



## Using cenograms to investigate gaps in mammalian body mass distributions in Australian mammals

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### ABSTRACT

Body size distribution and cenogram analyses both use body weight distributions of mammalian species to describe structural patterns within communities. Using these methods it has been possible to correlate modern mammalian community structure and habitat. In turn these correlations have been used to infer palaeohabitat from analysis of the structure of extinct mammal communities.

We used the cenogram method to construct the body size distribution of both contemporary and pre-European invasion lists of mammal taxa from 52 Australian national parks spanning all major environments. All modern Australian open environments showed a gap in body mass distribution.

Historical open environments showed no distinct gap in body mass distribution but had significantly less medium-sized species than closed environments. Large, introduced mammalian predators have been shown to prefer medium-sized prey over large or small prey and to contribute significantly to the extinction of medium-sized species in open environments.

Our results are consistent with previous studies which have found that mid-sized mammals are more extinction prone, and this has been suggested to be due to introduced cats and foxes, following the European colonization of Australia.

Two methods complementary to cenograms are introduced in this study, which are useful to infer vegetation coverages of fossil localities.

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### 1. Introduction

The term cenogram was first proposed by Valverde (1964, 1967) for a graph displaying the relationships between the size of predators and the size of their prey species in a mammalian community. His cenograms were constructed by plotting rank ordered taxa versus head–body length. Legendre (1986, 1989) adapted this method for palaeoecological studies. This adaptation excluded bats, as per Valverde's method, as well as carnivores. Body sizes were expressed in Log of body mass (g) instead of head–body length. Legendre (1986, 1989) made three visual observations regarding the structure of cenograms and their environments (see Fig. 1):

1. Cenograms of open environments have a gap in the medium-sized species (500–8000 g) whereas closed environments have a continuous distribution.
2. The slope of large species (over 8000 g) is steeper in more arid environments.

3. The slope of small species (under 500 g) is related to minimal temperatures.

Legendre (1986, 1989) recommended the use of these three rules for qualitative comparison between different faunal complexes. In order to formalise the methods outlined by Legendre (1986, 1989), Gingerich (1989) quantified the gaps and the slopes of cenograms.

The cenogram method is one of the most controversial palaeoecological methods in this discipline. A review of this methodology was undertaken by Rodríguez (1999), who showed that the relationships between cenogram patterns and climate are not statistically significant. Rodríguez's (1999) analysis does, however, support the fact that the gap in medium-sized mammals relates to vegetation structure in tropical communities. In a further review, Hernández Fernández et al. (2006) indicate that Rodríguez's (1999) concentrated on a quantitative analysis of the each of the cenogram variables (e.g. gap size, slopes) rather than a qualitative approach. In addition, Hernández Fernández et al. (2006) used a qualitative statistical approach in order to infer biomes using cenogram patterns, comparing the efficiency of cenograms in predicting biomes with four other commonly used ecological variables (taxonomic, trophic, locomotion and body size categories). They concluded that body size categories and cenogram variables were the most accurate for identifying biomes. Gómez Cano et al. (2006) showed that the method remains

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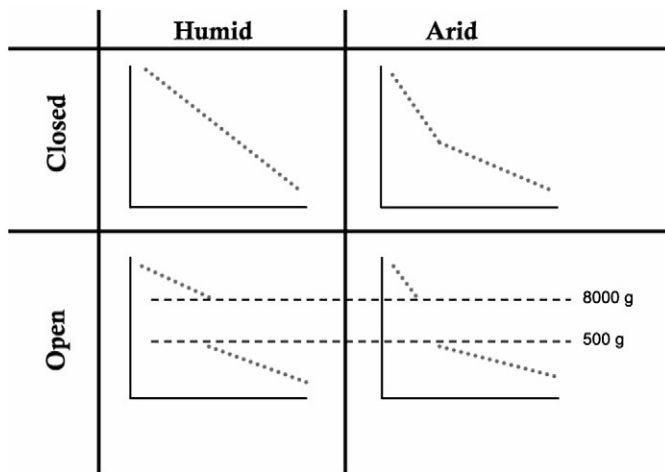


Fig. 1. Cenogram patterns identified by Legendre (1986, 1989).

efficient with a random species loss up to 60–70% in a fossil assemblage.

Body size categories or body size distribution is another commonly used method to describe faunal communities (Holling, 1992). The similarity of these methods with cenograms is obvious, as both rely on the differential distribution of body sizes with respect to biomes. Holling (1992), without knowing the work of Legendre (1986, 1989), found that patterns of gaps and clumps in the body size distribution of mammal and bird communities were correlated with changes in climate and vegetation structure. Interestingly for this study, Holling's (1992) largest gap in distribution data also represented medium-sized animals (sensu Legendre, 1986, 1989). Siemann and Brown (1999) re-examined Holling's (1992) method by testing the gaps in mammalian body size distribution. They compared the magnitudes of gaps in mammalian communities of North America and Australia to randomly generated models and found that the gaps were similar in structurally dissimilar but adjacent biomes that shared similar species. They concluded that the structure of body size distributions reflected taxonomic constraints on body size rather than climate/vegetation constraints. Allen et al.'s (2006) review on patterns in body mass distributions identified five competing hypotheses (including that of Siemann and Brown, 1999) as follows: Energetic, phylogenetic, biogeographical, textural discontinuity and community interaction hypotheses. This review concluded that each hypothesis only partially explained pattern in body mass distribution and that mechanisms underlying those patterns are more likely to be multicausal and vary with scale, perhaps explaining the different patterns found by Legendre (1986, 1989) and Holling (1992) using one dataset and by Rodríguez (1999) and Siemann and Brown (1999) using another.

However, it could be that the differences in conclusion between these authors could be a reflection that the original datasets used were not actually representative of the area from which they were sourced. Limitations should be addressed regarding species lists compilation and identification of vegetation structure, as well as the understanding of interaction between animals and their environment. Neither Rodríguez (1999) nor Siemann and Brown (1999) addressed these issues. As Sand-Jensen (2007) points out, the current trend in scientific writing in biology reduces all species to numbers and statistical elements without considering any interesting biological aspects of adaptation, behavior and evolution. The dataset that Siemann and Brown (1999) used was prior to European settlement for both North America and Australia. In their analysis, Australia was found to have no gaps statistically larger than random. However, since European settlement, 117 species are now listed as extinct, threatened, or vulnerable out of 245 (47% of the fauna) in Australia (Short and Smith, 1994; Anonymous, 1999c). Species most

affected are the medium-sized terrestrial species in the weight range 35 g to 5.5 kg (Australia's critical weight range) (Short and Smith, 1994).

The aim of this paper is to examine patterns in body size distribution in Australian datasets through time and space. In particular, it aims to identify factors producing gaps in the body size distributions and to develop new methodologies to improve on the current ones.

## 2. Methods

### 2.1. Mammal species database

We compiled a database of recent mammalian species lists from 52 national parks (NP) and reserves across Australia (Fig. 2). These parks and reserves were selected to cover all major habitat types in Australia. Mammal species lists were compiled from a number of sources. The Department for Environment and Heritage (DEH) of South Australia provided data from the Biological Database of SA (BDBSA) for Mount Remarkable, Flinders Ranges, Gawler Ranges, Vulkathunha – Gammon Ranges and Witjira NPs. The Department of Sustainability and Environment (DSE) of Victoria provided data for Wyperfeld, Little Desert, Mount Buffalo and Snowy River NPs. Online databases were used to collect data for Millstream–Chichester, Kalbarri and Karijini NPs using Western Australia Museum's FaunaBase (<http://www.museum.wa.gov.au/faunabase/prod/index.htm>), for Mutawintji, Kinchega, Mungo, Gundabooka, Bundjalung, Yuraygir, Deua, Wadbilliga, South East Forest, Abercrombie River, Blue Mountains, Ku-ring-gai Chase and Kosciuszko NPs using the NSW National Parks and Wildlife Services' Wildlife atlas database (<http://wildlifeatlas.nationalparks.nsw.gov.au/wildlifeatlas/watlas.jsp>), and for Mungkan Kandju, Iron Range, Mount Barney, Main Range, Boodjamulla, Simpson Desert, Currawinya, Diamantina and Carnarvon NPs using Queensland Parks and Wildlife Service's Wildlife Online database ([http://www.epa.qld.gov.au/nature\\_conservation/wildlife/wildlife\\_online/](http://www.epa.qld.gov.au/nature_conservation/wildlife/wildlife_online/)).

The faunal list of Lamington NP was taken from its website (<http://lamington.nrsrm.uq.edu.au>). The data from the following parks and reserves is from publications: Fitzgerald River (Chapman, 1995), Prince Regent River Nature Reserve (Miles and Burbidge, 1975), Purnululu (Woinarski et al., 1992), Stirling Range (Herford et al., 1999), Croajingo-long (Anonymous, 1998a), Grampians (McCann, 1985), Yumbera Conservation Park (Owens et al., 1995), Bookmark Biosphere Reserve (Anonymous, 1997), Shoalwater and Corio Bays Area Ramsar Site (Schodde et al., 1992; Anonymous, 1999a), Uluru (Burbidge and McKenzie, 1989; Balding, 2004), Gregory (Anonymous, 2001a), Nitmiluk (Anonymous, 2002a), Kakadu (Anonymous, 1999b), Savage River (Anonymous, 2001b), Ben Lomond (Anonymous, 1998b), Mount Field (Anonymous, 2002b) and Douglas-Apsley NPs (Anonymous, 1993).

Historical data were also collected from the same sources where available (Stirling Range, Karijini, Mutawintji, Uluru, Gundabooka, Kinchega, Wadbilliga, Ku-ring-gai Chase and Kosciuszko NPs). Interpretations from our historical data are limited because only Uluru NP has a pre-European record (Burbidge and McKenzie, 1989). All other historical data dates back to the opening of the National Park. Average body weight for each mammal species is from Strahan (1995).

### 2.2. Environmental data

Environmental data was collected for each national park from diverse sources. Annual Rainfall, Mean Annual Maximum (MAMT) and Minimum (MAMT) Temperature and climate (based on the Koeppen classification) information were taken from the Bureau of Meteorology website (<http://www.bom.gov.au/>). When environmental data was not available for a park, data from the closest meteorological station was used. Vegetation data (Major Vegetation Groups in

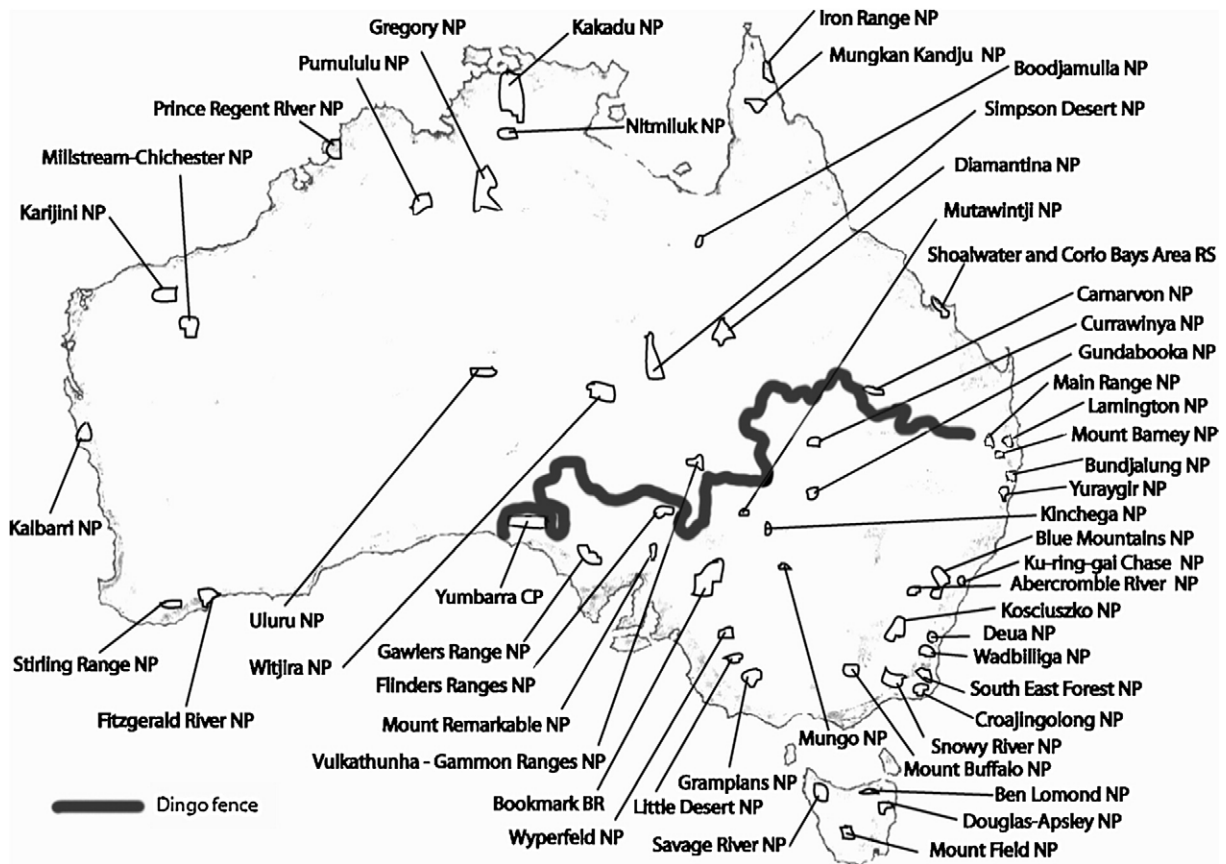


Fig. 2. Map of Australian National Parks and Reserves used in this study. Shapes of park are approximate and sizes of parks are not to scale. The position of the dingo fence is also indicated.

Australia) was taken from the Department of the Environment and Heritage website (<http://www.environment.gov.au/erin/nvis/publications/major-veg-map.html>).

Vegetation data are shown in Table 1 along with our simplified classifications (habitat type). Note that major vegetation groups are different to vegetation types: vegetation groups are much broader categories and include several vegetation types. For example, the vegetation group “eucalypt forests” refers to eucalypt tall open forest, eucalypt open forest and eucalypt low open forest, all of which are open forests. In Table 1, only the name of the broader vegetation groups (such as eucalypt forest) were included (as opposed to listing detailed vegetation types).

In Australia, the vegetation group “closed forests” specifically refer to rainforests, however, the habitat type “closed” has also been used in cenogram methods (Legendre, 1986, 1987) to refer not only to closed forests but also to any type of forests, including open forests. Similarly, in the cenogram method, the habitat type “open” includes the vegetation groups “shrublands”, “grasslands” and “deserts”. “Woodlands”, being an intermediate state between closed and open habitats, have been classified as both closed and open. Because these definitions of habitat types can be ambiguous, we have assigned our own classification. Parks containing major vegetation groups referred to as “rainforest” or “eucalypt forests” were classified as “closed” (equivalent to Legendre’s closed/humid habitat), parks containing “woodlands” were classified as “semi-open” (equivalent to Legendre’s open/humid habitat) and parks containing “shrublands” and “grasslands” were classified as “open” (equivalent to Legendre’s open/arid habitat).

In his study, Rodríguez (1999) also allocated a single habitat type to each National Park used. For example, he classified the Guadalupe Mountains National Park (USA) as a desert, a vegetation group which

is indeed present at the park. However, this park also contains riparian woodlands and mountaintop forests, which support a number of arboreal species such as squirrels and chipmunks (<http://www.nps.gov/gumo>). Therefore, this particular national park exhibits a mix of closed and open habitats. In modern ecology, the dominant vegetation group (in this case desert) is commonly used to describe the overall community of a national park. However, in the cenogram methodology, this way of classifying habitat type may be in fact problematic. Cenograms use presence/absence data of individual species as opposed to abundance data, (the latter usually used in modern ecology). In the case of Guadalupe Mountains National Park, abundance data would show a clear majority of desert species, but with presence/absence data of individual species, both forest and desert types would both be represented. The presence of arboreal species in Guadalupe Mountains National Park, as well as species that are only found in forested areas (e.g., black bears, skunks, porcupines) should therefore be acknowledged, particularly when using cenogram methods. Because the gap in open habitats will be obscured by the overlying closed habitat signature, Guadalupe Mountains National Park would be assigned to a “closed” habitat in a cenogram representation. Therefore, in our study, we classified parks with mixed closed and open vegetation (e.g. Kakadu NP) according to the highest density vegetation group present, e.g. a mix of forest and woodland is classified as “closed”.

### 2.3. Cenograms

We constructed cenograms for each of the parks studied. We follow Legendre’s (1986, 1989) method for the construction of cenograms, excluding bats and carnivorous taxa from the dataset.



**Table 1**

List of major vegetation groups and habitat types for each National park used in this study

Name	Major vegetation groups	Habitat type
Abercrombie River National park	Eucalypt forest	Closed
Ben Lomond National Park	Eucalypt forest and shrublands	Closed
Blue Mountains National Park	Eucalypt forest	Closed
Boodjamulla National Park	Eucalypt woodlands and grasslands	Semi-open
Bookmark Biosphere Reserve	Miscellaneous forests, woodlands and shrublands	Semi-open
Bunjalung National Park	Eucalypt forest	Closed
Camarvon National Park	Eucalypt forest and woodlands	Closed
Croajingolong National Park	Eucalypt forest	Closed
Currawinya National Park	Acacia forests and woodlands	Semi-open
Deua National Park	Eucalypt forest	Closed
Diamantina National Park	Shrublands and grasslands	Open
Douglas-Apsley National Park	Eucalypt forest	Closed
Fitzgerald River National Park	Shrublands	Open
Flinders Ranges National Park	Miscellaneous forests, woodlands and shrublands	Semi-open
Gawler Ranges National Park	Shrublands	Open
Grampians National Park	Eucalypt forest	Closed
Gregory National Park	Eucalypt woodlands	Semi-open
Gundabooka National Park	Miscellaneous forests, woodlands and shrublands	Semi-open
Iron Range National Park	Rainforests	Closed
Kakadu National Park	Eucalypt woodlands, eucalypt forest, rainforest and grasslands	Closed
Kalbarri National Park	Shrublands	Open
Karijini National Park	Shrublands and grasslands	Open
Kincheqa National Park	Miscellaneous forests, woodlands and shrublands	Semi-open
Kosciuszko National Park	Eucalypt forest	Closed
Ku-ring-gai Chase National Park	Eucalypt forest	Closed
Lamington National Park	Rainforests and eucalypt forest	Closed
Little Desert National Park	Eucalypt woodlands and shrublands	Semi-open
Main Range National Park	Rainforests and eucalypt forest	Closed
Millstream–Chichester National Park	Grasslands	Open
Mount Barney National Park	Rainforests and eucalypt forest	Closed
Mount Buffalo National Park	Eucalypt forest	Closed
Mount Field National Park	Eucalypt forest, rainforests and eucalypt woodlands	Closed
Mount Remarkable National Park	Eucalypt forest	Closed
Mungkan Kandju National Park	Eucalypt woodlands and rainforests	Closed
Mungo National Park	Miscellaneous forests, woodlands and shrublands	Semi-open
Mutawintji National Park	Miscellaneous forests, woodlands and shrublands	Semi-open
Nitmiluk National Park	Eucalypt woodlands, eucalypt forest, eucalypt woodlands	Closed
Prince Regent River Nature Reserve	Eucalypt woodlands	Semi-open
Purnululu National Park	Grasslands	Open
Savage River National Park	Rainforests	Closed
Shoalwater and Corio Bays Area Ramsar Site	Eucalypt forest, eucalypt woodlands	Closed
Simpson Desert National Park	Grasslands	Open
Snowy River National Park	Eucalypt forest	Closed
South East Forest National Park	Eucalypt forest	Closed
Stirling Range National Park	Miscellaneous forests	Closed
Uluru National Park	Shrublands and grasslands	Open
Vulkathunha–Gammon Ranges National Park	Shrublands	Open
Wadbilliga National Park	Eucalypt forest	Closed
Witjira National Park	Grasslands	Open
Wyperfeld National Park	Eucalypt woodlands and shrublands	Semi-open
Yumberra Conservation Park	Shrublands	Open
Yuraygir National Park	Eucalypt forest	Closed

We represented all large introduced mammals (those larger than the red kangaroo, *Macropus rufus*, such as cattle, sheep, camels, deer, horses, goats, pigs, donkeys and buffalo) by a different symbol, as their current distribution, reflects introduction by humans. Finally, because it is easier to visualise, we have used  $\log_{10}$  rather than the natural log of average body mass for each species.

Once the cenograms were constructed, we (visually) compared the cenogram shapes of each national park or reserve to the patterns found by Legendre (1986, 1989) (Fig. 1) as well as to known habitat types (Table 1). In order to investigate the relationship between the gap in medium-sized mammals and openness, we plotted the magnitude of the largest gap between two consecutive species within the whole fauna (excluding large introduced mammals, for the reasons mentioned above). These were plotted in log units versus the position of the largest gap within the cenogram, using the mean weight of the two species defining the largest gap in log units. We also compared the total number of mammal species for each habitat type in three different weight ranges: Legendre's (1986, 1989) gap range (500 g to 8000 g); Australia's critical weight range (35 g to 5500 g); and a new range found by our analyses (100 g to 1000 g).

#### 2.4. Arboreal taxa

We assume here that the presence of arboreal taxa in an area indicates the presence of trees. To our knowledge, no research had attempted to correlate the presence of arboreal taxa with habitat type. Defining arboreal taxa is arguably quite difficult. However, certain taxa require the presence of trees for feeding and predator avoidance. In Australia, for example, possums, koalas, tree-kangaroos, some dasyurids (quolls, antechinuses and phascogales) and some rodents can be classified as “arboreal” or “scansorial”. However, dasyurids and rodents are not fully restricted to closed habitats, and are quite capable of surviving in more open habitats (Strahan, 1995). For this reason, we are referring in this study only to possums, koalas and tree-kangaroos as our “arboreal” taxa, although, no tree-kangaroos are present in the data.

We examined the presence of these arboreal taxa (as opposed to all other taxa; referred to herein as non-arboreal) in different body classes graphically, and compared this with habitat type and cenograms.

#### 2.5. Body mass distribution

Cenograms are a type of representation of body mass distribution. However, patterns in cenograms can be difficult to distinguish (e.g. difference in slope between large and small mammals can be hard to see visually). The representation of body mass distributions, following Holling's (1992) method, will allow easier comparisons of body mass patterns when combined with cenograms patterns. Percentages of taxa in 5 body class categories (logarithmic mass in grams of the following ranges: 0–0.99, 1–1.99, 2–2.99, 3–3.99 and 4–4.99) for the mammal fauna (excluding large introduced herbivores) of each national park were represented as bar graphs. Arboreal species were represented separately on these graphs. We also compared the patterns found for each park with the overall pattern of body mass distribution of all non-volant Australian mammals, as well as between historical and modern faunas. Mammalian body mass distributions of New Guinea's closed forest (Flannery, 1995; Bassarova, 2005) were also examined.

#### 2.6. Analysis

Rodríguez (1999) used Kendall's  $\tau$  coefficient to find the probability of correlation between cenograms and environmental variables. The advantage of using Kendall's  $\tau$  is that it does not assume normal distribution of the data. We used Rodríguez (1999)'s method for our data, but modified the variables used. We used climate, major vegetation group (MVG), mean annual maximum temperature (MAMT), mean annual minimum temperature (MAMt), annual rainfall and habitat type (closed, semi-open, open) as our environmental variables. We used the following variables to describe cenogram, body mass distribution and arboreal taxa patterns: magnitude of largest gap; position of largest gap; percentage of taxa in the logarithmic

mass ranges of 0–0.99, 1–1.99, 2–2.99, 3–3.99 and 4–4.99; and percentage of arboreal taxa in the logarithmic mass ranges of 0–0.99, 1–1.99, 2–2.99, and 3–3.99.

### 3. Results

#### 3.1. Cenograms

A set of representative cenograms for the 52 Australian national parks and reserves are represented in Fig. 3. All other cenograms are available in the electronic supplementary material, Figs. A1a–A5. In this figure, cenograms have been arranged according to their habitat type in Fig. 3, with 3A to 3D being closed habitats (rainforest and temperate forest), 3E being semi-open and 3F being open habitats. As expected, most national parks we classified as being closed habitats, represented by Iron Range NP (rainforest) and Snowy River NP (temperate forest) in Figs. 3A and B, had a pattern similar to that habitat represented in Fig. 1 except for the following exceptions.

All the Tasmania national parks, represented by Ben Lomond NP in Fig. 3C (Douglas-Apsley, Mount Field and Savage River NPs) have a gap between log body mass of 2 and 3 (100 to 1000 g). Several other parks arguably have such a gap, represented by Abercrombie NP in Fig. 3D (Kosciuszko, Ku-Ring-Gai Chase, Mount Barney, Mount Buffalo, Mount Remarkable, Wadbilliga NPs). In the case of Abercrombie and Mount Remarkable NPs, there are very few mammal species less than 1000 g (3–4 species), possibly a result of poor surveying of smaller mammals.

Semi-open habitats, represented by Boodjamulla NP (Fig. 3E), were expected to resemble the pattern shown by closed/arid or open/humid cenograms (Fig. 1). No closed/arid patterns were found among Australian cenograms. However, the pattern displayed by Australian parks classified as semi-open habitat was very similar to Legendre's open/humid pattern (Fig. 1). There appears to be little difference between the open/humid and open/arid patterns, but all semi-open habitats display had a distinct gap varying from log body mass of 2 to 3, except for Fitzgerald River NP which showed no distinct gap.

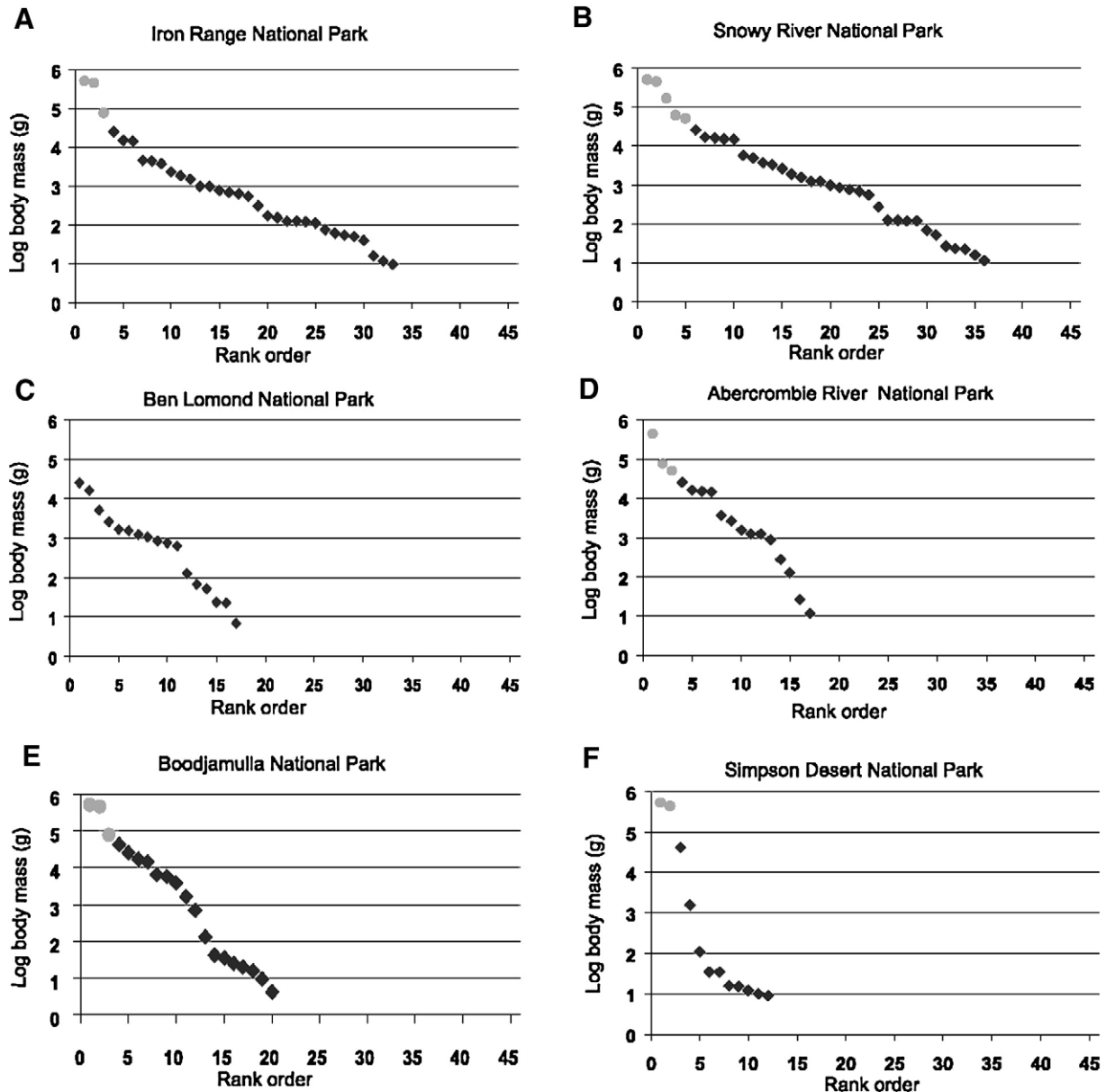


Fig. 3. Cenograms of the mammalian faunas of 6 representative National Parks classified as: A – Rainforest; B, C and D – Temperate forest; E – Woodland; F – Grassland/desert. Light grey circles represent large introduced herbivores; black diamonds represent all other mammal species.

## Historical vs modern

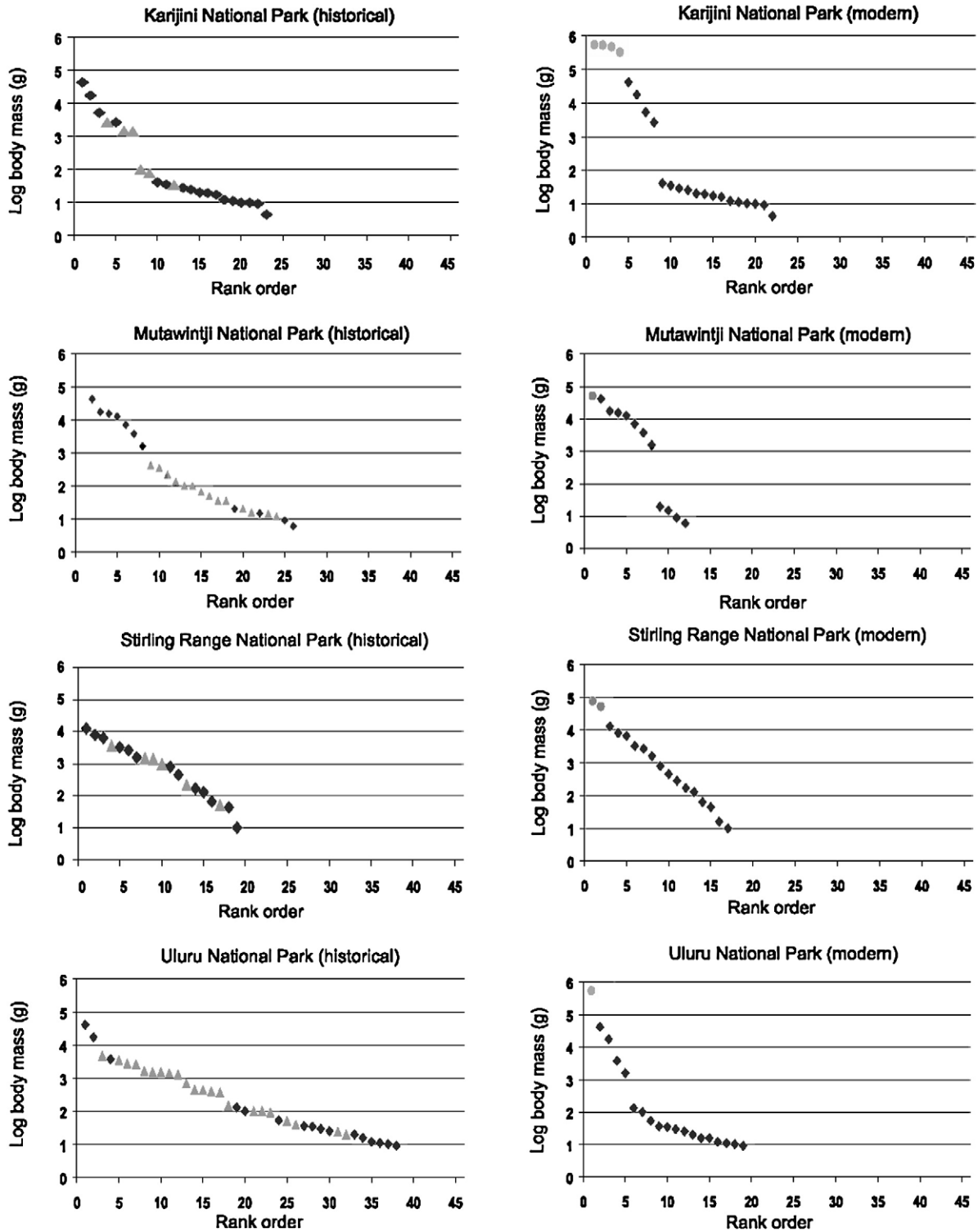


Fig. 4. Modern and historical cenograms of the mammalian faunas of four National Parks. Light grey circles represent large introduced herbivores; light grey triangles represent extinct species; black diamonds represent all other mammal species.

Open habitat patterns, represented by Simpson Desert NP (Fig. 3F), were very similar to Legendre's open/arid patterns (Fig. 1).

Fig. 4 shows cenograms of the historical data for four national parks (Karijini, Mutawintji, Stirling Range and Uluru National Parks) with their modern equivalents. Cenogram patterns for the modern

mammalian faunas of Karijini, Mutawintji, Stirling Range and Uluru NPs show patterns (Fig. 4) expected for their current habitat type (open, semi-open, closed and open respectively; Fig. 1). Historically, however, their patterns were different even though most environmental factors have not changed (i.e. rainfall, climate, major

vegetation group and temperatures can be assumed as homologous to conditions present today). Karijini NP's historical pattern was closer to Legendre (1989)'s open/humid pattern while Mutawintji's and Uluru's historical patterns more closely resembled a closed/humid pattern. The only exception among these is Stirling Range, whose historical pattern, although losing some taxa, still closely resembles the modern pattern.

When a gap occurs in Australian cenograms, it appears to consistently lie between log 2 and 3 (i.e. 100 to 1000 g) sometimes extending to log 1.5 or 3.5 (i.e. 50 to 5000 g). Legendre's (1989) gap was predominantly found between 500 and 8000 g (log 2.5 to 3.8). For each of the Australian national parks and reserves we plotted the magnitude of the largest gap and its position on the cenogram (Fig. 5). This graph clearly demonstrates that the gaps of largest magnitude were almost always features of parks that we classified as open or semi-open habitats, and all were between log 1.5 and 3.5. The majority (all except three) were between log 2 and 3, shifting the gaps in Australian cenograms to lower body masses.

We plotted the total number of species in our three habitat types in three body weight categories (Fig. 6): our new observed Australian cenogram gap (100 to 1000 g); Legendre's (1989) gap (500 to 8000 g); and Australia's critical weight range (35 to 5500 g) identified by Short and Smith (1994). In all three categories, there is significant overlap between semi-open and open habitats, with semi-open habitats having a lower mean number of species than open habitats for the weight ranges 100 to 1000 g and 35 to 5500 g. The lower end of the closed habitats also overlaps with the upper end of both semi-open and open habitats for all body weight ranges. However, the body weight range 100 to 1000 g is the only one that can be described as a true gap, having the lowest mean number of taxa and the closest to zero (with a large number of parks having no taxa in that range).

3.2. Arboreal taxa

For our investigation of the presence of "arboreal" taxa in habitat types (Fig. 7) we included only two body weight ranges, 100 to 1000 g and 1000 to 10,000 g, (these ranges were shown to strongly correlate with habitat types in Kendall's  $\tau$  results, see below), which we will refer herein as medium-sized and large respectively. For closed habitats, all parks contained both medium-sized and large arboreal taxa, except for Stirling Range and Prince Regent River NPs which included only large arboreal taxa. Most semi-open habitats included large but no medium-sized arboreal taxa. The exceptions were Mutawintji, Mungo and Gawlers Range NPS which contained no

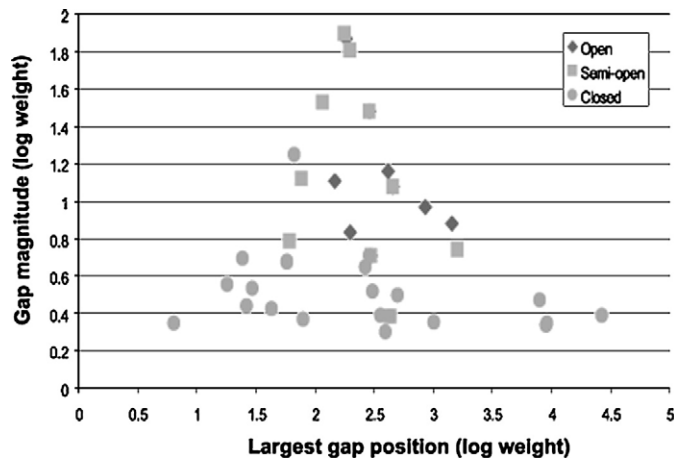


Fig. 5. Plot of the largest gap magnitude versus its relative position on the cenogram for each of the National Parks, divided into the three habitat types, closed, semi-open and open.

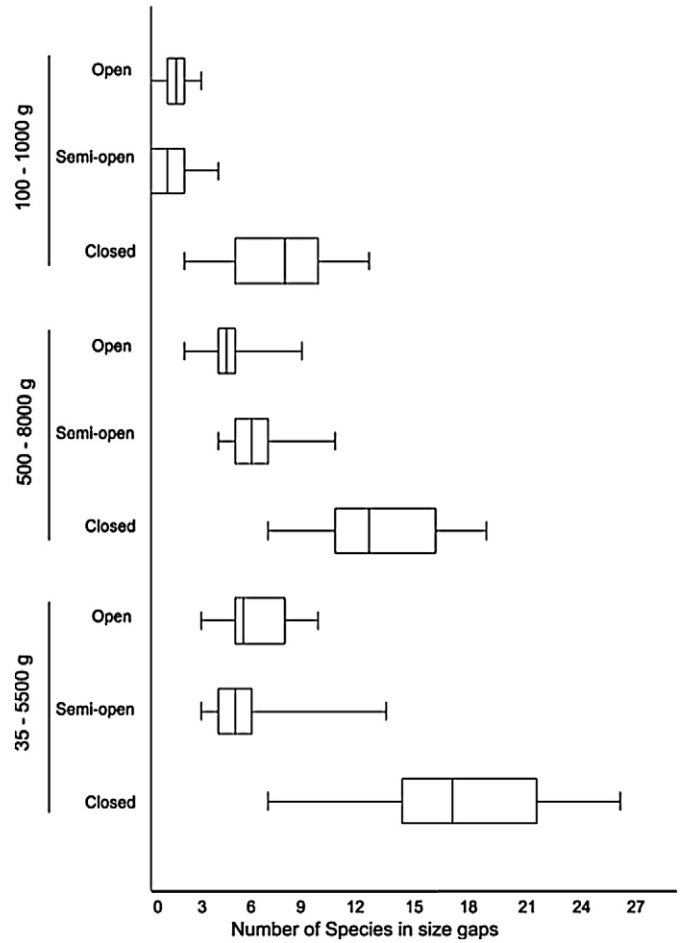


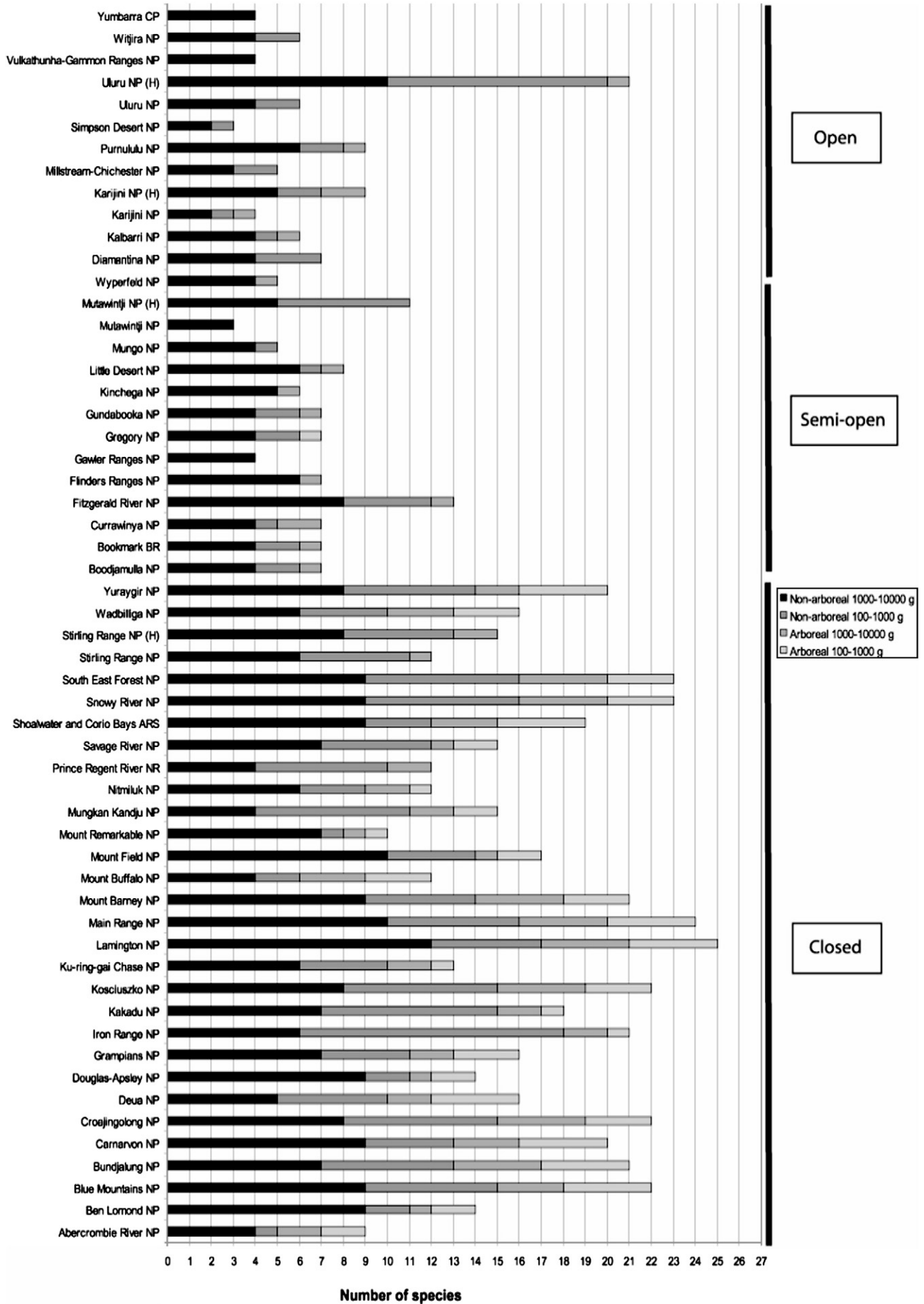
Fig. 6. Box plot of the number of mammal species in the size gaps 100–1000 g, 500–8000 g and 35–5500 g, in each of the three habitat types, closed, semi-open and open.

arboreal taxa, and Gregory NP which had a medium-sized taxon but no large arboreal taxa. Open habitats generally had no arboreal taxa, with the exception of Kalbarri, Karijini (modern and historical), Purnululu and historical Uluru NPs. Large non-arboreal taxa were always present in all habitats, but medium non-arboreal taxa were not always present in semi-open and open habitats. Overall, the patterns in presence of arboreal taxa in Australian habitats were very close to those expected.

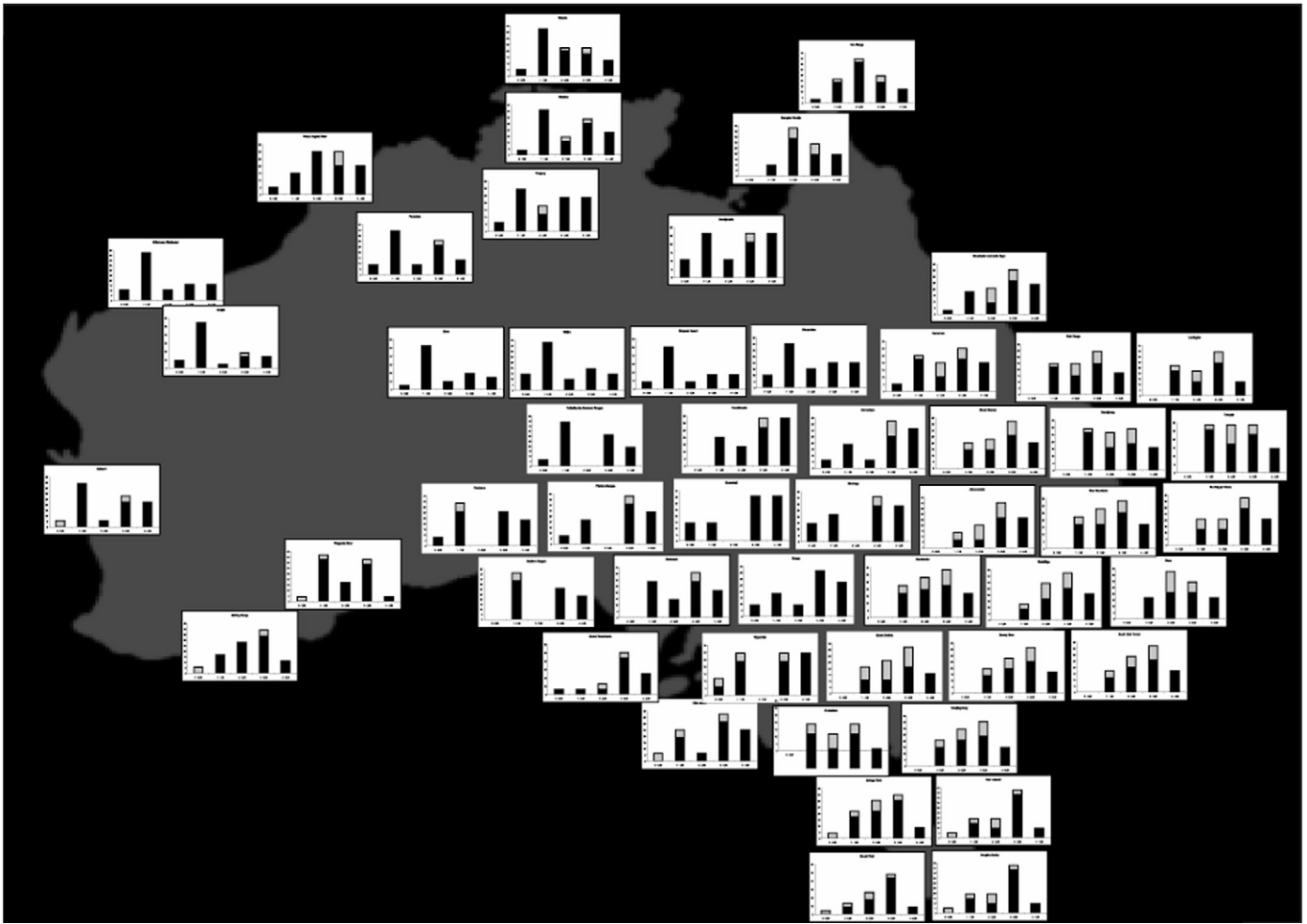
3.3. Body mass distribution

In Fig. 8, we represented the geographical distribution of the body mass distributions of each national park and reserve. Each bar graph shows the percentage of taxa in each of the body size categories selected (i.e. very small: 0 to 10 g; small: 10 to 100 g; medium: 100 to 1000 g; large: 1000 to 10,000 g; and very large: 10,000 to 100,000 g).

Fig. 9 shows the overall body mass distribution of Australian and New Guinean mammalian faunas. Australia's body mass distribution is characterised by having the greatest proportion of its taxa in the small size range, followed by large, medium-sized, very large and very small. The body mass distribution of all mammal species for Australia (except large introduced herbivores) represents a mix of habitats ranging from rainforest to desert. We would expect that a similar distribution pattern found at the scale of a national park would mean mixed habitats. The body mass distribution pattern for the closed forest of New Guinea is very different from Australia's pattern. The majority of taxa are medium-sized, followed by large, then small, with no very large or very small mammals. In Fig. 8, only the rainforests of







**Fig. 8.** Bar graphs of the proportion of mammal species in each of the body mass categories of the National Parks used in this study, with each bar graph representing on the map of Australia the approximate geographical position of each National Park. Body mass categories are in Log body mass, from left to right, 0–0.9, 1–1.99, 2–2.99, 3–3.99, 4–4.99. Bar graphs are coloured to represent non-arboreal taxa in black and arboreal taxa in light grey.

north-eastern Queensland (Iron Range and Mungkan Kandju NPs) and Deua NP have the same peak in medium-sized mammals as the New Guinea distribution. All Australian parks on the eastern, south-eastern and south-western coasts (all categorised as closed habitats in this study) had their highest distribution peak in large mammals (i.e. 1 kg to 10 kg). In contrast, all central and western Australian parks (categorised as open or semi-open) had their highest distribution peak in small mammals (i.e. 10 g to 100 g). Several individual parks had a distribution similar to Australia's overall body mass distribution pattern. These parks occur either in transitional areas between forest and grasslands (e.g. Fitzgerald River NP) or include a mix of forest and grassland (i.e. Nitmiluk and Kakadu NPs). Flinders Range, Mungo, Gundabooka, Kinchega and Mutawintji NPs had a different body mass distribution pattern, with most of their species being large and very large, with very few if any medium, small and very small mammals. Fig. 10 summarises the four major patterns in body mass distribution observed in Australia. A peak in medium sized mammals characterises rainforests, a peak in the large mammals characterises open forests, peaks in both small and large (and sometimes also very large) characterise mixed habitats (such as riparian woodlands) or transitional habitats, and a peak in small mammals characterises grasslands and deserts.

Fig. 11 plots the historical body mass distribution of Mutawintji and Uluru NPs versus their current distribution (Stirling Range and

Karijini NPs had the same historical distribution as their current distributions). Historical Mutawintji NP had a body mass distribution that resembles the distribution that observed for grasslands and deserts, displaying a peak in small mammals. Most mammals that went extinct at Mutawintji were small, between 10 and 100 g. In contrast, Uluru's historical distribution patterns resemble a mixed habitat distribution with medium-sized and large mammals subsequently becoming extinct.

### 3.4. Analysis

The results of Kendall's  $\tau$  to find correlations between our cenogram, body mass distribution, and arboreal taxa variables and environmental variables are shown in Table 2. The  $\tau$  coefficient varies between 1 (correlated) and  $-1$  (inversely correlated), with values close to 0 showing no correlation. Unlike Rodríguez (1999), we found many significant correlations between our cenogram variables and environmental variables. Magnitude of the largest gap correlated with all environmental variables except maximum (MAMT) and minimum (MAMT) temperatures, with the highest correlation being with annual rainfall. No correlations were found between the average position of the largest gap and any of the environmental variables. This was not unexpected because the average position of the largest gap in closed habitats revealed no particular pattern (see Fig. 5). The percentage of

**Fig. 7.** Bar graphs of the number of mammal species in each of the body mass categories 100–1000 g and 1000–10,000 g for non-arboreal and arboreal species in each of the National Parks studied, and grouped into the three habitat types, closed, semi-open and open.

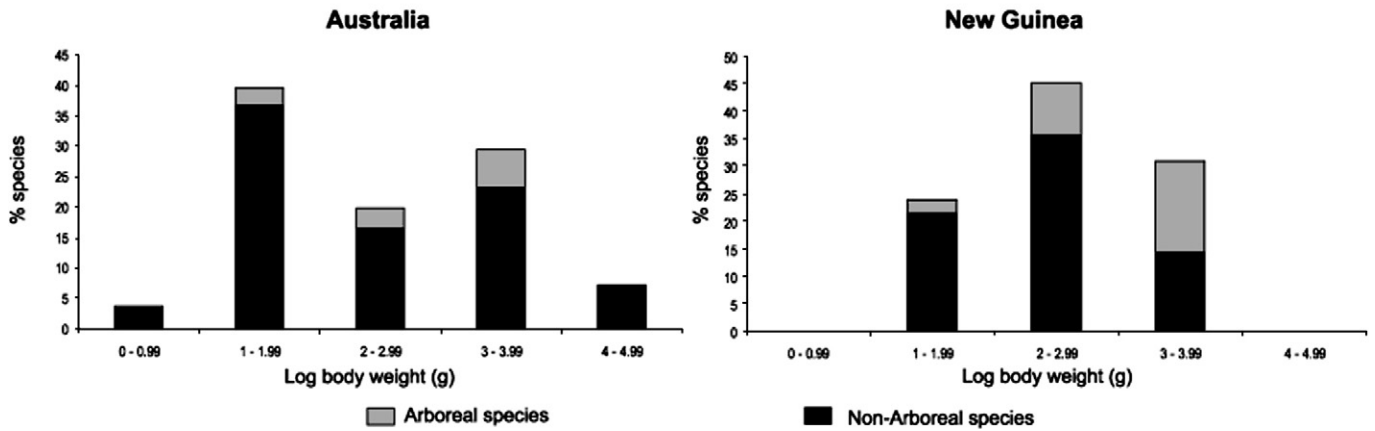


Fig. 9. Bar graphs of the proportion of mammal species in each of the body mass categories of Australia and New Guinea.

species in the very small (log 0–0.99 or 0 to 10 g) and small (log 1–1.99 or 10 to 100 g) body mass categories correlated with all environmental variables. Correlations for these two body mass categories range from fairly low correlations (Kendall's  $\tau$  values of 0.25) with temperatures, and fairly high correlations (Kendall's  $\tau$  values of 0.57) with habitat type. Of all body mass categories, medium sized mammals (log 2–2.99 or 100 to 1000 g) have the highest Kendall's  $\tau$  values (over 0.5) with all

the environmental variables, except for temperatures which had low or no correlation. Large mammals (log 3–3.99 or 1000 to 10,000 g) correlated with all variables weakly, with temperatures having the highest Kendall's  $\tau$  values ( $-0.459$  and  $-0.419$ ). Annual rainfall was the only variable correlating (weakly) with very large mammals (log 4–4.99 or 10,000 to 100,000 g). Very small arboreal species correlated only with temperatures and only very weakly. Small arboreal species correlated

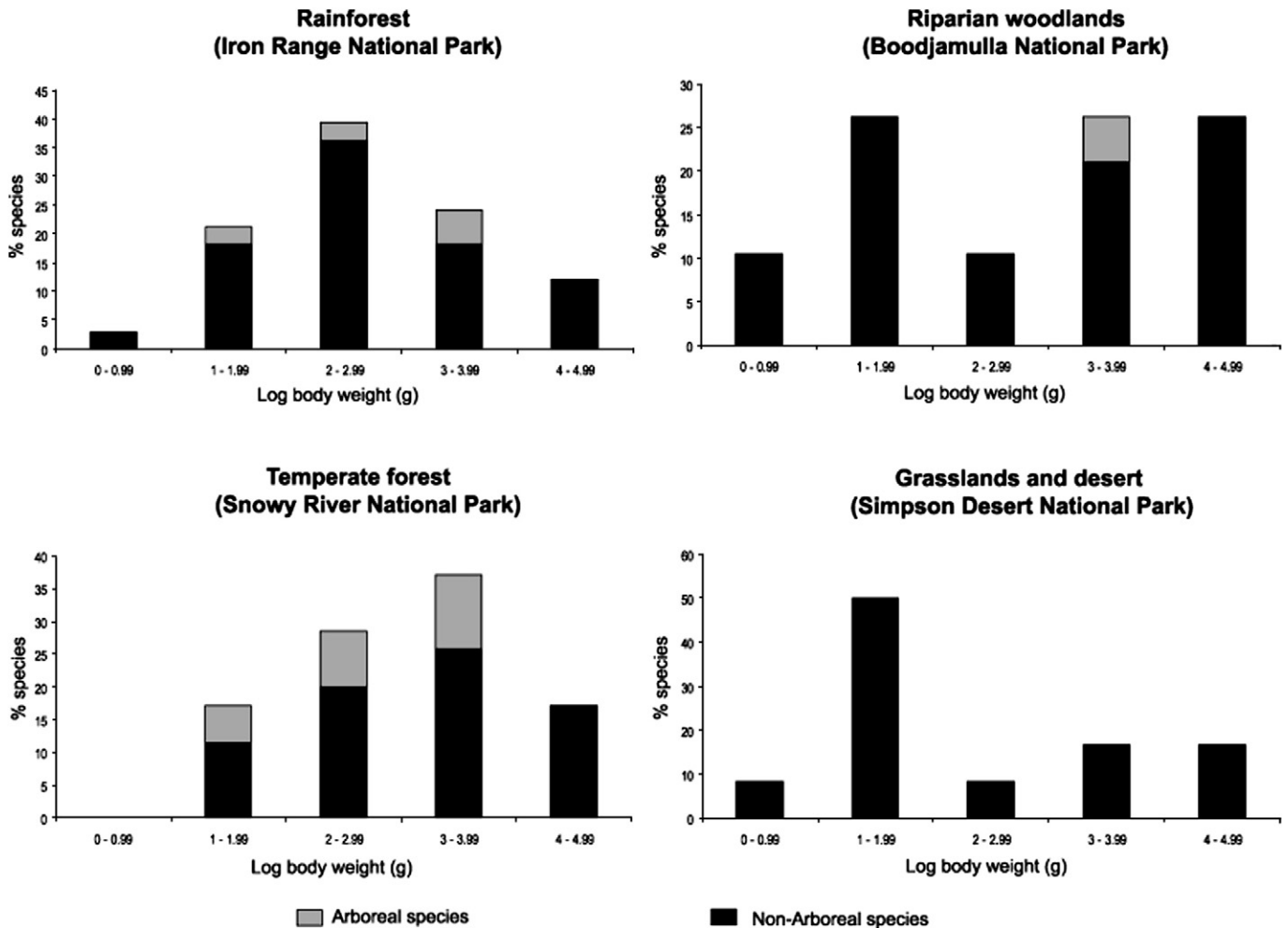


Fig. 10. Bar graphs of the proportion of mammal species in each of the body mass categories of four main patterns identified for Rainforest, Temperate forest, riparian woodlands and grasslands and desert.

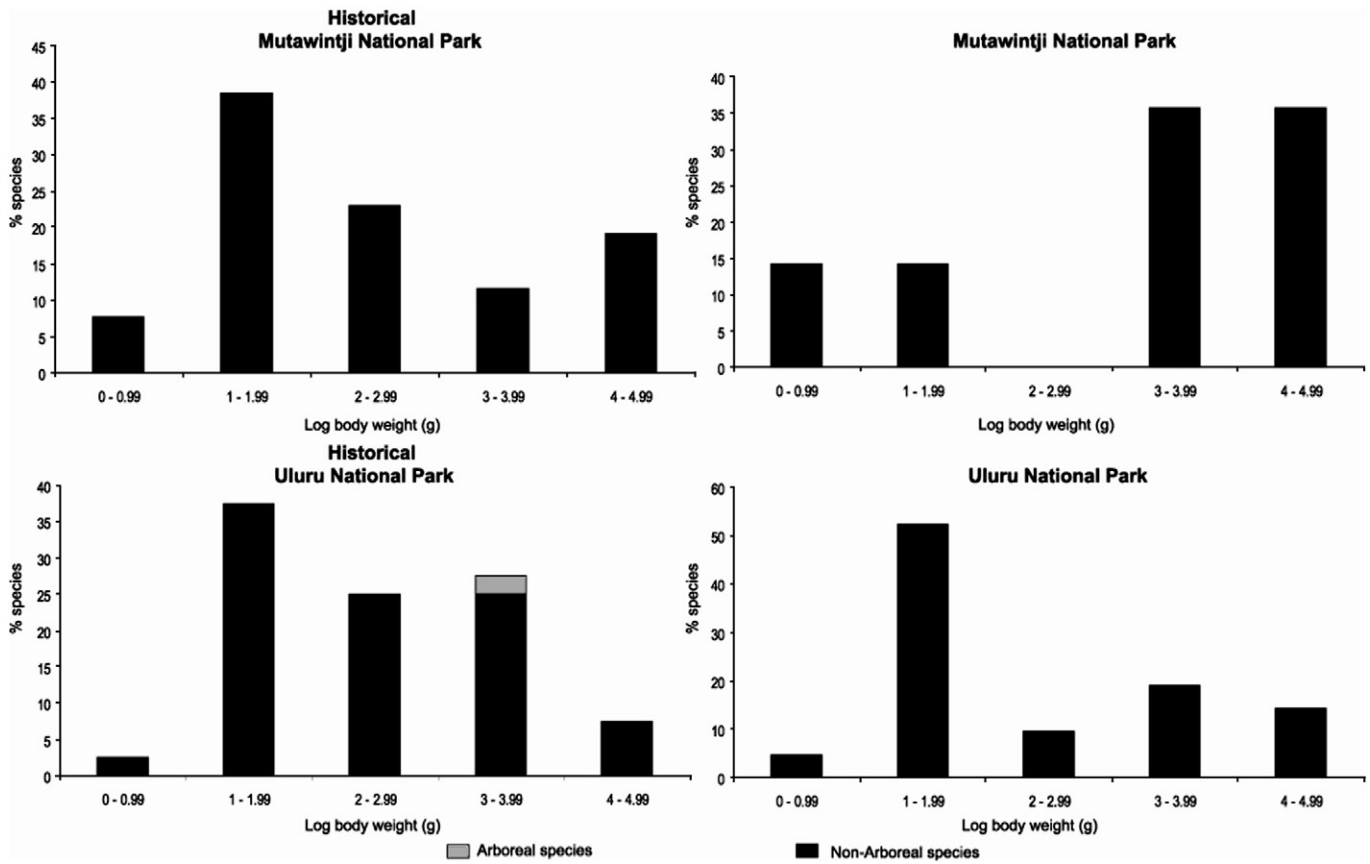


Fig. 11. Bar graphs of the proportion of mammal species in each of the body mass categories of Mutawintji and Uluru National Parks, comparing historical data versus modern data.

with all environmental variables and Kendall's  $\tau$  values were quite high for temperatures, MVG and habitat type. The highest Kendall's  $\tau$  values in the analysis were for correlations between medium-sized arboreal species and habitat type ( $-0.753$ ) and MVG ( $-0.607$ ). Medium-sized arboreal species also correlated with all other environmental variables.

Similar results, but with lower Kendall's  $\tau$  values, were found for large arboreal species. Overall, the results of Kendall's  $\tau$  analysis showed strong correlations between our cenogram, body mass distribution and arboreal taxa variables versus environmental variables, giving statistical support to the patterns examined visually.

Table 2

Kendall's  $\tau$  coefficient and probability ( $P$ -value) of uncorrelated pairs between cenogram, body mass distribution and arboreal taxa variables and environmental variables

		Climate	MVG	MAMT	MAmT	Habitat type	Annual rainfall
Magnitude of largest gap	Kendall's $t$	0.496	0.473	0.113	0.039	0.466	-0.506
	$P$ -value (uncorr.)	0.000	0.000	0.217	0.667	0.000	0.000
Average position of largest gap	Kendall's $t$	-0.010	-0.070	0.024	-0.017	-0.042	-0.012
	$P$ -value (uncorr.)	0.914	0.444	0.792	0.852	0.647	0.892
% species between Log 0–0.99	Kendall's $t$	0.428	0.506	0.345	0.253	0.570	-0.448
	$P$ -value (uncorr.)	0.000	0.000	0.000	0.006	0.000	0.000
% species between Log 1–1.99	Kendall's $t$	0.367	0.376	0.316	0.250	0.515	-0.226
	$P$ -value (uncorr.)	0.000	0.000	0.001	0.007	0.00	0.014
% species between Log 2–2.99	Kendall's $t$	-0.524	-0.527	-0.233	-0.140	-0.592	0.551
	$P$ -value (uncorr.)	0.000	0.000	0.011	0.129	0.000	0.000
% species between Log 3–3.99	Kendall's $t$	-0.183	-0.245	-0.459	-0.419	-0.378	0.103
	$P$ -value (uncorr.)	0.047	0.008	0.000	0.000	0.000	0.262
% species between Log 4–4.99	Kendall's $t$	0.140	0.106	0.105	0.034	0.132	-0.272
	$P$ -value (uncorr.)	0.127	0.248	0.255	0.709	0.151	0.003
% arboreal species between Log 0–0.99	Kendall's $t$	-0.008	0.004	-0.302	-0.296	-0.027	0.033
	$P$ -value (uncorr.)	0.931	0.967	0.001	0.001	0.768	0.719
% arboreal species between Log 1–1.99	Kendall's $t$	-0.197	-0.393	-0.502	-0.440	-0.430	0.278
	$P$ -value (uncorr.)	0.032	0.000	0.000	0.000	0.000	0.002
% arboreal species between Log 2–2.99	Kendall's $t$	-0.537	-0.607	-0.358	-0.203	-0.753	0.522
	$P$ -value (uncorr.)	0.000	0.000	0.000	0.027	0.000	0.000
% arboreal species between Log 3–3.99	Kendall's $t$	-0.348	-0.450	-0.281	-0.202	-0.513	0.380
	$P$ -value (uncorr.)	0.000	0.000	0.002	0.028	0.000	0.000

MVG, MAMT and MAmT stand for major vegetation groups, mean annual maximum temperature and mean annual minimum temperature, respectively.

## 4. Discussion

### 4.1. Australia's shifted gap

In our study, we identified a significant shift in the position of the gap in open habitats between 100 g to 1000 g, compared to gap between 500 g to 8000 g found by most researchers. [Holling's \(1992\)](#) "Core-Taxa Hypothesis" predicts that the greatest gaps should occur at different body sizes in structurally similar biomes on different continents but at similar sizes in structurally different biomes on the same continent. Our results do show that Australia does support part of this hypothesis, having its greatest gap at a different position to those of other continents (sensu [Siemann and Brown, 1999](#)), but do not support the other part of the hypothesis, as our closed habitats had their largest gap at different body sizes. In addition, Australia is, as far as we know, the only country which greatest cenogrammic gap is different from the rest of the world. [Siemann and Brown \(1999\)](#) accepted [Holling's \(1992\)](#) "Core-Taxa Hypothesis" only based on comparisons of body mass distributions between Australia and North America and rejected the Textural-Discontinuity Hypothesis which linked patterns of vegetation and mammalian body size. Textural-Discontinuity Hypothesis ([Holling, 1992](#)) predicts the exact reverse to the "Core-Taxa Hypothesis". [Siemann and Brown \(1999\)](#) concluded that patterns in body mass distributions were the results of geographical ranges and the history of phylogenetic radiations. Our results do not agree with their conclusions as cenogram patterns do reflect the closed/open patterns of the vegetations. Furthermore, the results of the Kendall's  $\tau$  correlations showed that body mass distributions correlated with most environmental variables. According to the "Core-Taxa Hypothesis", it should be expected that Australia have different cenogram patterns from the rest of the world as it is an isolated continent, however the cenogram patterns found in Australia are extremely similar to the rest of the world, showing only a shift down for the greatest gap of open habitats. Our results therefore support the Textural-Discontinuity Hypothesis and reject the "Core-Taxa Hypothesis", suggesting that body mass distributions and cenograms reflect patterns in vegetation.

### 4.2. Explaining the gap

Even though most of our closed habitats exhibited a continuous distribution of mammalian body sizes, some showed a small gap in the medium-sized range. Small gaps in body weight distributions are present in all Tasmanian parks (Ben Lomond, Douglas-Apsley, Mount Field and Savage River NPs). Mammals filling this gap on the mainland are not present in Tasmania and, indeed there are no Tasmanian mammal species ([Strahan, 1995](#)) that could fill this gap. Since European arrival over 200 years ago, only the Tasmanian tiger (*Thylacinus cynocephalus*) is known to have gone extinct in Tasmania ([Strahan, 1995](#)). At this point, the cause of the medium-sized mammal gap in Tasmania is unknown. The last land bridge occurred about 12,000–13,000 years ago ([Alexander, 2005](#)) possibly providing the opportunity for more medium-sized mammals to colonise Tasmania. However, land bridges between Tasmania and the mainland occurred during glacial maxima that perhaps mitigated against successful establishment of Tasmanian population. This hypothesis can only be tested by an examination of the fossil record of Tasmania. [Burbidge et al. \(1997\)](#)'s study on Australian island species richness demonstrated that the size of the island is highly correlated to its species richness. The gap could therefore be the response to an "island effect". A similar gap is also found in some mainland national parks (Abercrombie, Kosciuszko, Ku-Ring-Gai Chase, Mount Barney, Mount Buffalo, Mount Remarkable, Wadbilliga NPs). Considering that all other parks adjacent to them had a continuous size distribution, two possible explanations can be hypothesised: medium-sized mammals were less well sampled than other mammal sizes, or medium-sized

mammals have been well sampled but they are locally going extinct. In the latter case, these absences/extinctions could be the result of habitat fragmentation and edge effects, in turn due to the cleared lands (urban and agricultural areas) found outside of national park boundaries. Habitat fragmentation and edge effects have been shown to have a serious impact on mammalian communities, resulting in the loss of species or decline in population size due to increasing competition for food and predation ([Andr n, 1994](#); [Abensperg-traun et al., 1996](#); [Turner, 1996](#); [Williams and Pearson, 1997](#); [Lidicker, 1999](#); [Debinski and Holt, 2000](#); [Schneider, 2001](#)). [Legendre \(1989\)](#) did identify an edge effect (calling it an island effect) from the fauna of Transvaal (type 10), a small tropical forest surrounded by open areas. This fauna was identified as being too small to support a forest community, hence showing an open pattern, reflecting the community outside of the forest. The inverse of this pattern was identified in the faunas of Lamto (Ivory Coast) and Caatinga (Brazil) being mixes of closed and open habitats (perhaps similar to that of Kakadu NP) or open habitats surrounded by closed habitats (not observed in our study). Although [Legendre \(1989\)](#) identified these effects, until now they have not been recognised as independent cenogram patterns themselves.

The cenogram method becomes less credible if both island and edge effects create gaps in the cenograms of closed habitats. In both cases, a closed habitat could be mistakenly identified as an open habitat. In addition, historical data from Uluru and Mutawintji National Parks show no distinct gaps in either cenogram. In this case, open habitats could be mistakenly identified as closed habitats. [Legendre \(1986, 1989\)](#) only identified aridity and openness as the only environmental "pressures" affecting cenograms patterns. In our study, we can identify two new environmental "pressures": pressure caused by island effect, habitat fragmentation and edge effect, and lack of pressure caused by the isolation of Australia for millions of years, resulting in lower predator numbers than the rest of the world ([Wroe et al., 2004](#)). When dingoes were introduced by humans to Australia around 3500–4000 years ago ([Strahan, 1995](#)), the largest carnivore on the mainland were the Tasmanian tiger (*Thylacinus cynocephalus*), the Tasmanian devil (*Sarcophilus harrisii*) and the four quoll species (*Dasyurus maculates*, *Dasyurus viverrinus*, *Dasyurus geoffroi* and *Dasyurus hallucatus*). At that time, Australia was already lacking carnivorous mammals over 50 kg, which are found on all other continents ([Wroe et al., 2004](#)). Following the introduction of dingoes to the mainland, both the Tasmanian tiger and Tasmanian devil went extinct from the mainland, diminishing the overall number of large predators ([Johnson and Wroe, 2003](#)). The introduction of cats and foxes by Europeans increased predation rates, bringing in a new predatory pressure on medium-sized Australian mammal fauna.

### 4.3. Two new methods complementary to the cenogram method

Because of these two new pressures (island, edge and fragmentation effects and increased predation), the cenogram method becomes less accurate for inferring habitat types, perhaps explaining why [Rodr guez \(1999\)](#)'s results showed very little correlation between cenogram patterns and environmental variables (using both historical and modern data, and possibly data with island or edge effects) and why [Siemann and Brown \(1999\)](#) found few or no statistically significant gaps (using mainly historical data). However, used in combination with other methods, an alternative use of the cenogram method may in fact be very informative. In this study, we examined two other ways to infer habitat type: using arboreal species (possums and koalas) and using the percentage of mammals in each of the selected body mass categories. We found that closed habitats contain arboreal species of all sizes (large, medium and small) while semi-open habitats contain only large arboreal species and open habitats contain no arboreal species. Arboreal species tend to be found in



higher rainfall areas in Australia. With decreasing numbers of trees, there is more competition for food and less shelter from predators, and this helps explain the absence of arboreal species in open areas. Arboreal species are less at risk from introduced predators such as foxes and cats.

The common brushtail possum (*Trichosurus vulpecula*) is the only arboreal species whose geographical range extends into more open areas, and historically, its geographical range covered most of Australia, even into the arid zone provided trees were present (Strahan, 1995). They are now restricted to forests and woodlands only. We have also identified patterns in body mass distributions using a bar graph of the percentage of mammals in each of the selected categories (logarithmic mass in grams of the following ranges: 0–0.99, 1–1.99, 2–2.99, 3–3.99 and 4–4.99). The patterns identified, using this method, are able to infer habitat type where cenograms may be misleading. For example, all parks showing a gap in medium-sized mammals due to island or edge effect, showed the same pattern in body mass distribution as any other closed habitat, in having a peak in the large sized mammals. Similarly, the cenogram of historical Mutawintji National Park was a straight line, but the body mass distribution showed a peak in the small sized mammals, characterising open habitats. Overall, the presence of arboreal species and the proportion of body mass categories are most likely better methods to infer habitat type, but neither of these methods is able to visualise pressures on mammalian communities in the way that the cenogram method does, by showing the magnitude of the gap in medium-sized mammals. Using all three methods in conjunction should allow accurate identification of habitats as well as visualisation of pressures caused by diverse ecological phenomenon. Fig. 12 gives a revised summary of the cenogram patterns proposed by Legendre (1986, 1989), including the presence of arboreal taxa and body mass distribution patterns. We propose that these patterns should be used, at least for Australian habitat type identification.

#### 4.4. The impact of introduced predators

Special attention should also be given to some of the patterns found using the body mass distribution method (also seen in cenograms). Mutawintji, Currawinya, Mungo, Kinchega, Gunda-booka, Flinders Range, Bookmark, Gawlers Range, Little Desert and Yumbarra NPs, all share one pattern in common which separates them from other semi-open/open habitats. They have a relatively low number of small mammal species (or low proportion compared to large mammals) compared to a high number of small mammal species found everywhere else in the arid and semi-arid zone of Australia. Three possible explanations for this pattern are: sampling for small mammals in those parks was poor; the pattern may be caused by an environment that does not favour small mammals; or it is the result of another unidentified phenomenon. Historical data from Mutawintji National Park help eliminate two of these explanations. First, Mutawintji NP historically contained many small mammals (12 small and very small species versus only four currently found at Mutawintji NP), eliminating the explanation of poor sampling. Second, if this pattern was caused by an environment unfavourable to small mammals then no changes would be found between historical and modern data. This suggests that the pattern is the result of another phenomenon or “pressure” that has resulted in a different pattern in body mass distribution to the other open habitats. Having fewer small species, the cenograms of these ten parks show a larger gap extending into the small mammals, shifting downwards the gap from 1000 g to 50 g.

Valverde (1964, 1967) hypothesised that the gap in medium-sized mammals was the result of predator–prey relationships. If this relationship between gap size and gap position is correct, then the position of the gap will correlate with the size of the predators, and the magnitude should reflect the degree of predation. A shift in the gap to smaller sizes should therefore imply that the main predators

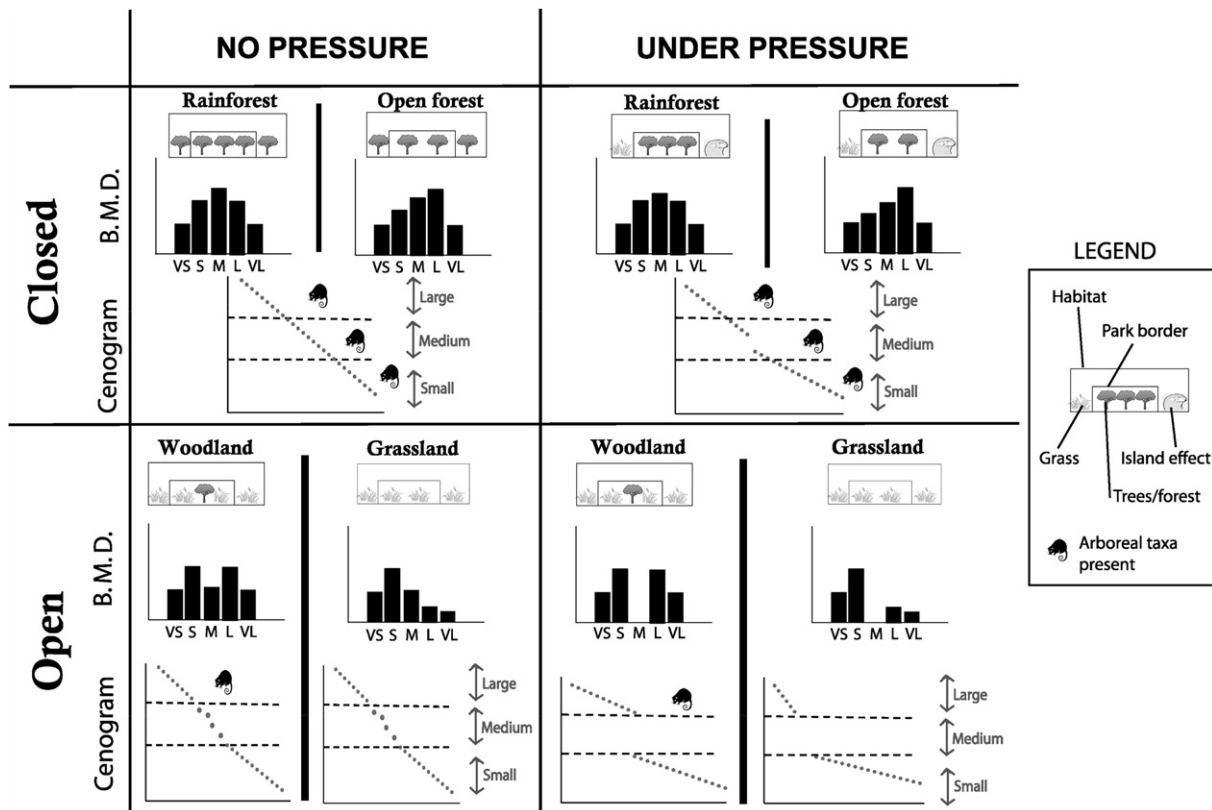


Fig. 12. Summary of new cenogram and body mass distribution patterns hypothesised in this study for Australian closed (rainforest and open forest) and open (woodland and grassland) habitats. B.M.D.=body mass distribution; VS=very small; S=small; M=medium; L=large; VL=very large (see text for definition of size categories).

are also smaller. Geographically, all the parks showing this pattern are located in the area where dingoes have been excluded by the dingo proof fence (Fig. 2). It has been hypothesised that top predators such as the dingo may control smaller predator populations, such as foxes and cats (Risbey et al., 2000; Glen and Dickman, 2005; Johnson et al., 2007). The observed pattern may be the result of the removal of dingoes and increases in the populations of foxes and cats and increasing predation on small and medium-sized mammals. The geographical distributions of sheep and rabbits have also been shown to be correlated with areas of high extinctions, caused by the depletion of food and ground-level shelter by these two species (Burbidge and McKenzie, 1989; Morton, 1990; Short and Smith, 1994; Smith and Quin, 1996; Fisher et al., 2003; Glen and Dickman, 2005; Johnson et al., 2007). The two different patterns observed for semi-open/open habitats in our study may be the result of the combination of presence and absence of dingoes, sheep and rabbits.

#### 4.5. Mid-domain effect

The other noteworthy, and cautionary, pattern found in our analyses is that based on historical data from Uluru National Park. Uluru's pattern in body mass distribution (Fig. 11) was very similar to that of the overall pattern for the Australian continent today (Fig. 9). This pattern might be expected in parks with mixed closed and open habitats, but Uluru's habitat is exclusively open. The pattern could be explained by the mid-domain effect (Colwell and Lees, 2000). This model (still being debated Davies et al., 2005; McClain and Etter, 2005) predicts that centrally located areas tend to have higher species richness than other areas because they share common species with all other areas, thus increasing the overall species richness of that area. Historically, many Australia mammal species' distributions extended from west to east, or north to south, meeting in the centre of the continent. Today, most of these very broad distributions have been disrupted and reduced to small isolated areas, with many taxa now locally extinct at Uluru.

#### 4.6. Limitations

The first step of any interpretation of statistical results should be the identification of possible errors (Sand-Jensen, 2007). Limitations inherent in the data used in our analyses and their possible effects on our results and their interpretation are as follow. First, the data used in all cenogram and body mass distribution studies, both by ourselves and other authors (e.g. Legendre, 1986, 1989; Rodríguez, 1999) is derived from national parks and reserves. These data are very useful for ecological studies: they are delimited in space, and the fauna and flora are monitored and studied. Rarely are there data of this quality available outside national parks. However, data from national parks are subject to several sources of error, such that they may not be truly representative of patterns between habitats (Louys et al., unpublished manuscript). Ideally comparisons would be between data from uniform habitats of the exactly the same size, with homogenous vegetation and equal sampling effort. However, in reality each national park is of different size, contains usually more than one habitat, has heterogeneous vegetation and unequal sampling effort. This may in fact not be a problem when patterns found using national parks are compared to fossil sites. Fossil sites are certainly collecting fossils from areas of different sizes, may collect fossils from different habitats (although one may be dominant), and taphonomic biases can be considered as an analogue to modern sampling effort.

In our own analysis, we have identified several sources of error. Firstly, we know that our national park data has not been uniformly sampled. Some parks have had decades of intense sampling effort, while others have had only a few years of sampling effort. Sampling effort information is not readily available, and therefore we can only rely on observation of the raw data to identify possible sampling

biases. As yet, there have been very few statistical treatments of this problem (Louys et al., unpublished manuscript). In our study, we suspect that Abercrombie and Mount Remarkable NPs may have been surveyed less than other national parks, and therefore may be heavily biased because smaller mammals are poorly represented.

The second potential source of error in our study is the identification of vegetation type/habitat type. We used a single vegetation map to minimise the problem of inconsistencies in vegetation identification, which can frequently occur when these are sampled across several countries (Lawesson, 1994; Louys et al., unpublished manuscript). Nevertheless, vegetation maps have been recognized to have several problems, including their robusticity (they do not account for spatial and temporal variability) and generality (simplification of complex interactions between vegetation, climate, fire and grazing) that can potentially be misleading for ecological studies (Bastin and Ludwig, 2006). Further, national parks that contain only one major vegetation group are rare. In our study, Kakadu National Park, at 1,980,400 km<sup>2</sup> the largest National Park in Australia, contains at least five different major vegetation types, ranging from rainforest to grasslands. Current statistical analyses require that only one vegetation type describes the data from a single park. This is one possible source of error in Rodríguez's (1999) results, as he assigned one vegetation type per park, which can lead to further errors if the vegetation type was not assigned properly. So how does one assign a vegetation type? If, for example, a park contains 10% forest and 90% grassland, that the park would in all likelihood be assigned to grassland, however grasslands may not be the dominant pattern. Using the cenograms patterns, if you were to overlap the pattern of a closed forest with a desert, the resulting pattern would still look like a closed forest, because the medium-sized mammals of the forest would fill in the gap in the desert cenogram. Therefore, in the cenogram method, closed habitats have a dominant pattern over open habitats. In the case of the previous example, the hypothetical park with 10% forest and 90% grassland, using the cenogram method will not assign it to grasslands, as this will not be the pattern observed. As an example, Kakadu National Park displays a closed habitat pattern, yet a large portion of the park is actually grasslands. In our study, we chose to simplify the vegetation types to three habitat types (closed, semi-open and open) because we wanted to minimise error caused by incorrectly assigning a park to the wrong vegetation types. Our results from the Kendall's  $\tau$  analysis do show that our assignment of a park to the three habitat types works very well, as they showed the highest correlation with mammalian body mass patterns. However, this does not imply that we assigned correctly all our park to the correct habitat type, and it is possible that we did incorrectly assigned some parks.

Assuming that we have correctly assigned most national parks to habitat type, two major points can be made about our cenograms. Firstly, they are not infallible identifiers of habitats in Australia, and secondly, it is often very difficult to identify a pattern visually when the slopes of small or large mammals are made of only a few data points.

There are definite inconsistencies (e.g. weight range of the gap, interpretations of the slopes...) in the way cenograms, as defined by Legendre (1986, 1989), have been used in the past by many authors. Despite those inconsistencies in their use, this method was considered amongst the best methods to infer habitat types along with body mass distributions (Hernández Fernández et al., 2006). As Montuire (2000) pointed out that cenograms are only meant to be used to identify whether a fauna is closed or open, and are not accurate predictors of temperatures.

## 5. Conclusion

This study suggests that the current cenogram methodology cannot reliably infer habitat types from cenogram patterns. However, with new cenogram patterns for modern and historical habitats identified and

used in conjunction with two other measures described here (presence of arboreal taxa and body mass distribution), cenogram methodology should prove to be a useful ecological tool. Cenograms are able to visualise pressures caused by several well-recognised ecological phenomena. These pressures can significantly affect the patterns of the cenograms and body mass distributions, and include island effect, habitat fragmentation, edge effects, predator removal (viz. Australian dingo-proof fence) and introduced species (cat, fox, sheep and rabbit). The gap in cenograms is the result of these pressures and its position is correlated with predator size. Australia has smaller predators with a smaller preferred prey range than the rest of the world and there is a resulting shift downwards in the position of the cenogram gap. Historical data indicates that Australia was under very little environmental pressure before European arrival, with no distinct gaps in the cenograms of open habitats, evidently reflecting Australia's isolation from other continents for millions of years and its lack of large carnivores. Cenogram methodology should prove to be an increasingly useful tool both to infer habitat type in Australia for fossil communities and identify pressures caused by diverse pressures on the mammalian community.

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.palaeo.2008.11.009](https://doi.org/10.1016/j.palaeo.2008.11.009).

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