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

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Forecasts of range dynamics now incorporate many of the mechanisms and interactions that drive species distributions. However, connectivity continues to be simulated using overly simple distance-based dispersal models with little consideration of how the individual behaviour of dispersing organisms interacts with landscape structure (functional connectivity). Here, we link an individual-based model to a niche-population model to test the implications of this omission. We apply this novel approach to a turtle species inhabiting wetlands which are patchily distributed across a tropical savannah, and whose persistence is threatened by two important synergistic drivers of global change: predation by invasive species and over-exploitation. We show that projections of local range dynamics in this study system change substantially when functional connectivity is modelled explicitly. Accounting for functional connectivity in model simulations causes the estimate of extinction risk to increase, and predictions of range contraction to slow. We conclude that models of range dynamics that simulate functional connectivity can reduce an important source of bias in predictions of shifts in species distributions and abundances, especially for organisms whose dispersal behaviours are strongly affected by landscape structure.

1. 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 [2] systems. This is because such models provide direct predictions of spatio-temporal patterns of abundance, allowing extinction risk to be estimated and conservation management efforts evaluated and prioritized [3]. The drawbacks are that these models are data intensive and require a robust understanding of the population dynamics of the focal species for effective parameterization [4].

When embedded in demographic frameworks, models of species' range dynamics typically make use of simplifying assumptions to minimize 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
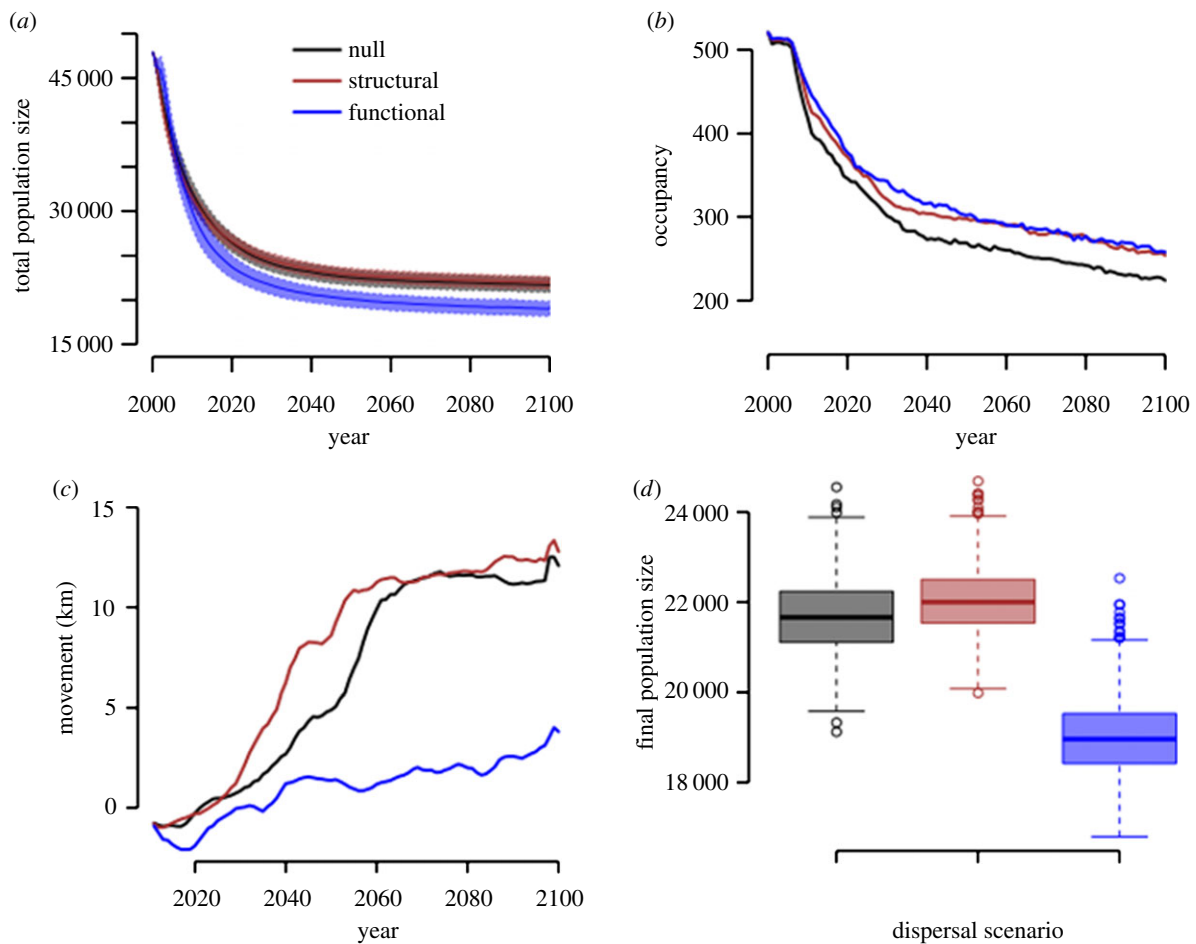
Figure 1. The influence of structural and functional connectivity on predicted range dynamics and extinction risk. Shown are mean population estimates (solid line), including fifth and 95th percentiles of population size (a), average number of extant populations (b), movement of the southern range boundary in a northerly direction (c) and final population size (d) derived from a stochastic metapopulation model for the freshwater turtle *Chelodina rugosa* according to three connectivity scenarios: null (black), structural (red) and functional (blue). Note that there is strong agreement in forecast population size according to the null and structural dispersal scenarios.

priority, especially because 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, whereas 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 integrated into forecasts of range dynamics using spatially explicit demographic models [10], mainly via least-cost pathway approaches that identify the optimal route between two patches on the basis of a gridded cost surface representing the resistance of the intervening matrix [11]. By contrast, functional connectivity is rarely considered in forecasts of species' range dynamics (but see [12]) and has not been considered in detail in spatially explicit

demographic models. This is despite the development of mechanistic individual- or agent-based models capable of assigning behaviour to individuals and allowing them to interact directly with their surroundings [13].

Niche-population models couple ecological niche models with stochastic demographic models and have recently been used to link multiple mechanisms and interactions that together drive species distributions and abundances [3]. In this study, we determine the sensitivity of niche-population model forecasts of range dynamics and extinction risk to characterizations of landscape connectivity as strictly structural, or as truly functional—incorporating both landscape structure and animal-movement behaviour. To account for functional connectivity, we link niche-population models to spatially explicit individual-based models. We then apply this novel approach to a well-studied freshwater turtle species from northern Australia (*Chelodina rugosa*), which is threatened by synergistic drivers of global change (predation by invasive species, habitat degradation and overexploitation) in a tropical wetland environment [14].

2. Material and methods

We constructed spatially explicit stage- and sex-based stochastic matrix models for *C. rugosa* in two neighbouring water catchments in northern Australia using the RAMAS GIS v. 5

software [15]. The region is bounded by distinct northern (saltwater) and southern (sandstone escarpment) local range boundaries. We modelled the influence of invasive species and overexploitation (and their interaction) [14] on local population dynamics at 521 waterholes, patchily distributed within a terrestrial habitat. We used repeat survey data from 50 waterholes (1999–2007) and linear regression to determine waterhole ephemerality (frequency of drying and hydroperiod). The surveyed waterholes captured the environmental features of the study region, meaning that the statistical model was not used to extrapolate to novel environmental conditions. The ephemerality of waterholes varied spatio-temporally (based on observed local rainfall between 1980 and 2005), affecting rates of turtle predation by pigs and humans and their interaction [16], and resulting in some refuge populations with low predation rates. We did not consider an effect of future global warming on ephemerality.

We modelled dispersal between distinct habitat patches using: (i) a simple distance-based dispersal kernel extrapolated from field-based estimates of average and maximum *C. rugosa* movement (*null model*); (ii) a least-cost pathway method that combined a friction map with a distance-based dispersal kernel [15], thus allowing dispersal patterns to be affected by habitat characteristics such as dispersal barriers as well as inter-patch distance (*structural connectivity model*); and (iii) a spatially explicit individual-based model that incorporated mechanisms linking complex turtle movement behaviour to habitat structure (*functional connectivity model*). The influence of dispersal on spatial abundance patterns and local range limits was simulated using 10 000 stochastic replicates, run over a 101 year period (i.e. 2000–2100) with a 10 year initial burn-in (stabilization) period. Population viability was assessed using expected minimum abundance (EMA) calculated for the period 2010–2100. Range movement between 2010 and 2100 was calculated annually based on the latitude of the geographical centre of the most southern subpopulation [17]. Change in the number of occupied waterholes and total population abundance (of persistent model runs) over time were also investigated. See the electronic supplementary material, appendices S1 and S2 for additional technical details.

3. Results

Accounting for functional connectivity caused turtle population abundance to decline at a faster rate compared with models that did not link movement behaviour to landscape structure explicitly (figure 1). Populations with high predation pressure tended to persist for longer (83 versus 62 pig-predated populations remained extant in 2100), and refuge populations (no pig predation) tended to have lower EMA (49 versus 59) under the functional connectivity scenario compared with the null scenario (table 1, percentage decline in high predation populations; figure 2a). The median size of refuge populations in 2100 was smaller for the functional connectivity scenario (28) compared with the structural (77) and null scenarios (55) (electronic supplementary material, figure S1). Although the predicted number of extant populations in 2100 was similar under the functional and structural connectivity scenarios (table 1), the populations that were predicted to experience extirpation differed between these scenarios (figure 2). The southern range boundary contracted in a northerly direction at a much slower rate under the functional connectivity scenario (figure 1), moving 3.81 km by 2100, compared with more than 12 km for the null and structural connectivity scenarios (table 1). Turtle populations with high predation rates tended to persist for shorter periods in savannah versus floodplain environments (electronic supplementary material, figure S2).
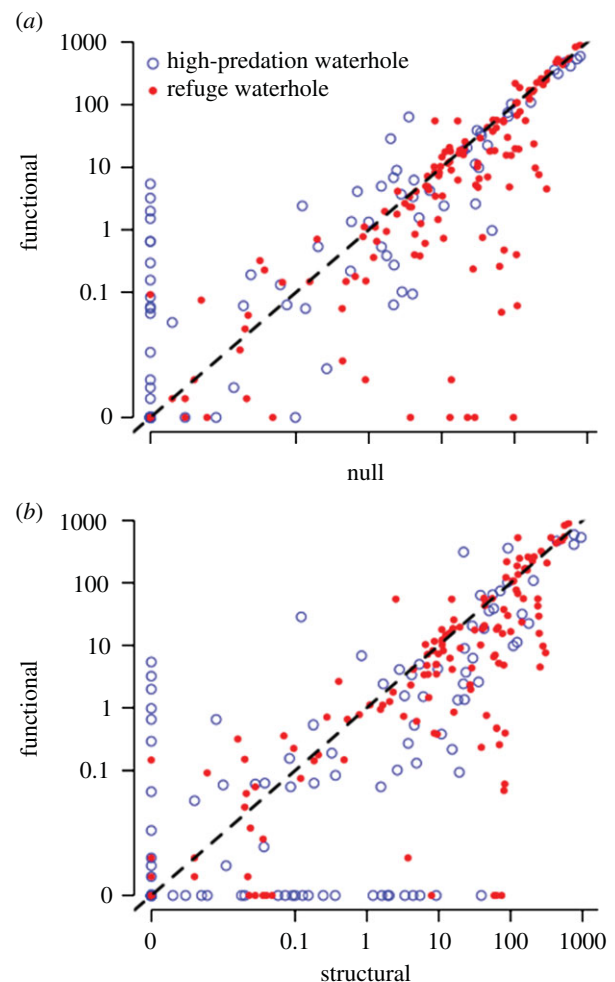

Figure 2. The influence of functional connectivity on local expected minimum abundance ($\log_{10}$ scale) in populations subject to high (high-predation waterhole) and low (refuge waterhole) levels of predation. Plots compare results from simulations with functional connectivity to those without (top) and with (bottom) structural connectivity.

4. Discussion

By coupling individual-based and niche-population models, we show that estimates of extinction risk and local range movement are sensitive to alternative characterizations of landscape connectivity. Accounting for the interaction between animal behaviour and landscape structure (functional connectivity) in model simulations for *C. rugosa* results in elevated local population-level extinction risk and slower rates of local range contraction. Projected shifts in turtle abundance and range margins derived from the null (distance-based dispersal) and structural connectivity models (dispersal affected by land cover characteristics as well as inter-patch distance) were more similar to each other than to results obtained from the functional connectivity model. These results suggest that: (i) functional connectivity should be considered in models of species' range dynamics when the behaviour of the dispersing organism is affected by landscape structural elements and processes; and (ii) high rates of extirpation of populations along a trailing range boundary can occur without causing extensive range movement, despite resulting in substantial declines in population abundance and occupancy.

The influence of landscape connectivity on plant and animal movement is a vital component of metapopulation ecology,

Table 1. Range movement and extinction risk according to three contrasting methods of modelling connectivity. Expected minimum abundance as a proportion of initial population size (EMA), number of subpopulations in the metapopulation (metapop size), movement of the southern range boundary in a northerly direction, and percentage of high-predation (predation) and low predation (refuge) populations remaining in savannah and floodplain habitats in 2050 and 2100 according to three connectivity scenarios: null, structural and functional (see Material and methods for details).

year	connectivity scenario	EMA	metapop size	movement (km)	high-predation savannah (%)	high-predation floodplain (%)	refuge savannah (%)	refuge 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

influencing fundamental processes such as population dynamics and evolution [18]. However, the simplifying assumptions commonly used for modelling connectivity in metapopulation models and ecological network analysis are likely to bias forecasts of population persistence [19] and range movement. During the wet season, *C. rugosa* move to the shallows to feed at the expanding margins of waterholes. This feeding behaviour results in increased contact with streams, allowing turtles to more easily disperse to geographically distant and isolated waterholes. Simulations that included this behaviour resulted in slower rates of range contraction owing to pig predation and an increased mean frequency of dispersal into populations experiencing high predation rates (demographic sinks), resulting in lower densities in refuge populations (demographic sources). This suggests a more general result—that failing to consider important functional connectivity in models of range dynamics is likely to underestimate extinction risk and overestimate range shifts for species such as *C. rugosa* that interact with landscape features such as dispersal corridors (natural or artificial).

Our spatio-temporally complex wetland system is well suited for examining the importance of functional and structural connectivity. The preferred habitat of *C. rugosa*—ephemeral wetlands that occasionally or regularly dry—provides a gradient in resource quality that varies through both space and time. While our results suggest that many demographic-based forecasts of range movement and extinction risk will be improved by including functional connectivity, it is likely that biases in model forecasts for some species can be addressed adequately without the need for behaviourally explicit individual-based models. For example, previous niche-population model predictions for marine species with free-swimming larval stages [5] almost certainly would be improved by simulating dispersal as a passive process driven principally by oceanic currents.

Using spatially explicit demographic models with functional connectivity, we have confirmed that present-day estimates of turtle predation by pigs [14,16] are so high that the extirpation of many *C. rugosa* populations is very likely in the near term, particularly in waterholes embedded within savannah landscapes. Our results for floodplain turtle populations are likely to underestimate extinction risk, because we did not account for future sea-level rise, which is likely to result in severe regional habitat loss [20], further threatening the persistence of *C. rugosa*.

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