomads.

87   There are several possible approaches to prioritizing conservation actions in light of spatio-

88   temporal dynamics in nomadic species distributions. Currently, the nature of movements of

89   nomadic birds is poorly known (Chan, 2001; Dean, 2004; Burbidge & Fuller, 2007) and can

90   differ across regions (Wyndham, 1982; Ziembicki & Woinarski, 2007). As a consequence, it

91   remains difficult to determine the most effective conservation strategy for highly dynamic

92   species. One approach may be to prioritize refugia or bottlenecks, places to which species

93   contract during times of limited habitat suitability across the wider landscape. If such refugia

94   exist, they may be crucial to long-term persistence (Reid & Fleming, 1992; Morton *et al.*,

95   1995; Bateman *et al.,* 2015). Currently, very little is known about the consistency of refugial

96   sites over long time frames (Manning *et al.*, 2007) and their role in population persistence is

97   not fully understood (Bennetts & Kitchens, 2000; Tischler *et al.,* 2013). Conservation of

98   refugia may only guarantee a species survival during a small part of its lifetime. In some

99   species it may be more important to protect a good sample of suitable habitat across space

100   and time (Dickman *et al.*, 1995; Stojanovic *et al.,* 2015). It is unclear how those differing

101   approaches will affect population persistence, given the lack of ecological knowledge on

102   many nomadic species. A bet-hedging approach may be to undertake conservation actions in

103   refugia (where known) in combination with broader landscape management.

104   Here we present an approach for incorporating spatio-temporal dynamics into a spatial

105   prioritization for mobile species, using a case study of data-poor nomadic birds in the

106   rangelands of Australia. Our objective was to compare the minimum set of areas identified

107   for protected area designation (though the results are also applicable to any ecologically

108   favourable management involving loss of agricultural profitability) under five scenarios of

109   species representation that varied according to plausible beliefs about where and when the

110   most important places for maintaining nomadic populations occur. This approach could

111   inform conservation planning for any suite of species with dynamic distributions across time,

112   from short-term migratory movements to long-term distributional changes driven by climate

113   change. We then examine the impact of different temporal choices of distributional

114   information on the configuration and cost of spatial priorities and suggest how that

115   information might be used to guide both conservation and ecological research.

116   **(A) Methods**

117   *(B) The study region*

118   We explore a conservation network for a suite of nomadic birds found within the rangelands

119   of Australia, including the arid and semi-arid zones of central Australia, and adjoining

120   monsoonal tropics. The rangelands of Australia occupy an area of over 6.2 million km^2 and

121 large areas of the region are grazed, predominantly for cattle and sheep production, with
122 smaller regions of cropping and irrigated agriculture (State of the Environment, 2011). The
123 study region was divided into grid cells of 10x10km for analysis, resulting in 66,179 planning
124 units.

125 Spatially explicit cost data are a key component of conservation planning, often driving the
126 location of priority areas (Carwardine *et al.*, 2008). We estimated conservation feasibility
127 using data on agricultural profit at full equity for the period 2005-2006 (Marinoni *et al.*,
128 2012). These data were calculated in a period of widespread drought, and to avoid
129 underestimating landholder values negative profitability values were set to zero. We adjusted
130 for inflation to December 2013 (ABS, 2013) and multiplied the average profitability per
131 hectare in each planning unit by the area of that planning unit. We determined the net present
132 value of foregone annual profitability as per Carwardine *et al.,* (2008) in Australian dollars. A
133 transaction cost (the cost associated with negotiating and managing land use) of $10 000 was
134 applied to each planning unit where agricultural activity occurred within that planning unit.
135 Valuation has yet to be mapped for parts of the region, including Indigenous lands and
136 regions where no or very low intensity agricultural activity currently occurs. Conservation
137 actions in such places will still incur costs and there is still very little guidance about how to
138 aggregate costs when land valuation is not linked to monetary value or is borne by different
139 stakeholders (Ban & Klein 2009). We assigned unvalued locations a transaction cost of
140 $5000 per planning unit so they would not be automatically protected. The simplified
141 transaction cost data used in this study only approximate actual reserve establishment and
142 management costs, which will likely be heterogeneous over time and space, and dependent
143 on a range of factors including the type of conservation project undertaken, the size and
144 context of the planning unit, and the level of trust and confidence between parties (Garrick *et*
145 *al.*, 2013; Pannell *et al.*, 2013). While we focus on protected area designation, the
146 conservation feasibility metric used here, agricultural profitability, provides a surrogate
147 estimate for a diversity of actions; from adopting lower stocking rates to setting aside
148 wetlands and remnant woodlands facilitated by agreements with landholders or by
149 designation of formal protected areas. The prioritization method used is sensitive to the
150 relative values of planning units, rather than their absolute values.

151 *(B) Conservation features and targets*

152   We derived distribution maps for a phylogenetically diverse but non-comprehensive subset of
153   bird species thought to be nomadic and predominantly occurring in the rangelands of
154   Australia (42 species; Appendix S1) from Runge *et al.,* (2015). Nomadic species range over
155   large areas, and may show different movement patterns under different environmental
156   conditions (Dean, 2004), limiting the ability of field experts to reliably classify species as
157   nomadic. While recognizing that classification of movement patterns in the study region is
158   subject to ongoing discussion, we include species where nomadism is indicated in part or all
159   of their range according to the *Handbook of Australian, New Zealand and Antarctic Birds*
160   (HANZAB; Marchant & Higgins 1993; Higgins & Davies 1996; Higgins 1999; Higgins,
161   Peter & Steele 2001; Higgins & Peter 2002; Higgins, Peter & Cowling 2006a,b) and a key
162   reference where classification was based on other than HANZAB (Ziembicki & Woinarski
163   2007). Though many water birds in the region are also highly nomadic (Kingsford *et al.*
164   2010), they were excluded from the analysis as they present different conservation challenges
165   to nomadic land birds. We use IOC nomenclature for all species. The aim of this paper is to
166   outline and test a new approach for spatial prioritization of dynamic species. We use a subset
167   of the species found within the region to illustrate this approach, and our findings should not
168   be taken as a prescriptive conservation plan for the region.

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

182   We accounted for coastal and spring bias in bird survey effort by drawing 10 000 background
183   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 10x10km resolution by calculating the product of the area of the planning unit in km^2 and the area-weighted mean habitat suitability of the distribution map cells (0.05°) that overlapped the planning unit (10x10km), 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 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 the prioritization problem remained computationally tractable, while still representing seasonal habitat use.

3. **Annual** scenario representing a goal of accounting for inter-annual 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

214   distributions which had been averaged across all occurrences of each month in the

215   study period (12 conservation features per species, 504 conservation features in total).

216   5. **Bottleneck** scenario representing a goal of protecting each species' distribution when

217   its geographic range is at its minimum. This was based on the mapped species

218   distributions in the month of the minimum geographic range extent across the time

219   series for each species, and yielded one conservation feature per species, ignoring

220   their distributions at other times (42 conservation features in total). We defined

221   refugia as the absolute minimum distribution across the time period, though refugia

222   could alternately be defined as distributions that drop below a threshold range size,

223   allowing comparison of refugial stability across time.

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

225   Supporting Information.

226   To explore priority sites for the expansion of the current Australian protected area network,

227   we additionally ran each of the above scenarios with planning units that are already covered

228   by protected areas locked in to the final prioritization. Planning units were defined as

229   protected where at least 50% of their area was covered by a protected area listed in the

230   Collaborative Australian Protected Areas Database as IUCN management category I-IV

231   (CAPAD: AGDEWR, 2012). We also calculated how the temporal distribution of nomadic

232   species is covered by existing protected areas (Appendix S4). Geospatial analyses were

233   conducted in Python 2.6.5 (https://www.python.org/) and ArcGIS 10.0

234   (http://www.esri.com/).

235   The area prioritized under each scenario is a function of the geographic size of each

236   conservation feature, and the bottleneck scenario will have the smallest spatial footprint. We

237   acknowledge concerns regarding the setting of arbitrary representation targets (Carwardine *et*

238   *al.,* 2009), and welcome research into more realistic targets (Addison *et al.,* 2015). In the

239   absence of data to inform target selection and for the purposes of a comparative analysis, we

240   set representation targets at 30% for each conservation feature, that is, aiming to protect 30%

241   of each species' distribution according to the scenarios above.

242   *(B) Prioritizing habitats for nomads*

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

(A) Results

257 The conservation planning scenarios that accounted for the movements of nomadic birds
258 prioritized more area than the static scenario, with priority areas located in different places
259 compared with a simple static approach that ignores species' changing distributions over time
260 (Table 1). The 'time-sliced' scenario required the greatest area for protection, with a higher
261 cost than other scenarios ($177 million, 2.02 million km^2). It also showed only limited spatial
262 congruence with the static scenario, with a Bray–Curtis dissimilarity of 21.7% (Table 2). As
263 expected, total cost and reserve area were lowest under the bottleneck prioritization, which
264 attempts to represent species distributions only when they are at their minimum ($104
265 million, 1.59 million km^2).

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

275   When spatial dynamics were incorporated into planning, the conservation planning goal had a
276   large impact on both the cost and spatial pattern of the resulting conservation prioritization
277   (Fig 1). For example, sites prioritized across eastern Australia showed high selection
278   frequency under every scenario, where high agricultural profitability across the region limits
279   conservation action to the few remaining intact patches. However the bottleneck scenario,
280   which emphasized very different spatial priorities compared to the other scenarios, placed
281   less emphasis on protection of sites in eastern Australia. During bottleneck times highest
282   species richness for the species analysed is concentrated in a band across central northern
283   Australia, with low richness across the eastern third of the continent (Fig. 2a). In contrast,
284   overall species richness for the subset of species analysed (as represented by aggregated
285   distributions across time) is spread widely across the central inland (Fig. 2b), though it is
286   more consistently focused on sites in central and north-western deserts across time (Fig. 2c).

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

291   **(A) Discussion**

292   Protecting mobile species requires that their movement dynamics be incorporated into
293   systematic conservation tools (Runge *et al.*, 2014). Despite increasing awareness of the need
294   for movement dynamics to be included in systematic planning and attempts to incorporate the
295   dynamics of predictable migrations (Martin *et al.*, 2007; Iwamura *et al.*, 2014; Nicol *et al.*,
296   2015), it has proven more difficult to deal with nomadic species (Runge *et al*., 2014).

297   The currently accepted approach for incorporating the distributions of most species into
298   systematic conservation planning pools their spatial distribution across time, without
299   considering the dynamics within that distribution (Gilmore *et al.*, 2007; Watson *et al.*, 2011;
300   Venter *et al.*, 2014). Our results show that spatial prioritizations under such an approach
301   differ substantially from those that incorporate movement dynamics, and risk leaving
302   dynamic species unprotected at certain times. We discovered that incorporating the temporal
303   dynamics of species distributions into spatial prioritization increases the area of land selected
304   for conservation action and reduces the selection frequency of any one site. Patterns of
305   expansion and contraction in dynamic species vary among years, and as a consequence a

306 broad range of sites need to be prioritized even though many sites will be at times
307 unoccupied. The resulting spatial prioritization is affected by the time scale across which
308 distributions are summarized, and the different goals (i.e. planning to maintain habitat across
309 time, or maintain bottleneck refugia, or maximize coverage of overall range) result in
310 spatially divergent prioritization schemes (Fig. 1). Prioritizing bottlenecks, sites critical to the
311 species when its distribution is at a minimum, is the cheapest and most spatially constrained
312 solution, and for many nomadic species this will be the time when conservation actions are
313 most required (Runge *et al*., 2015).The potential scale of misspending is large, ranging
314 between 31-53% of total budget ($40.6m to $68.9m), with inefficient protection of
315 930,000km^2 of the rangelands by ignoring species dynamics (Table 3), and this is likely to
316 increase if more species are considered.

317 The relatively low agricultural value of much of the region means the cost of purchasing the
318 land suggested for conservation action by our study is not prohibitive. However, the large
319 area and isolation of the sites required for protection under each scenario (one third of the
320 landscape under the time-sliced scenario to one quarter under the bottleneck scenario) means
321 conflict with land users combined with high cumulative management costs will soon limit the
322 feasibility of a conservation approach based solely on protected area designation, consistent
323 with previous studies on dynamic systems (Lourival *et al.*, 2011). A move away from
324 reliance on static protected areas into large-scale integrated land management, where
325 conservation actions and human land use are intertwined will be crucial for the majority of
326 nomadic species. Conservation actions outside of protected areas could involve working with
327 landholders to limit overgrazing of shrubs and native grasses, maintain vegetation along
328 waterways or in ephemeral swamplands, or manage feral predators, although the different
329 costs associated with these actions may change the location of some priority areas. Inclusion
330 of the full suite of rangeland species, and more ecologically realistic conservation targets will
331 only increase the amount of land required for conservation, lending further support to our call
332 for landscape-scale conservation management.

333 While in some systems knowledge on species distributions may be available on a daily basis
334 (Fink *et al.,* 2010), the temporal rate at which a distribution should be mapped will depend in
335 part on the rate of change in the distribution, but also whether temporal resolution changes
336 the management actions or decreases management uncertainty. For instance, in Neotropical
337 migrants a single seasonal time slice may be sufficient to capture species' breeding

338 distributions. However, during migration when species can move large distances very quickly

339 (DeLuca *et al.,* 2015), the temporal scale at which distributions should be sampled will

340 depend on how rapidly conservation actions can be implemented. Actions implemented in

341 real-time such as stopping wind turbines will require daily knowledge on distributions,

342 whereas aggregating distributions seasonally will be sufficient for actions with slow rates of

343 implementation such as land protection. While our study was not designed to evaluate the

344 value of temporal information for informing choice between management options, this is a

345 key area for future research.

346 Generating time-sliced habitat suitability models is a time-consuming exercise, and relies on

347 specialist skills and adequate data with which to build models. Our study benefited from

348 eleven years of citizen science surveys across a generally data-poor region (Mac Nally *et al.,*

349 2004; Szabo *et al.*, 2007). Lack of long-term survey data would limit applicability of this

350 approach for many non-avian species. Where budget, data or time constraints limit the

351 generation and use of time-sliced habitat suitability models, estimates of spatial distribution

352 can be generated through expert elicitation approaches such as Bayesian Belief Networks

353 (Smith *et al.*, 2007; Murray *et al.*, 2009). Our results indicate that a prioritization based on the

354 annual distribution of these birds is a good surrogate for one incorporating shorter time-scale

355 dynamics.

356 Lack of ecological knowledge might often limit our understanding of whether managing

357 species across time or during bottlenecks is the more suitable approach. This lack of certainty

358 could result in significant misspending of limited conservation funding where conservation of

359 nomadic species was the primary goal. However, a suite of 'no-regrets' sites in eastern

360 Australia are consistently prioritized across all planning goals and resilient to differing

361 hypotheses or approaches to dealing with nomadic behaviour (Fig. 4c; Carvalho *et al.*, 2011).

362 Other sites are robust to uncertainty in the conservation goal in some but not all scenarios, so

363 planners will need to decide which of the scenarios are more likely to represent the resource

364 needs of species. The mechanisms driving the response of nomads to resource availability are

365 most likely species- and threat-dependent – some species might best be represented by a

366 bottleneck planning approach, but other species with high inter-annual variability in

367 distribution might be best represented by an inter-annual approach.

368 Ecological uncertainty is just one of the many uncertainties that make conservation decisions

369 difficult, particularly when it comes to managing data-poor species. The prioritization

370 approach illustrated here is based entirely on distributional information, and neglects the
371 interactions of resource and site use across time, which may often have unexpected
372 population consequences (Hostetler *et al.*, 2015). The modelled distributions are themselves
373 subject to uncertainty, and the model variables may only approximate the complex drivers of
374 resources such as flowering events (Runge *et al.,* 2015). Strategies for buffering against
375 uncertainty include setting high conservation targets (Steele 2006), or increasing the size of
376 protected areas (Tulloch *et al.,* 2013), and it is likely that explicitly accounting for uncertainty
377 would further increase the area under conservation management in this study.

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

389 The simple approach outlined here can be applied to other mobile species including regular
390 migrants or wide ranging species such as large carnivores, and is most useful when species
391 have irregular movement patterns that are not readily predicted and limit use of more
392 sophisticated approaches (e.g. Nicol *et al.,* 2015), such as seabirds or facultative migrants
393 (Stojanovic *et al.,* 2015). This approach can be also adapted to include connectivity. There
394 has been much recent research on incorporating connectivity into conservation planning, and
395 current approaches rely on setting either species-specific dispersal distances (Moilanen *et al.,*
396 2005), or assigning values to the connections between planning units (Beger *et al*., 2010;
397 Pouzols & Moilanen, 2014). In this study we explored changes in priority areas based on
398 temporal changes in habitat suitability for nomadic species, without imposing additional
399 assumptions about connectivity requirements based on very little empirical data. Some
400 species might depend heavily on adequate connectivity across time and space, especially
401 those with limited or constrained dispersal capabilities (e.g. ground-dwelling mammals that

402 require corridors for movement, or species in marine environments constrained by currents
403 and other environmental factors). For such species, the approach outlined here could be
404 adapted to incorporate connectivity by estimating the strength of connectivity among
405 planning units (e.g. Kool *et al.,* 2013). This would also allow connectivity between non-
406 contiguous planning units to influence the prioritization, for example species that can travel
407 long distances, using sites as 'stepping stones' rather than requiring continuous connectivity.

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

418 **(A) Conclusions**

419 The success of conservation planning for dynamic species will depend on identifying actions
420 that maintain viable populations across both space and time and discovering ways to integrate
421 those actions into human land use. By incorporating time-sliced distributions of each single
422 species as multiple conservation features in the spatial prioritization problem we present a
423 simple approach for accounting for temporal and spatial dynamics in spatial prioritization
424 schemes for highly mobile species. We have shown that dynamic distributions strongly
425 influence the optimal spatial configuration of conservation actions. Our results highlight that
426 movements of species are often far from simple, and conservation of dynamic species
427 depends on accounting for these complex patterns.

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433 **(A) Supporting Information**

434 Additional Supporting Information may be found in the online version of this article:
435 **Appendix S1** Methods for species distribution modelling of bird distributions
436 **Appendix S2** Mathematical formulation of MARXAN with temporal dynamics
437 **Appendix S3** Sensitivity analysis exploring effect of number of species on overall area under
438 conservation
439 **Appendix S4** Protected area coverage of nomadic species across time
440
441 **(A) Biosketch**

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

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

448 **(A) References**

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716 **Table legends**

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

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

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

722

Figure legends

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 e) bottleneck; Dark blue = PU chosen in 100 runs, white = PU never chosen; .and difference maps of static vs f) time-sliced g) annual h) monthly 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.

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 c) average species richness for the period 2000 to 2011.

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

740 **Tables**

741 Table 1

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

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750 Table 2

	Static	Time-sliced	Annual	Monthly
751	Static	Time-sliced	Annual	Monthly
752 Time-sliced	21.7 %			
753 Annual	15.0 %	16.5 %		
754 Monthly	10.2 %	18.0 %	12.6 %	
755 Bottleneck	30.9 %	34.7 %	31.7 %	31.3 %

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758   **Table 3.**

759   Dynamic scenario   Area selected by dynamic scenario that was not selected in static
760   scenario (million km2)   Area selected by static scenario that was not selected by
761   dynamic scenario (million km2)   Cost of Static area not represented in dynamic scenario
762   (million $)   Amount misspent as percentage of cost of static scenario

763   1 Time-sliced 0.84   0.70   45.3   34.9 %
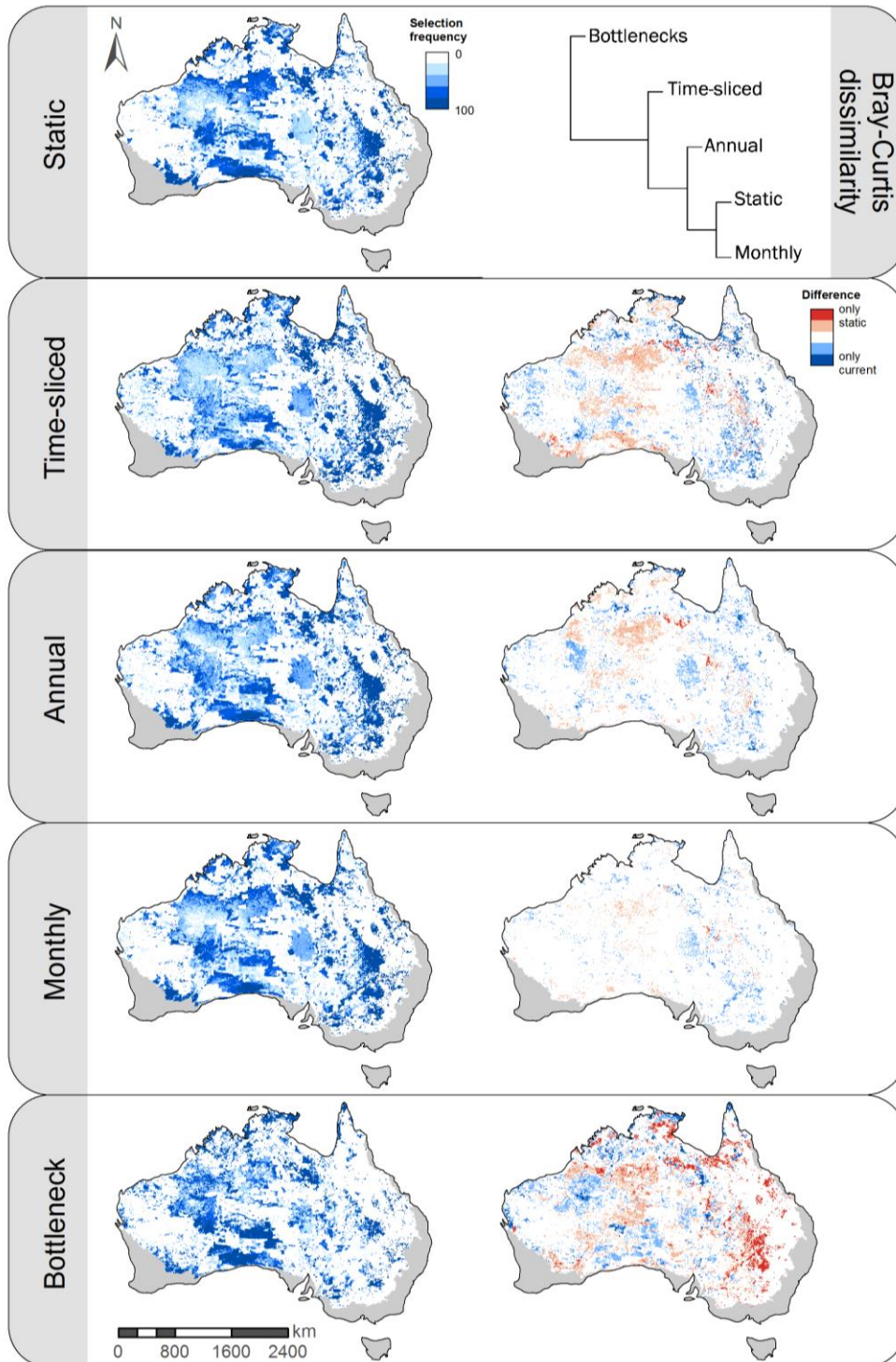
764   2 Annual   0.73   0.65   42.9   33.1 %

765   3 Monthly   0.67   0.61   40.6   31.3 %

766   4 Bottleneck   0.63   0.93   68.9   53.1 %
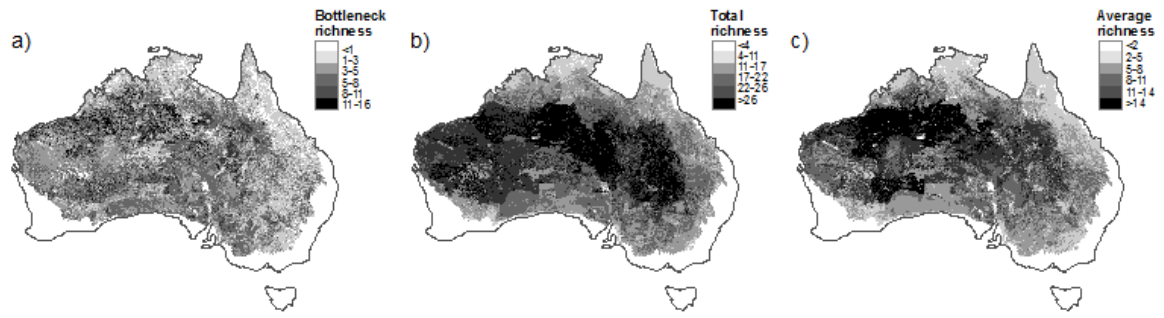
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768   **Figures**
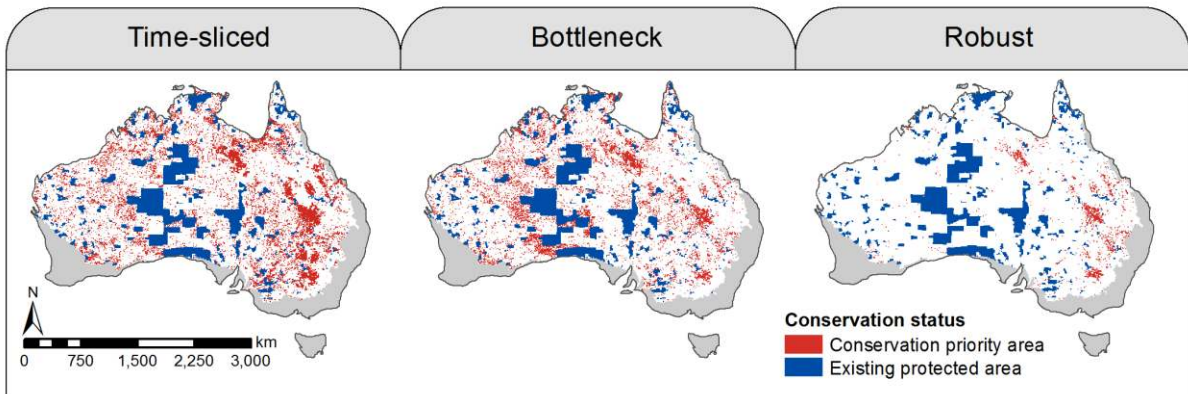
769   Figure 1

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772

773   Figure 2

778   Figure 3

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