Separating the influences of environment and species interactions on patterns of distribution and abundance: competition between large herbivores

Euan G. Ritchie[1]*, Jennifer K. Martin[1,2], Christopher N. Johnson[1] and Barry J. Fox[3]

[1]*School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia;* [2]*Department of Zoology, University of Melbourne, Vic. 3010, Australia; and* [3]*School of Biological, Earth & Environmental Science, University of New South Wales, Sydney, NSW 2052, Australia*

Summary

1. Much recent research has focused on the use of species distribution models to explore the influence(s) of environment (predominantly climate) on species' distributions. A weakness of this approach is that it typically does not consider effects of biotic interactions, including competition, on species' distributions.

2. Here we identify and quantify the contribution of environmental factors relative to biotic factors (interspecific competition) to the distribution and abundance of three large, wide-ranging herbivores, the antilopine wallaroo (*Macropus antilopinus*), common wallaroo (*Macropus robustus*) and eastern grey kangaroo (*Macropus giganteus*), across an extensive zone of sympatry in tropical northern Australia.

3. To assess the importance of competition relative to habitat features, we constructed models of abundance for each species incorporating habitat only and habitat + the abundance of the other species, and compared their respective likelihoods using Akaike's information criterion. We further assessed the importance of variables predicting abundance across models for each species.

4. The best-supported models of antilopine wallaroo and eastern grey kangaroo abundance included both habitat and the abundance of the other species, providing evidence of interspecific competition. Contrastingly, models of common wallaroo abundance were largely influenced by climate and not the abundance of other species. The abundance of antilopine wallaroos was most influenced by water availability, eastern grey kangaroo abundance and the frequency of late season fires. The abundance of eastern grey kangaroos was most influenced by aspects of climate, antilopine wallaroo abundance and a measure of cattle abundance.

5. Our study demonstrates that where census and habitat data are available, it is possible to reveal species' interactions (and measure their relative strength and direction) between large, mobile and/ or widely-distributed species for which competition is difficult to demonstrate experimentally. This allows discrimination of the influences of environmental factors and species interactions on species' distributions, and should therefore improve the predictive power of species distribution models.

Key-words: climate change, distribution, habitat preference, interspecific interaction, niche

Introduction

In response to the pressures of global climate change and habitat loss, there has been increasing interest in quantitative studies of factors predicting the distribution and abundance of species (Peterson 2001; Hughes 2003; Rondinini, Stuart & Boitani 2005; Sagarin, Gaines & Gaylord 2006). Much of this work has taken the form of species distribution models (SDM) that explore the relationships between species presence data and environmental variables (typically climate). While this approach is powerful, it does not adequately consider biotic interactions that may affect observed patterns (see Araujo & Luoto 2007). SDMs constructed solely on environmental data reflect a species' fundamental niche rather than its realized niche and actual distribution as shaped by biotic interactions such as competition and predation (Hutchinson 1978). Attempts to preserve biodiversity that do not take this distinction into account may overestimate the total area available to species (Preston *et al.* 2008).

*Correspondence author. E-mail: euan.ritchie@jcu.edu.au

Competition can have significant effects on distribution and abundance of species as well as influencing community structure (Connell 1983; Schoener 1983; Fox 1987, 1999; Dickman 1988; Fox & Brown 1993; Kelt, Taper & Meserve 1995; Anderson, Peterson & Gomez-Laverde 2002). It should therefore be included in attempts to understand factors determining species' distributions. However, competition between species (interspecific competition) is notoriously difficult to measure experimentally, particularly for larger-bodied and/or wide-ranging species.

Ecologists have long sought to resolve this problem using statistical techniques to estimate values for interaction coefficients from census data combined with habitat variables. Difficulties with MacArthur & Levins' (1967) method of estimating interspecific interaction coefficients led to the development of the regression techniques of Schoener (1974) and Crowell & Pimm (1976). In this method, stepwise multiple regression was used to build models describing habitat effects on abundance, before the effects of other species were tested by adding them to the habitat model (Hallett & Pimm 1979). The simplicity of the method made it attractive, particularly for multispecies analyses (Hallett 1982). However, Rosenzweig, Abramsky & Brand (1984) and Rosenzweig *et al.* (1985) maintained that any detectable effects may be an artefact of the variance, with rare species having strong effects on common species while common species have weak effects on rare species, and that there was a lack of experimental support for the method. These criticisms caused the technique to fall into disfavour, despite a strong defence from Pimm (1985).

Fox & Luo (1996) demonstrated the existence of the statistical artefact that Rosenzweig *et al.* (1985) had warned of, but showed that it could be removed if species' abundances were standardized using a normal standardization (zero mean and variance of one). They developed a revised standardized regression technique to estimate competition coefficients, and then validated it using field removal experiments (Higgs & Fox, 1993; Thompson & Fox, 1993) of rodents. Fox & Luo (1996) also showed that using principal component analyses (PCA) to reduce the dimensionality of habitat variables gave better results than the use of non-PCA techniques with habitat variables only.

A large-scale study on the ecology of large herbivores conducted across the tropical savannas of northern Australia (Ritchie *et al.* 2008) detected a non-random (negative) association between two congeneric macropodid species (family Macropodidae), the antilopine wallaroo (*Macropus antilopinus*) and eastern grey kangaroo (*Macropus giganteus*). The antilopine wallaroo is endemic to tropical northern Australia, whereas the eastern grey kangaroo has an extensive distribution along Australia's eastern coast and inland regions, including the island state of Tasmania (see Ritchie *et al.* 2008). The eastern grey kangaroo may be expanding its range northward in the tropics (Ritchie 2005), bringing it into increased contact with the antilopine wallaroo. Both species are grazers, which overlap in their macrohabitat preferences and have similar social behaviour (Dawson 1995; Fossan 2005; Ritchie 2008; Ritchie *et al.* 2008). Another species, the common wallaroo (*Macropus robustus*) is also sympatric with antilopine

wallaroos and eastern grey kangaroos in large parts of its distribution, but did not show a non-random association with either species in the study of Ritchie *et al.* (2008). The common wallaroo, in comparison to the other two species, is a generalist herbivore (eating both grass and shrubs), usually occupies rockier habitats and has different social behaviour (essentially solitary, versus gregarious for the other species) (Dawson 1995). These factors provide an opportunity to study interspecific competition in large, free-ranging herbivores, and more broadly, to compare biotic versus environmental influences on species distribution and abundance.

We present an analysis which seeks to assess the potential for competitive interactions between antilopine wallaroos, common wallaroos and eastern grey kangaroos, across a 225 000-km^2 zone of sympatry in tropical North Queensland, Australia. We used standardized habitat and abundance data and the information theoretic approach (ITA; Burnham & Anderson 2002) to construct models of herbivore abundance, and compared support for models constructed using habitat variables only and those using both habitat variables and the abundance of the other species. We then used these models to derive estimates and assess the competitive influence of each species on the other. We chose this technique in preference to stepwise model selection (detailed above) due to statistical concerns about the reliability of the latter (see Methods section).

Our aims were to compare the effects of habitat versus species interactions in influencing the abundance of each species, and to quantify the direction and intensity of competition between them. We predict that the best supported models of antilopine wallaroo and eastern grey kangaroo abundance will include the abundance of each species, reflecting the likelihood of competition between the two species as suggested in Ritchie *et al.* (2008). Due to differences in diet, microhabitat preference and social behaviour, we do not expect models of common wallaroo abundance to be influenced strongly (negatively) by either antilopine wallaroos or eastern grey kangaroos.

Materials and methods

STUDY REGION

Our study was conducted at 27 sites in North Queensland, Australia (Fig. 1). The majority of this region is in the monsoonal dry tropics, with most rainfall occurring in the summer months of December to March followed by an extended dry season with little to no rainfall. The vegetation is generally tropical savanna, but varies from tall open forest to woodland and scattered woodlands, all with a grassy understorey (Williams *et al.* 2005; Woinarski *et al.* 2005). The antilopine wallaroo, common wallaroo and eastern grey kangaroo are sympatric in all of these habitats and there are no evident differences in their detectability (Ritchie *et al.* 2008).

DATA COLLECTION AND STATISTICAL ANALYSES

Habitat, abundance data and field methods are fully described in Ritchie *et al.* (2008). Statistical analysis followed the methods established by Fox & Luo (1996) in their re-examination of the regression
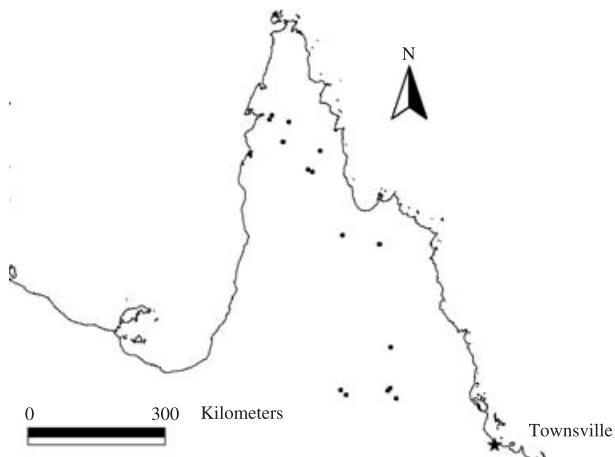
Fig. 1. Map of North Queensland, Australia showing the location of study sites (solid dots).

techniques for estimating competition coefficients. We also followed Luo, Monamy & Fox (1998) in excluding sites that had zero abundance values for all species, which applied to two sites from Ritchie *et al.* (2008), leaving a total of 27 sites at which at least one species was present.

We applied a normal standardization to abundance data for each species, (i.e. giving zero mean and variance of one). The use of such standardized values for species abundances removed any effect of the significant negative relationship between variance and estimated competition coefficients found by Fox & Luo (1996). Because of the large number of habitat variables measured, factor analysis on related variables was performed using PCA. Four separate PCAs were performed on (i) climatic variables, (ii) vegetation structure variables, (iii) grass variables, and (iv) substratum variables. Each of the principal components by definition has zero mean and variance one. Seven additional variables were included for the analyses representing: (i) an index of cattle abundance; (ii) the total number of permanent water bodies; (iii) the number of artificial permanent water bodies; (iv) the number of natural permanent water bodies; (v) the number of late season (hot) fires; (vi) the number of early season (cool) fires; and (vii) the total number of fires (see Ritchie *et al.* 2008 for details). These variables were also standardized to ensure effect sizes between modelled variables were directly comparable.

Generalized linear models of macropodid abundance [compared using Akaike's information criterion (AIC)] were constructed with the normal standardized abundance census for each species. AIC is a measure of the goodness-of-fit of an estimated statistical model which simultaneously accounts for its precision against its complexity (Burnham & Anderson 2002). We used an ITA and constructed all possible configurations of habitat variables and the abundance of each species (best subsets). As a conservative precaution, we included only PCA axes with variances (eigenvalues) greater than one in the model sets, as axes with values less than one generally contribute little and often spurious information due to problems of overfitting (see Quinn & Keough 2002). We chose an ITA over a stepwise approach, as stepwise selection suffers from bias in parameter estimation, inconsistent model selection algorithms, multiple hypothesis testing, and the inappropriate focus on a single 'best' model (Whittingham *et al.* 2006). In contrast, the ITA allows the identification of competing models that could describe the data equally well, thereby acknowledging that ecological inference should not be restricted to one model only. We compared the support for models using differences in their AIC scores (Burnham & Anderson 2002), as well as calculating Akaike model weights (w_i), the weight of evidence in favour of model i being truth given that truth is represented in the model set (Link & Barker 2006). These Akaike model weights were then used to compare evidence ratios between models. The competition coefficient of antilopine wallaroos on eastern grey kangaroos (α_{GA}) and the competition coefficient of eastern grey kangaroos on antilopine wallaroos (α_{AG}) were estimated as the standardized coefficient estimates for each appropriate variable, based on the standardized abundance census data.

Results

MACROPOD ABUNDANCE AND OCCURRENCE

Antilopine wallaroos occurred at an average abundance of 2·1 (± 0·5) animals per square kilometre, and at 19 of the 27 (70%) sites. In comparison, common wallaroos occurred at an average abundance of 0·6 (± 0·2) animals per square kilometre and at 15 sites (56%), and eastern grey kangaroos occurred at an average abundance of 0·4 (± 0·2) animals per square kilometre, and only at 11 sites (41%) (Fig. 2).
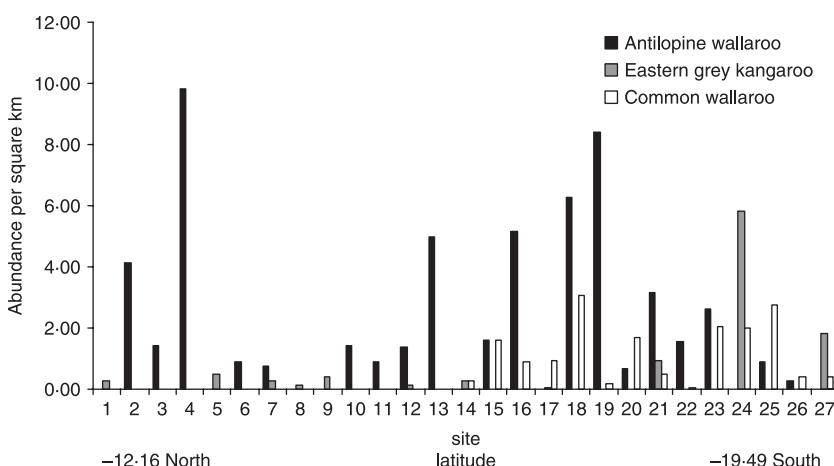

Fig. 2. Abundance of antilopine wallaroos, common wallaroos and eastern grey kangaroos in North Queensland. Abundance is shown for sites furthest to the north (left) to furthest to the south (right).

Table 1. Principal components (rotated varimax) of climate in North Queensland

Climate variable	PCA Clim 1	PCA Clim 2
Annual mean temperature	0·63	**0·75**
Maximum temperature, hottest period	−0·24	**0·94**
Minimum temperature, coldest period	**0·95**	0·23
Temperature range	**−0·95**	0·22
Temperature, wettest quarter	0·20	**0·95**
Temperature, driest quarter	**0·80**	0·50
Annual precipitation	**1·00**	0·04
Precipitation, wettest period	**0·99**	0·09
Precipitation seasonality	0·11	**0·70**
Precipitation, wettest quarter	**0·99**	0·12
Variance	5·89	3·23
Variation percentage	58·88	32·32
Cumulative variation percentage	58·88	91·20

Values in bold represent factor loadings contributing the most to each axis.

Table 2. Principal components (rotated varimax) of vegetation structure in North Queensland

Structure variables	PCA structure 1	PCA structure 2	PCA structure 3
Canopy height	−0·27	**0·57**	−0·23
Canopy cover	−0·20	**0·95**	0·03
Tree circumference	0·13	0·01	**−0·99**
Canopy coverage > 5 m	**−0·58**	0·28	0·09
Canopy coverage 2–5 m	**−0·85**	0·12	0·12
Canopy coverage 1–2 m	**−0·92**	0·24	0·12
Variance	2·05	1·37	1·06
Variation percentage	34·09	22·85	17·69
Cumulative variation percentage	34·09	56·94	74·62

Values in bold represent factor loadings contributing the most to each axis.

PRINCIPAL COMPONENTS OF ENVIRONMENTAL VARIABLES

Climate variables were reduced to two factors (PCA clim 1 and PCA clim 2), which explained 91% of the variation in climate data (Table 1). PCA clim 1 described increased precipitation, higher temperatures of the coolest period and driest quarter, and a reduced temperature range. PCA clim 2 described higher overall temperatures, including during the hottest period and wettest quarter, and greater precipitation seasonality.

Vegetation structure variables were reduced to three factors (PCA structure 1, PCA structure 2 and PCA structure 3), explaining 75% of the variation (Table 2). PCA structure 1 described reduced cover of the understorey, PCA structure 2 described an increase in canopy height and cover and PCA structure 3 described habitat with smaller trees. Grass layer variables were reduced to three factors (PCA grass 1, PCA

Table 3. Principal components (rotated varimax) of the grass layer in North Queensland

Grass layer variable	PCA grass 1	PCA grass 2	PCA grass 3
Percent cover, 0-1m	0·36	−0·24	−0·07
Clump height	**0·85**	0·15	0·07
Greenness	0·18	0·28	0·06
Seeding	0·05	0·12	**0·99**
Biomass	0·43	−0·10	0·18
Percentage grass	−0·06	**−0·97**	−0·08
Percentage nongrass	0·04	**0·98**	0·08
Variance	1·09	2·09	1·03
Variation percentage	15·53	29·84	14·71
Cumulative variation percentage	15·53	45·37	60·09

Values in bold represent factor loadings contributing the most to each axis.

Table 4. Principal components of the substratum in North Queensland

Substratum variable	PCA subs 1	PCA subs 2
Boulders	0·45	0·40
Rocks	**0·68**	−0·16
Pebbles	0·38	**0·59**
Sand	−0·43	**0·68**
Eigenvalue	1·68	1·22
Variation percentage	41·98	30·50
Cumulative variation percentage	41·98	72·49

Values in bold represent factor loadings contributing the most to each axis.

grass 2 and PCA grass 3), explaining 60% of the variation (Table 3). PCA grass 1 described increased height of grass, PCA grass 2 described an increase in the percentage of non-grass and subsequent decrease in the percentage of grass in the grass layer and PCA grass 3 described an increase in the amount of grass that is seeding. Substratum variables were reduced to two factors (PCA subs 1 and PCA subs 2), explaining 72% of the variation (Table 4). PCA subs 1 described increased rockiness and PCA subs 2 described increased pebbles and sand.

Abundance models

ANTILOPINE WALLAROO

Nine models of antilopine wallaroo abundance had considerable support ($\Delta_i < 2$), with little difference in the evidence ratios between models (the relative evidence for model 1 being truth was only 2·7 times more likely than model 9; Table 5). Therefore, there is a great deal of variation in which model best describes antilopine wallaroo abundance from sample to sample. Sixty per cent of models contained the abundance of eastern grey kangaroos but no models contained the abundance of common wallaroos. In order of most importance (w_i), the

Table 5. Generalized linear models of herbivore abundance using best subsets (AIC) for (A) Antilopine wallaroo, (B) Common wallaroo, (C) Eastern grey kangaroo

Model					AIC	Δ_i	w_i
(a)	**Antilopine wallaroo**	**Deviance 6·74**					
1	Eastern grey kangaroo	Water 1	Late season fire		54·71	0·00	0·19
2	Eastern grey kangaroo	Water 1	Late season fire	PCA grass 2	55·44	0·73	0·13
3	Water 1	Late season fire			55·92	1·21	0·11
4	Water 1	Late season fire	PCA grass 2		56·07	1·36	0·10
5	Eastern grey kangaroo	Water 1			56·12	1·41	0·10
6	Water 1				56·37	1·66	0·08
7	Eastern grey kangaroo	Water 1	Late season fire	PCA structure 3	56·53	1·82	0·08
8	Water 1	PCA grass 2			56·64	1·93	0·07
9	Eastern grey kangaroo	Water 1	Late season fire	PCA structure 1	56·69	1·98	0·07
10	Eastern grey kangaroo	Water 1	PCA grass 2		56·89	2·18	0·07
(b)	**Common wallaroo**	**Deviance 2.2**					
1	PCA clim 1				36·65	0·00	0·16
2	PCA clim 1	Cow			37·36	0·71	0·11
3	PCA clim 1	PCA subs 2			37·60	0·95	0·10
4	PCA clim 1	PCA subs 1			37·67	1·03	0·10
5	PCA clim 1	PCA grass 1			37·81	1·16	0·09
6	PCA clim 1	Water 3			38·07	1·42	0·08
7	PCA clim 1	Cow	Eastern grey kangaroo		38·43	1·78	0·07
8	PCA clim 1	Cow	Water 3		38·57	1·92	0·06
9	Cow	PCA subs 1	Eastern grey kangaroo		38·61	1·96	0·06
10	PCA clim 1	PCA structure 2			38·61	1·96	0·06
11	PCA clim 1	Eastern grey kangaroo			38·64	1·99	0·06
12	PCA clim 1	Cow	PCA subs 1		38·78	2·13	0·06
(c)	**Eastern grey kangaroo**	**Deviance 2.14**					
1	Antilopine wallaroo	Cow	PCA clim 2		30·35	0·00	0·12
2	Antilopine wallaroo	PCA clim 2			30·69	0·34	0·10
3	PCA clim 2				31·47	1·12	0·07
4	Cow	PCA clim 2			31·49	1·14	0·07
5	Antilopine wallaroo	Cow	PCA subs 2		31·53	1·18	0·06
6	Antilopine wallaroo	Cow	PCA clim 2	PCA subs 2	31·59	1·24	0·06
7	Antilopine wallaroo	PCA clim 2	PCA subs 2		31·69	1·34	0·06
8	Antilopine wallaroo	Cow	PCA clim 2	PCA structure 3	31·80	1·45	0·06
9	Antilopine wallaroo	Cow	PCA clim 2	Common wallaroo	31·82	1·47	0·06
10	Antilopine wallaroo	Cow	PCA clim 2	PCA grass 1	32·12	1·77	0·05
11	Antilopine wallaroo	PCA clim 2		Fire frequency	32·19	1·84	0·05
12	Antilopine wallaroo	Cow	PCA structure 3		32·27	1·92	0·04
13	Cow	PCA clim 2	PCA grass 1		32·27	1·92	0·04
14	Antilopine wallaroo	Cow	PCA clim 2	Water 2	32·30	1·95	0·04
15	Antilopine wallaroo	Cow	PCA clim 2	Fire frequency	32·34	1·99	0·04
16	Antilopine wallaroo	Cow	PCA clim 2	PCA structure 2	32·35	2·00	0·04
17	Cow	PCA clim 2	PCA structure 3		32·36	2·01	0·04

Only models with considerable support ($\sim\Delta_i \leq 2$) are shown. PCA = principle component axis (refer to tables in text for abbreviations not explained). Water 1 = permanent water (total), water 2 = permanent water (artificial), water 3 = permanent water (natural). AIC = model score, models with smaller scores have more support than models with larger scores. Δ_i = model score differences, 0 has most support; values between 0 and 2 have substantial support; values greater than 2 have considerably less support. w_i = Akaike model weights, which is the weight of evidence in favour of model *i* being truth given that truth is represented in the model set.

variables affecting antilopine wallaroo abundance were total permanent water, the frequency of late season (hot) fires and the abundance of eastern grey kangaroos (Table 6). Three other habitat variables contributed to abundance models but were much less important ($w_i < 0·4$).

COMMON WALLAROO

Similar to antilopine wallaroos, there were a number of models of common wallaroo abundance that had considerable support ($\Delta_i < 2$), with little difference in the evidence ratios (< 3) between models 1 and 11 (Table 5). None of the models with most support included antilopine wallaroo abundance and less than 30% contained abundance of eastern grey kangaroos. In addition, in relation to other variables, the evidence for an effect of eastern grey kangaroo abundance on common wallaroos was weak (Table 6). Instead, climate (PCA clim 1) was the single most important variable influencing common wallaroo abundance.

EASTERN GREY KANGAROO

Similar to the other two species, there were many models explaining variation in the abundance of eastern grey kangaroos

Table 6. Relative importance (weighted) of variables predicting herbivore abundance

Antilopine wallaroo	w_i	Estimated coefficient	Eastern grey kangaroo	w_i	Estimated coefficient	Common wallaroo	w_i	Estimated coefficient
Intercept		−0·12	Intercept		−2·23	Intercept		−2·44
Water 1	**1·00**	**0·55**	**PCA clim 2**	**0·89**	**−0·54**	**PCA clim 1**	**0·94**	**−0·86**
Late season fire	**0·68**	**0·38**	**Antilopine wallaroo**	**0·78**	**−0·55**	Cow	0·36	1·03
Eastern grey kangaroo	**0·64**	**−1·39**	**Cow**	**0·73**	**−0·60**	PCA subs 1	0·21	0·35
PCA grass 2	0·37	−0·28	PCA subs 2	0·19	−0·65	Eastern grey kangaroo	0·19	1·67
PCA structure 3	0·08	−0·10	PCA structure 3	0·14	−0·07	Water 3	0·14	0·31
PCA structure 1	0·07	0·03	Fire frequency	0·09	−0·05	PCA subs 2	0·10	0·41
			PCA grass 1	0·09	−0·29	PCA grass 1	0·09	0·26
			Common wallaroo	0·06	0·18	PCA structure 2	0·06	−0·42
			Water 2	0·04	−0·80			
			PCA structure 2	0·04	0·25			

Estimated relative importance (w_i) was calculated by summing w_i across all models in which variables occurred (increasing values signify increasing importance up to a maximum of 1). The estimated value for the standardized coefficient of each standardized variable included in the models are also shown, including what is interpreted as the competition coefficients for each species. Variables with w_i greater than 0·5 are shown in bold.

(Table 5). In addition, there were more potential explanatory variables (habitat) in the best subsets with considerable support. A large number (76%) of models contained the abundance of antilopine wallaroos, which along with climate (PCA clim 2) and cattle density, were among the most important predictor variables (Table 6). The abundance of common wallaroos (a positive effect) appeared in only one of the top 16 models (Table 5).

ESTIMATED COMPETITION COEFFICIENTS

The competition coefficient of antilopine wallaroos on eastern grey kangaroos (α_{GA}) was −0·55 while the competition coefficient of eastern grey kangaroos on antilopine wallaroos (α_{AG}) was −1·39 (Table 6). Although this large difference (~150%) in estimates may be indicative of asymmetry in interspecific competition between these two species, the relative importance of each species' abundance on the other was found to be roughly equivalent across models according to w_i values (Table 6).

Discussion

Species' habitat preferences and interspecies interactions are strongly linked, and both affect species' distributions and community structure (Araujo & Luoto 2007). Our results provide evidence of how competition, together with aspects of the environment, may influence the distribution and abundance of two sympatric, large herbivores. Interspecific competition has previously been suggested as a possible cause of contemporary patterns of co-occurrence among large mammalian herbivores (Young, Palmer & Gadd 2005; Wegge, Shrestha & Moe 2006), but because of the difficulties of demonstrating competition between large and wide-ranging species, its importance is unknown for the majority of species. To our knowledge, this is the first study to explore competition between large macropodids, a diverse, ecologically and evolutionary significant group of grazing marsupials, at a large scale and with detailed environmental information. Our study is not experimental, but our statistical technique, which substituted a generalized linear model (AIC) for stepwise multiple regression, is a modification of that by Fox & Luo (1996) and Luo *et al.* (1998), which was validated by reciprocal removal experiments (Higgs & Fox 1993; Thompson & Fox 1993; Fox & Luo 1996). Hence, we were able to quantify and isolate the contributions of environment versus competition, in influencing variation in herbivore abundance.

Consistent with predictions, our results suggest that competition occurs between antilopine wallaroos and eastern grey kangaroos (two ecologically similar species) and reduces each species' respective abundance. Contrastingly, there was no evidence that another ecologically dissimilar congener, the common wallaroo, is either negatively affected or affects the abundance of the other species. A positive association between eastern grey kangaroos and common wallaroos was a surprising result and requires further investigation; however, its overall importance in relation to other factors may be questionable (Table 6). By one statistical measure, the strength of competition between antilopine wallaroos and eastern grey kangaroos appears asymmetrical, possibly suggesting that eastern grey kangaroos (which are up to 67% heavier and 92% larger than antilopine wallaroos, Van Dyck & Strahan 2008) may have a stronger negative effect on antilopine wallaroos than the reverse (Dickman 1988). However, by assessing the relative importance of variables across models, the abundance of each species on the other species' abundance was roughly equal. This demonstrates the benefit of an ITA in assessing variation in the importance of variables among competing models rather than ecological inference based on a single 'best model'. Shenbrot & Krasnov (2002) have shown that interspecific competition detected by the regression technique is most likely to be interference competition rather than

exploitation competition. Further research is required to determine if interference – rather than exploitation – competition is the nature of the interaction between antilopine wallaroos and eastern grey kangaroos. However, it does appear clear that under certain situations, both antilopine wallaroos and eastern grey kangaroos may place limits on each other's distribution and abundance in north-eastern Australia.

In a landmark paper concerning drivers of mammalian patterns of distribution, Caughley *et al.* (1987) suggested that the distribution of large macropodids would most probably reflect their independent responses to climate, rather than the outcomes of species interactions. Our results provide evidence both for and against this assertion. For common wallaroos and eastern grey kangaroos, climate indeed appears to be an important factor affecting their abundance in North Queensland. In our study region, both common wallaroos and eastern grey kangaroos are at the northern limits of their distributions, and their negative associations with climate may suggest possible physiological limitations that reduce their overall abundance with increasing tropical conditions (higher temperatures, annual rainfall and rainfall seasonality; Table 1). In contrast, the antilopine wallaroo's abundance was not influenced by climate at the scale of this study, but see Ritchie *et al.* (2008) for a discussion on the relationship between species' niches and the spatial scale of studies. Counter to Caughley *et al.* (1987), our study suggests that the abundance of both antilopine wallaroos and eastern grey kangaroos was influenced by a reciprocal negative association (competition). Other factors that appear important for antilopine wallaroos are the availability of permanent water and the frequency of late season fires, consistent with previous work (Ritchie *et al.* 2008). Eastern grey kangaroos appear to be more abundant in areas of higher cattle numbers, which may indicate beneficial habitat changes associated with areas that are heavily grazed for cattle.

It is noteworthy that despite the antilopine wallaroo occurring at much higher average densities and being more widespread in the region than the eastern grey kangaroo, it appears to be affected by competition with the eastern grey kangaroo. However, abundance does not necessarily determine competitive ability. Considering a shared-preference model of habitat selection developed by Rosenzweig (1981), both Hallett (1982) and Pimm & Rosenzweig (1981) proposed that competitive ability is determined by specialization in the use of habitat. Under this scenario, common species that are less specialized may have only weak competitive effects on rarer, less abundant species that are more specialized. The two species shared the habitat structure variable PCA structure 3 in common but contrasted in other habitat variables. In particular, the antilopine wallaroo's abundance was influenced strongly by the availability of water. From our results, it would appear that the eastern grey kangaroo's abundance is influenced by a larger suite of habitat features, indicating greater habitat specialization (Pimm & Rosenzweig 1981; Hallett 1982). One possibility is that where eastern grey kangaroos are not significantly adversely affected by climate, local habitat specialization may provide a competitive advantage

over antilopine wallaroos. Contrastingly, where eastern grey kangaroos are already at their limits of climatic suitability, antilopine wallaroos (a species adapted for tropical conditions) may have competitive advantages over eastern grey kangaroos. This provides for interesting future research exploring the possible synergies between biotic and abiotic factors in influencing large herbivore patterns of distribution and abundance at varying scales. Of course, it could also be that other aspects of the environment not measured by this study account for apparent differences in specialization between the two species.

Our study demonstrates that the distribution and abundance of two large herbivores, one common species (the antilopine wallaroo), and one rarer species (the eastern grey kangaroo), appears to be influenced by competition as well as abiotic factors. Our results illustrate the value of the ITA (using standardized abundance and habitat data) for disentangling the effects of abiotic versus biotic effects in understanding patterns of distribution and abundance, and in estimating the strength and direction of competitive interactions. We would therefore advocate its increased use in community studies where experimental methods may not be feasible. In doing so, our understanding of patterns of species distribution and abundance at the macro-scale will be greatly improved (see Heikkinen *et al.* 2007). Furthermore, we will gain a better understanding of how community structure and ecosystem function are likely to change in the future under different biotic and abiotic scenarios (Tylianakis *et al.* 2008). Our findings not only contribute to a greater understanding of the influence of competition on large herbivore community assembly and the limits to distribution and abundance more widely, but have implications for the conservation of the antilopine wallaroo, a species restricted to the tropics. The eastern grey kangaroo is evidently expanding its range into areas occupied by the antilopine wallaroo (Ritchie 2005), which may already be under threat (Ritchie & Bolitho 2008). Any further changes to habitat brought about by increased development of the region and/or climate change could have a negative impact on the antilopine wallaroo and management will need to address this.

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