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How interactions between animal movement and landscape processes modify local range dynamics and extinction risk

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Manuscripts

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2   range dynamics and extinction risk

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17   **Summary:**

18   Forecasts of range dynamics now incorporate many of the mechanisms and interactions that drive

19   species distributions. However, connectivity continues to be simulated using overly simple

20   distance-based dispersal models with little consideration of how the individual behaviour of

21   dispersing organisms interacts with landscape structure (functional connectivity). Here we link an

22   individual-based model to a niche-population model to test the implications of this omission. We

23   apply this novel approach to a turtle species inhabiting wetlands which are patchily distributed

24   across a tropical savanna, and whose persistence is threatened by two important synergistic drivers

25   of global change: predation by invasive species and overexploitation. We show that projections of

26   local range dynamics in this study system change substantially when functional connectivity is

27   modelled explicitly. Accounting for functional connectivity in model simulations causes the

28   estimate of extinction risk to increase, and predictions of range contraction to slow. We conclude

29   that models of range dynamics that simulate functional connectivity can reduce an important source

30   of bias in predictions of shifts in species distributions and abundances, especially for organisms

31   whose dispersal behaviours are strongly affected by landscape structure.

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Introduction

Spatially explicit demographic models are increasingly being used to forecast the influence of

global change on species' range dynamics in terrestrial [1] and marine systems [2]. This is because

such models provide direct predictions of spatiotemporal patterns of abundance, allowing extinction

risk to be estimated and conservation management efforts evaluated and prioritised [3]. The

drawbacks are that these models are data intensive, requiring a robust understanding of the

population dynamics of the focal species for effective parameterisation [4].

When embedded in demographic frameworks, models of species' range dynamics typically

make use of simplifying assumptions to minimise the complexity of interactions between biotic and

landscape processes. Such simplifications increase uncertainty and can result in unwanted bias in

forecasts of extinction risk and range shifts, potentially affecting conservation actions [5]. Methods

used to estimate and model connectivity have been singled out as particularly important sources of

uncertainty in climate-driven predictions of species ranges and abundances [6]. Improving

techniques for simulating dispersal in models of range dynamics should therefore be viewed as a

research priority, especially since enhancing connectivity is the most commonly proposed solution

for conserving biodiversity under climate change [7].

In demographic models of species' range dynamics, the dispersal process is usually

approximated using a simple distance-based dispersal kernel, which is often extrapolated from

field-based estimates of average and maximum path lengths observed within a single or limited

number of populations [8]. Actual dispersal patterns depend on structural and functional

connectivity. Structural connectivity refers to the effects of population-level dispersal conduits or

barriers, while functional connectivity refers to interactions between the behaviour of dispersing

individuals and structural elements of the landscape and environmental processes [9]. For example,

streams may serve as dispersal conduits for a species (structural connectivity), and long-distance

dispersal may occur primarily via sporadic flood events that carry young-individuals searching for

territories in a downstream direction (functional connectivity). Structural connectivity has been

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64   integrated into forecasts of range dynamics using spatially explicit demographic models [10],

65   mainly via least-cost pathway approaches that identify the optimal route between two patches on the

66   basis of a gridded cost surface representing the resistance of the intervening matrix [11]. In contrast,

67   functional connectivity is rarely considered in forecasts of species' range dynamics [but see 12],

68   and has not been considered in detail in spatially explicit demographic models. This is despite the

69   development of mechanistic individual- or agent-based models capable of assigning behaviour to

70   individuals and allowing them to interact directly with their surroundings [13].

71   Niche-population models couple ecological niche models with stochastic demographic

72   models, and have recently been used to link multiple mechanisms and interactions that together

73   drive species distributions and abundances [3]. In this study, we determine the sensitivity of niche-

74   population model forecasts of range dynamics and extinction risk to characterisations of landscape

75   connectivity as strictly structural, or as truly functional − incorporating both landscape structure and

76   animal-movement behaviour. To account for functional connectivity, we link niche-population

77   models to spatially explicit individual-based models. We then apply this novel approach to a well-

78   studied freshwater turtle species from northern Australia (*Chelodina rugosa*), which is threatened

79   by synergistic drivers of global change (predation by invasive species, habitat degradation and

80   overexploitation) in a tropical wetland environment [14].

81   **Materials and Methods**

82   We constructed spatially explicit stage- and sex-based stochastic matrix models for *C. rugosa* in

83   two neighbouring water catchments in northern Australia using the RAMAS GIS v5 software [15].

84   The region is bounded by distinct northern (saltwater) and southern (sandstone escarpment) local

85   range boundaries. We modelled the influence of invasive species and overexploitation (and their

86   interaction) [14] on local population dynamics at 521 waterholes, patchily distributed within a

87   terrestrial habitat. We used repeat survey data from 50 waterholes (1999-2007) and linear

88   regression to determine waterhole ephemerality (frequency of drying and hydroperiod). The

89   surveyed waterholes captured the environmental features of the study region, meaning that the

                                                                              4

90   statistical model was not used to extrapolate to novel environmental conditions. The ephemerality

91   of waterholes varied spatiotemporally (based on observed local rainfall between 1980 and 2005),

92   affecting rates of turtle predation by pigs, humans, and their interaction [16], and resulting in some

93   refuge populations with low predation rates. We did not consider an effect of future global warming

94   on ephemerality.

95   We modelled dispersal between distinct habitat patches using: (i) a simple distance-based

96   dispersal kernel extrapolated from field-based estimates of average and maximum *C. rugosa*

97   movement (*null model*); (ii) a least-cost pathway method that combined a friction map with a

98   distance-based dispersal kernel [15] thus allowing dispersal patterns to be affected by habitat

99   characteristics such as dispersal barriers as well as inter-patch distance (*structural connectivity*

100   *model*); and (iii) a spatially explicit individual-based model that incorporated mechanisms linking

101   complex turtle movement behaviour to habitat structure (*functional connectivity model*). The

102   influence of dispersal on spatial abundance patterns and local range limits was simulated using

103   10,000 stochastic replicates, run over a 101 year period (i.e., 2000 - 2100) with a 10-year initial

104   burn-in (stabilisation) period. Population viability was assessed using expected minimum

105   abundance (EMA) calculated for the period: 2010 - 2100. Range movement between 2010 and 2100

106   was calculated annually based on the latitude of the geographic centre of the most southern sub-

107   population. Change in the number of occupied waterholes and total population abundance (of

108   persistent model runs) over time were also investigated. See Appendix S1 and Appendix S2 for

109   additional technical details.

110   **Results**

111   Accounting for functional connectivity caused turtle population abundance to decline at a faster rate

112   compared to models that did not link movement behaviour to landscape structure explicitly (Figure

113   1). Populations with high predation pressure tended to persist for longer (83 versus 62 pig-predated

114   populations remained extant in 2100), and refuge populations (no pig predation) tended to have

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115   lower expected minimum abundance (49 versus 59) under the functional connectivity scenario

116   compared to the null scenario (Figure 2; Table 1). The median size of refuge populations in 2100

117   was smaller for the functional connectivity scenario (28) compared to the structural (77) and null

118   scenarios (55) (Figure S1). Although the predicted number of extant populations in 2100 was

119   similar under the functional and structural connectivity scenarios (Table 1), the populations that

120   were predicted to experience extirpation differed between these scenarios (Figure 2). The southern

121   range boundary contracted in a northerly direction at a much slower rate under the functional

122   connectivity scenario (Figure 1), moving 3.81 km by 2100, compared to >12 km for the null and

123   structural connectivity scenarios (Table 1). Turtle populations with high predation rates tended to

124   persist for shorter periods in savanna versus floodplain environments (Figure S2).

125   **Discussion**

126   By coupling individual-based and niche-population models, we show that estimates of extinction

127   risk and local range movement are sensitive to alternative characterizations of landscape

128   connectivity. Accounting for the interaction between animal behaviour and landscape structure

129   (functional connectivity) in model simulations for *C. rugosa* results in elevated local population-

130   level extinction risk and slower rates of local range contraction. Projected shifts in turtle abundance

131   and range margins derived from the null (distance-based dispersal) and structural connectivity

132   models (dispersal affected by land cover characteristics as well as inter-patch distance) were more

133   similar to each other than to results obtained from the functional connectivity model. These results

134   suggest that functional connectivity should be considered in models of species' range dynamics

135   when the behaviour of the dispersing organism is affected by landscape structural elements and

136   processes.

137   The influence of landscape connectivity on plant and animal movement is a vital component

138   of metapopulation ecology, influencing fundamental processes such as population dynamics and

139   evolution [17]. However, the simplifying assumptions commonly used for modelling connectivity

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140   in metapopulation models and ecological network analysis are likely to bias forecasts of population

141   persistence [18] and range movement. During the wet-season *Chelodina rugosa* move to the

142   shallows to feed at the expanding margins of waterholes. This feeding-behaviour results in

143   increased contact with streams, allowing turtles to more easily disperse to geographically distant

144   and isolated waterholes. Simulations that included this behaviour resulted in slower rates of range

145   contraction due to pig predation, and an increased mean frequency of dispersal into populations

146   experiencing high predation rates (demographic sinks), resulting in lower densities in refuge

147   populations (demographic sources). This suggests a more general result – that failing to consider

148   important functional connectivity in models of range dynamics is likely to underestimate extinction

149   risk and overestimate range shifts for species like *C. rugosa* that interact with landscape features

150   such as dispersal corridors (natural or artificial).

151   Our spatiotemporally complex wetland system is well suited for examining the importance

152   of functional and structural connectivity. The preferred habitat of *C. rugosa* − ephemeral wetlands

153   that occasionally or regularly dry − provides a gradient in resource quality that varies through both

154   space and time. While our results suggest that many demographic-based forecasts of range

155   movement and extinction risk will be improved by including functional connectivity, it is likely that

156   biases in model forecasts for some species can be addressed adequately without the need for

157   behaviourally explicit individual-based models. For example, previous niche-population model

158   predictions for marine species with free-swimming larval stages [5] almost certainly would be

159   improved by simulating dispersal as a passive process driven principally by oceanic currents.

160   Using spatially explicit demographic models with functional connectivity, we have

161   confirmed that present-day estimates of turtle predation by pigs [14, 16] are so high that the

162   extirpation of many *C. rugosa* populations is very likely in the near term, particularly in waterholes

163   embedded within savanna landscapes. Our results for floodplain turtle populations are likely to

164   underestimate extinction risk because we did not account for future sea-level rise, which is likely to

165   result in severe regional habitat loss [19], further threatening the persistence of *C. rugosa*.

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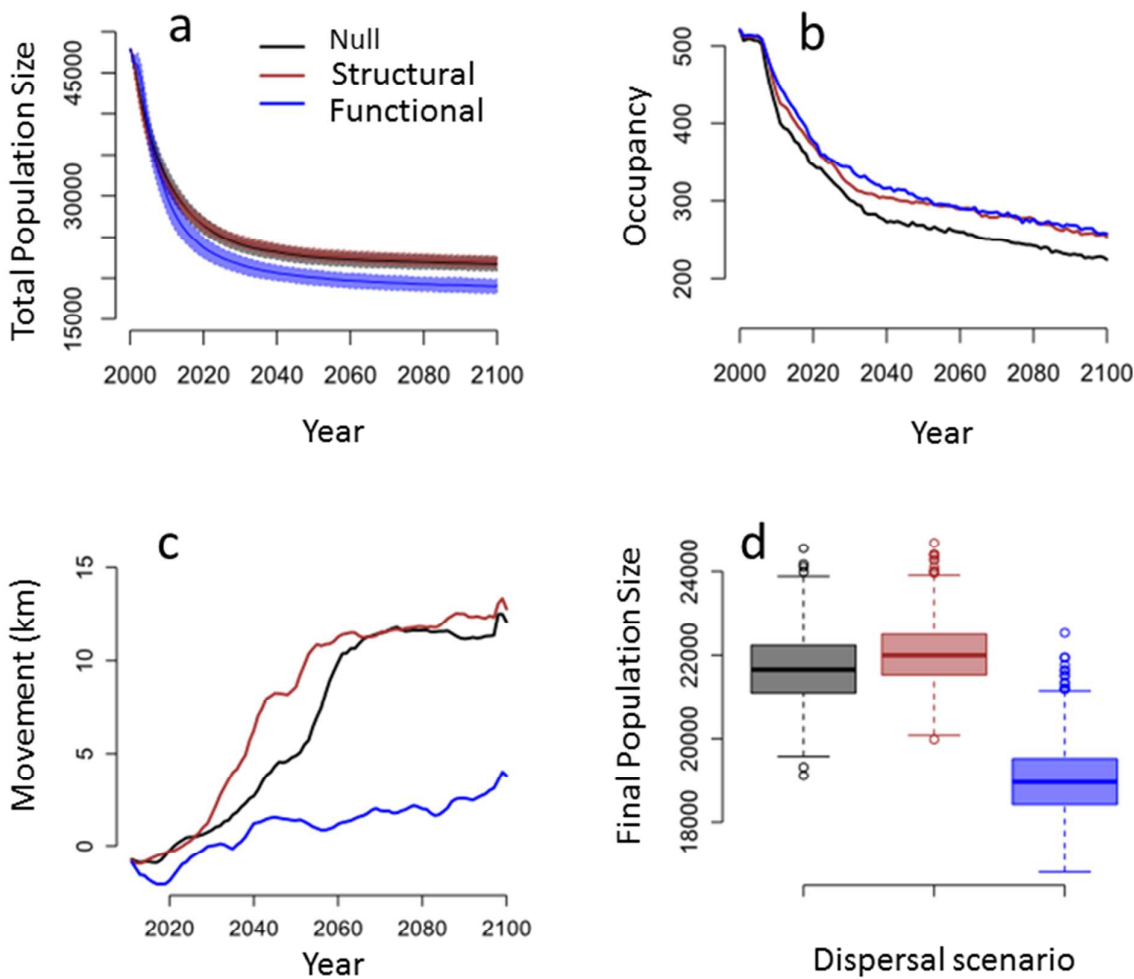
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227   **Figure 1:** The influence of structural and functional connectivity on predicted range dynamics and

228   extinction risk. Shown are mean population estimates (solid line), including 5th and 95th percentiles

229   of population size (**a**), average number of extant populations (**b**), movement of the southern range

230   boundary in a northerly direction (**c**) and final population size (**d**) derived from a stochastic

231   metapopulation model for the freshwater turtle *Chelodina rugosa* according to three connectivity

232   scenarios: null (black), structural (red) and functional (blue). Note that there is strong agreement in

233   forecast population size according to the null and structural dispersal scenarios.

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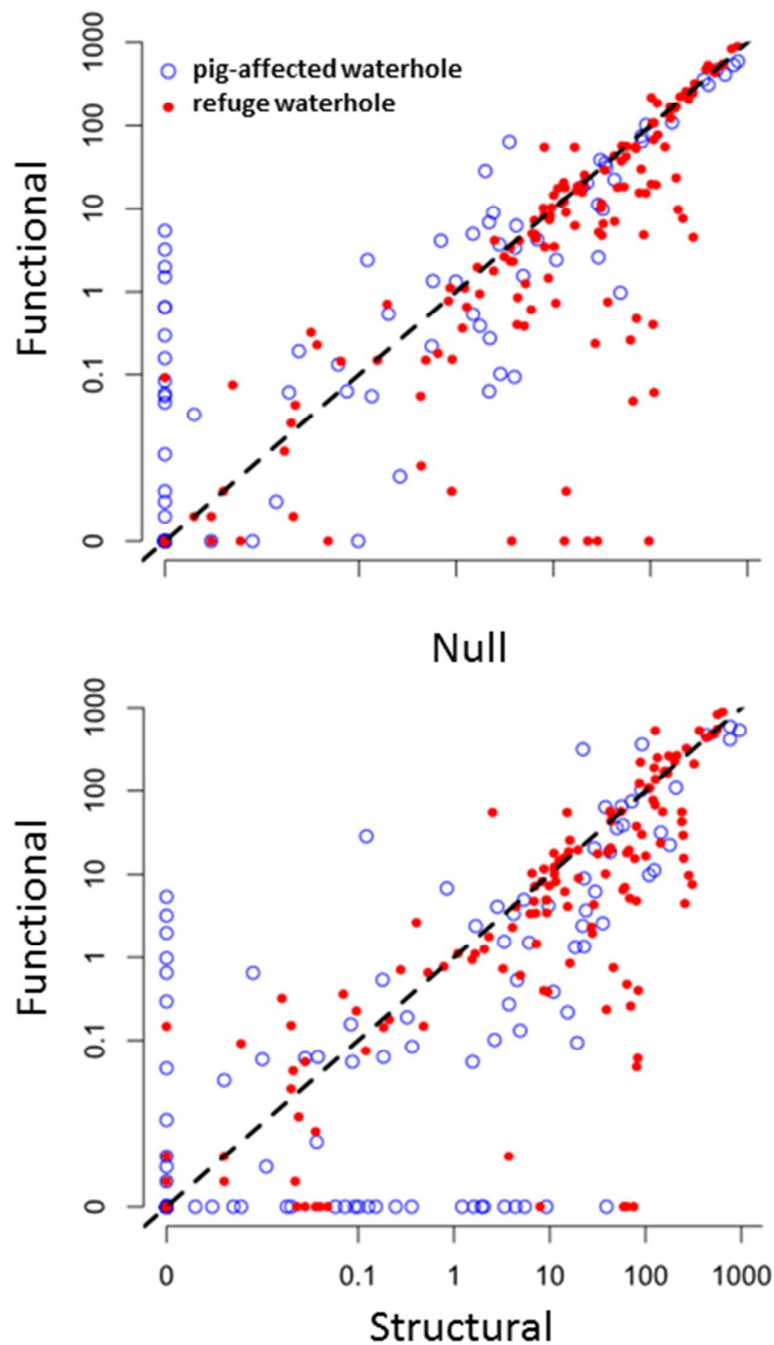
Figure 2: The influence of functional connectivity on local expected minimum abundance (log10

scale) in populations subject to high (pig affected waterhole) and low (refuge waterhole) levels of

predation. Plots compare results from simulations with functional connectivity to those without

(top) and with (bottom) structural connectivity.

Table 1: Range movement and extinction risk according to three contrasting methods of modelling connectivity

Year	Connectivity scenario	EMA	Metapop size	Movement (km)	High-predation savannah (%)	High-predated floodplain (%)	Refugia savannah (%)	Refugia floodplain (%)
2050	*Null*	0.46	269	4.89	15	28	74	68
	Structural	0.47	298	8.6	22	41	76	68
	Functional	0.41	302	1.38	20	33	70	63
2100	*Null*	0.43	224	12.09	14	25	54	63
	Structural	0.44	254	12.79	20	32	66	58
	Functional	0.43	258	3.8	20	30	67	57

Expected minimum abundance as a proportion of initial population size (EMA), number of sub-populations in the metapopulation (Metapop size), movement of the southern range boundary in a northerly direction, and percent of high predation (Predation) and low predation (Refuge) populations remaining in savanna and floodplain habitats in 2050 and 2100 according to three connectivity scenarios: Null, Structural and Functional (see methods for details).

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