Climate-driven variation in food availability between the core and range edge of the endangered northern bettong (*Bettongia tropica*)

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Abstract. The endangered northern bettong (*Bettongia tropica*) occurs in four disjunct populations in far north Queensland, Australia, at a high density only in its range core (RC). A recent study suggested that *B. tropica* populations are sparse at the northern and southern range edges (SRE) due to more severe droughts and variable climatic conditions causing fluctuations in the availability of their principal food resource, truffle-like fungi. Truffle availability in the Australian tropics is affected by climate, specifically seasonality of precipitation. We aimed to determine whether the differences in weather patterns between the RC and SRE could be translated to actual differences in truffle availability. Truffle density was consistently lower on the SRE although biomass was slightly higher there due to dominance by drought-tolerant truffle taxa that produce few but large truffles. Lower densities of truffles on the SRE could explain why *B. tropica* is also less abundant there and why they may be less resilient to competition from the more generalist rufous bettong (*Aepyprymnus rufescens*). Increasing temperatures and, more importantly, harsher droughts predicted for this region as a result of climate change, may have further detrimental impacts on truffle availability and thus population densities of *B. tropica* and other mycophagous species.

Additional keywords: *Bettongia tropica*, endangered species, truffles, range edge, range core, climate change.

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Introduction

Recent studies have shown that species are already responding to increasing global temperatures by shifting their distributions polewards or upwards in elevation (Parmesan and Yohe 2003; Root et al. 2003, 2005; Parmesan 2006; Murphy et al. 2010; Chen et al. 2011). However, there is growing evidence that climatic changes other than increasing temperature also impact species distributions (Jentsch et al. 2007; Jentsch and Beierkuhnlein 2008; Zimmermann et al. 2009; Bateman et al. 2011). Climatic variability, short-term changes in weather patterns, and extreme events (e.g. more severe droughts) may be particularly important drivers of species range shifts, and are often not assessed in these global studies (Zimmermann et al. 2009; Bateman et al. 2011). Populations near the edge of species ranges may be the first to exhibit detectable changes, as they are likely to already experience conditions near physiological tolerances for persistence (Parmesan et al. 2000; Thuiller et al. 2008; Brook et al. 2009).

Fluctuations in the abundance of a population are often directly tied to the availability of resources such as food, which can be regulated by weather (Lewellen and Vessey 1998; White 2008 and references therein). This is particularly true for ecological specialists, which depend on a narrow range of resources. The northern bettong (*Bettongia tropica*), an endangered marsupial endemic to north-eastern Australia, is a specialist mycophagist. It feeds mainly (60% or more) on ‘truffles’, the fruiting bodies of hypogeous (below-ground) ectomycorrhizal fungi (Johnson 1996; McIlwee and Johnson 1998; Abell et al. 2006). Truffle availability is strongly influenced by rainfall (Johnson 1994; Claridge et al. 2000, 2009; Jumpponen et al. 2004; Abell et al. 2006) and in north-eastern Australia truffle availability declines when rainfall is low during the annual dry season or droughts (Abell et al. 2006). Truffle availability is highest in sclerophyll woodlands that occur in a zone of high, although seasonal, rainfall on the western edge of the Wet Tropics bioregion (Vernes 1999), and *B. tropica* is restricted to these habitats (Johnson 1996; Abell et al. 2006). Rainforest habitats form an abrupt boundary for the northern bettong because rainforest mycorrhizae produce small fruiting bodies (Johnson and McIlwee 1997).
Bettongia tropica occurs in four known upland areas in the Wet Tropics: the Lamb Range, Coane Range, Carbine Uplands, and Windsor Uplands (Fig. 1). Only the populations occurring within the centrally located Lamb Range – hereafter referred to as the range core (RC) – have high densities (trap success up to 20%) (Winter 1997a; Pope et al. 2000; Vernes and Pope 2006). The outlying populations on the northern (Carbine and Windsor Uplands) and southern range edge (SRE, situated on the Coane Range) occur at much lower densities (trap success 1.0–2.4%) (Winter 1997a; McIlwee and Freeman 1998; Dennis 2001). Local declines have been recorded from both of the northern range edges (Winter 1997a) and the SRE. At the SRE a recent survey failed to detect a single individual over several years of intense effort (Bateman 2010; Bateman et al. 2011). Periods of severe droughts and variable temperatures, in combination with competitive pressure from the generalist rufous bettong (Aepyprymnus rufescens), are implicated as the cause of this decline (Bateman et al. 2011). The RC of this species is more stable climatically than northern and southern portions of the Wet Tropics, experiencing lower seasonality in both temperature and precipitation (Williams and Middleton 2008). It is possible that the range edges experience climate and weather conditions that are less suitable for the production of truffles.

The aim of this study was to determine whether the differences in weather and population status of B. tropica between the RC and SRE described by Bateman et al. (2011) are associated with actual differences in truffle availability between these two regions. There are many species of truffles, but we combined them into a single category because B. tropica has been shown to feed non-selectively on the full range of species found within this region (Vernes et al. 2001). The distribution and habitat factors influencing truffle availability at the SRE of the distribution of B. tropica in comparison to the RC were specifically examined in this study, using new data from the SRE in comparisons with data collected from the RC (Abell-Davis 2008; Mathams 2008). This will help us to understand if the climate in the SRE affects truffle availability, making truffles less reliable as a food resource for B. tropica there and explaining the lower density of B. tropica.

**Methods**

**Study area**

Truffle surveys in the SRE were conducted in sclerophyll woodlands on the Australian Wildlife Conservancy–managed Mt Zero-Taravale wildlife sanctuary on the Coane Range, in the Wet Tropics of north-eastern Queensland, Australia (19°07’S, 146°11’E) (Fig. 1). These sites occur within suitable habitat for B. tropica. Annual precipitation varied along this gradient from 2000 mm in the north-east to less than 800 mm on the western border of the property (Stanton 2007), creating a steep transition in vegetation from rainforest to dry sclerophyll forests. A total of eight survey sites were selected along this gradient. Forest types were Allocasuarina very tall open forests (type 10 and 11 of Stanton 2007), and Eucalyptus woodlands (type 40 and 64 of Stanton 2007) and were situated at different altitudes due to the nature of the vegetation gradient. Sites were spaced at least 500 m apart.

Truffle records from across the Wet Tropics region of Australia were used to evaluate regional-scale influences of climate on truffles. Data on truffle occurrence were obtained from this survey and other field surveys (during 2004–07) conducted using the same field methods in the region (Abell-Davis 2008; Mathams 2008) (Fig. 1). Due to limited sampling in the region, truffle records were restricted to the wet to dry sclerophyll woodlands gradient, occurring adjacent to rainforest.

**Field survey methods**

Truffle sampling followed the methodology of Abell et al. (2006). At each sampling site (n = 8), four replicate 50 m by 20 m (1000 m²) quadrats were established adjacent to each other. Quadrats were sampled once only to minimise habitat disturbance and to allow fungal recovery after surveys. All quadrats were set up with the long axes of the four quadrats aligned to the same contour to limit topographical variation among quadrats. Sites were surveyed four times (once on each quadrat) giving a total of 32 surveys, in December 2006 (transition period from dry to wet...
season), April 2007 (late in the wet season), July 2007 (early in the dry season), and December 2007 (transition period from dry to wet season).

Although studies elsewhere show that different taxa of truffles may respond differently to environmental cues (Johnson 1994; Jumpponen et al. 2004), in the Australian Wet Tropics the availability of truffles responds consistently to precipitation (Abell et al. 2006). Density and biomass of truffles collected within a total survey area of 32,000 m² were converted to a per-hectare measure (as per Abell et al. 2006). Estimates of truffle density and biomass from the SRE were compared with density and biomass measures on the RC (from Abell et al. 2006; Abell-Davis 2008) using one-way ANOVA. Surveys conducted on the RC during the late dry season, where truffle availability is low (Abell et al. 2006), were excluded from this comparison, as no late dry season survey was conducted on the SRE.

Climate data were long-term climate means derived from ANUCLIM 5.1 software (McMahon et al. 1995) using monthly averages and an 80-m DEM resampled from ~250 m (GEODATA 9 Second DEM Version 2; Geoscience Australia, http://www.ga.gov.au/). Eight climate variables were selected with the aims of maximising climate information and minimising the number of highly intercorrelated variables. Variables were: annual mean temperature (°C), temperature seasonality (coefficient of variation (CV)), maximum temperature of warmest period (°C), minimum temperature of coldest period (°C), annual precipitation (mm), precipitation seasonality (CV), precipitation of wettest quarter (mm), and precipitation of driest quarter (mm). Climate data were extracted from GIS layers (ANUCLIM) for each of the eight fungal survey sites as well as all truffle records from within the Wet Tropics. Climate and weather data were derived for each of the sites, rather than for each quadrat within sites (as these were too close together to have distinct climate or weather attributes). In addition, precipitation data were extracted from the Bureau of Meteorology (BOM) (http://www.bom.gov.au/climate/data/), for the month before each of the surveys. Data were extracted from two weather stations, Paluma (12.2 km east of the study site; Wet BOM) and Horse Shoe Bend, Qld (12.7 km west of the study site; Dry BOMF), and averaged to provide one measure (Average BOM) as the study site is situated halfway between these weather stations along the east–west rainfall gradient.

Analysis

Relationships of truffle availability to precipitation (from BOM data) were tested using linear regression analysis, which compared effects of precipitation one and two months before survey. To determine if the relationships differed for the SRE and RC, we used ANCOVA with site as a random factor and precipitation as the covariate. The one-month preceding precipitation values for each survey were then compared with long-term means to determine if the survey had above- or below-average precipitation values. Truffle availability in above-average precipitation surveys was compared with below-average precipitation surveys using a Kruskal–Wallis (H) one-way non-parametric analysis of variance.

Maxent (ver. 3.3.1) (Phillips et al. 2006) was used to correlate occurrence of truffles with the eight selected climate variables to estimate probabilities of presence across the landscape. Probability of presence was used as an indicator of availability, as truffles are presumably ubiquitous throughout this region given appropriate conditions but some areas are more likely to be consistently productive and thus are more likely to provide occurrence records. Maxent is a presence-only modelling algorithm that has been shown to outperform other such algorithms (Elith et al. 2006; Hernandez et al. 2006; Hijmans and Graham 2006; Guisan et al. 2007). Maxent was parameterised with default settings (Phillips and Dudík 2008) with the exception of the removal of threshold and hinge features, because this produces more ecologically realistic response curves. We addressed spatial bias in the dataset by using both a spatial buffer and drawing the 10,000 background points from near locations where records are known (VanDerWal et al. 2009), and developing a bias-corrected null-model (as per Raes and ter Steege 2007). These approaches provide better model discrimination and remove spatial biases that are often inherent in datasets on species distributions. Although Maxent models were trained on the full dataset, a 10-fold cross-validation was undertaken for model evaluation making use of the area under the receiver operating characteristic (ROC) (Le Brocque and Buckney 2003) curve, the AUC (area under curve), as a model performance parameter. Values that are significantly better than the bias-corrected null-model (95% CI) are considered better than random predictions (Raes and ter Steege 2007).

Individual Maxent models were also created for both the RC truffle records only and the SRE truffle records only, to compare these with the full Wet Tropics model. Models were developed using the Wet Tropics (Fig. 1) to define background and extent so that models were comparable (VanDerWal et al. 2009). Results are presented here to determine where truffle records from both the RC and SRE are situated in relation to climatic variables. In addition, to determine the climatic seasonality of each region where truffle occurrences were recorded in the Wet Tropics, the values for the ANUCLIM variables of temperature seasonality and precipitation seasonality were extracted for each location and compared using a scatter plot.

Once the top three climate variables contributing to models of truffles across the Wet Tropics were determined, the values for each of those climate variables were extracted for all of the SRE truffle occurrences so that they could be compared with the response curves developed by Maxent. In addition, the extracted climate values were used to observe the differences between the top four sites in truffle availability (highest values of truffle density and biomass) with the bottom four sites in relation to the top three variables.

Results

Site scale

A total of 44 patches (including individual fruiting bodies, or sporocarps) of truffles were found in surveys in the SRE, containing 162 total sporocarps with a total weight of 137.85 g. This represented an average of 13.75 patches per hectare, with patches tending to contain few truffle sporocarps (3.68 per patch) that were large (3.13 g per sporocarp). Truffle density per hectare on the SRE (52.18 ha = 3.68 per patch) was significantly less than the RC (174.44 ha = 56.92 s.d.) (from Abell et al. 2006) when surveys from the same time of year were compared (F_{1,5} = 13.54,
Truffle biomass in the SRE (44.61 g ha\(^{-1}\) ± 26.96 s.d.) was higher than biomass measures from the RC (27.96 g ha\(^{-1}\) ± 9.63 s.d.; Abell-Davis 2008) although not significantly so (\(F_{1,2} = 1.00, P = 0.36\)). This indicates that biomass was more variable on the SRE (60.3% CV) than on the RC (34.44% CV). Ten genera were identified in surveys in the SRE: *Castoreum, Mesophellia, Scleroderma, Gummiglobus, Labyrinthomyces/ Dingleya, Stephanospora, Hysterangium, Malajczukia, Sclerogaster*, and *Pogiesperma*. One of these genera, *Mesophellia*, represented 47% of the overall biomass and 23.5% of the total density of all truffles found, followed by *Castoreum* with 24% of the total biomass and 14% of the overall biomass.

There was no significant difference in truffle availability between survey periods on the SRE (density, \(H = 4.97, P = 0.17\); biomass, \(H = 2.69, P = 0.44\)) and thus no patterns of seasonality could be discerned. This may be due to a failure to survey during the late dry season (September) when truffles are typically found, followed by *Castoreum* with 24% of the total biomass and 14% of the overall biomass.

There was a positive relationship of biomass to precipitation in the preceding month (average BOM data: \(r = 0.86, P = 0.12\)) although more surveys are needed to determine whether the relationship is significant (Fig. 2a). This is comparable with the relationship found on the RC (Abell-Davis 2008), where truffle density was significantly positively related to precipitation two months before surveys on the RC, as well as positively related to precipitation one month before surveys (Fig. 2a). ANCOVA revealed that for both one- and two-month precipitation time lags, there was no site effect on truffle density between the SRE and RC (precipitation two months prior: \(F = 1.31, P = 0.31\); precipitation one month prior: \(F = 0.43, P = 0.66\)), but there was an effect of precipitation (precipitation two months prior: \(F = 44.71, P < 0.0001\); precipitation one month prior: \(F = 16.20, P = 0.01\)).

There was a positive relationship of biomass to precipitation one month prior in the SRE (average BOM data: \(r = 0.84\)) (Fig. 2b). However, truffle biomass had a stronger relationship with precipitation in the preceding one month on the SRE than on the RC (Fig. 2b). There was a site effect (\(F = 4.89, P = 0.13\)), but no precipitation effect (\(F = 4.11, P = 0.07\)), on biomass.

On the SRE, higher density and biomass were positively related to above-average rainfall in the preceding month. Significantly higher density (7.75 sporocarps ± 6.6 s.d.) was found during surveys with above-average precipitation (Table 1) the month preceding the survey (\(H = 4.43, P = 0.05\)) than the other surveys (3.17 sporocarps ± 4.71 s.d.). Biomass followed a similar pattern, with higher values in surveys with above-average precipitation (Table 1) in the preceding month (6.57 g ± 9.47 s.d.) than the other surveys (2.73 g ± 5.50 s.d.), although this was not significant (\(H = 2.31, P = 0.13\)).

In the surveys with above-average precipitation (Table 1), *Mesophellia* (32.58%), *Gummiglobus* (28.30%), and *Castoreum* (22.64%) made up the highest percentage of biomass, while *Gummiglobus* (30.39%), *Hysterangium* (19.61), and *Pogiesperma* (14.71%) made up the highest percentage of density. In the surveys with below-average precipitation (Table 1), *Castoreum* (50.73%), *Mesophellia* (30.03%), and *Scleroderma* (18.34%) made up the highest percentage of biomass, while *Castoreum* (38.46%), *Scleroderma* (28.21%),

### Table 1. Precipitation data for the preceding one month to each truffle survey on the SRE

<table>
<thead>
<tr>
<th>Survey</th>
<th>Dry BOM</th>
<th>Survey rainfall Wet BOM</th>
<th>Mean</th>
<th>Dry BOM</th>
<th>Long-term mean rainfall</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. December 2006</td>
<td>0.0</td>
<td>24.9</td>
<td>12.45</td>
<td>55.2</td>
<td>170.6</td>
<td>112.90</td>
</tr>
<tr>
<td>2. April 2007</td>
<td>51.4</td>
<td>213.3</td>
<td>132.35</td>
<td>124.1</td>
<td>349</td>
<td>236.55</td>
</tr>
<tr>
<td>3. July 2007</td>
<td>99.8</td>
<td>187.6</td>
<td>143.70</td>
<td>12.1</td>
<td>59.6</td>
<td>35.85</td>
</tr>
<tr>
<td>4. December 2007</td>
<td>19</td>
<td>271.8</td>
<td>145.40</td>
<td>55.2</td>
<td>170.6</td>
<td>112.90</td>
</tr>
</tbody>
</table>
and *Mesophellia* (20.51%) made up the highest percentage of density.

**Regional scale modelling**

Truffles on the SRE experienced both high temperature and precipitation seasonality in comparison with the RC (Fig. 3). This was further corroborated by the individual Maxent models developed for the RC (temperature seasonality range = 0.65–1.15) and SRE (temperature seasonality range = 1.05–1.20), indicating that the SRE is at the upper limits of temperature seasonality associated with truffle occurrence across the Wet Tropics (temperature seasonality range = 0.70–1.40).

The AUC value for the truffle model was 0.98 ± 0.01 s.d., significantly higher than the bias-corrected null model AUC of 0.84 ± 0.07 s.d. (*P* < 0.05), indicating that model discrimination was high and this model can be considered highly accurate (Guisan *et al.* 2007; Raes and ter Steege 2007). The distribution model for truffles indicates that suitable habitat for truffles occurs throughout the Wet Tropics (Fig. 4), but suitability is highest in upland regions close to *B. tropica* habitat (see Fig. 1 for reference). Maximum temperature of the warmest period had the strongest influence on the distribution (51.4% contribution), followed by precipitation of the driest quarter (18% contribution) and annual mean temperature (12.5% contribution). The probability of presence peaked when the maximum temperature of the warmest period was 24.5°C (Fig. 5a), precipitation during the driest quarter was 125 mm (Fig. 5b), and mean annual temperature was 16°C (Fig. 5c). Suitability declined as temperature increased, with probability of presence being low where temperatures were above 30°C in the warmest period.

Only a portion of the climatic niche modelled for the Wet Tropics was represented at the survey sites on the SRE. Sites with truffle occurrences ranged from 28.5 to 29.7°C for maximum temperature of the warmest period ranges, which is at the higher end of the range for the entire Wet Tropics model and on the decreasing slope of probability of occurrence (Fig. 5a). Truffle sites on the SRE also experienced conditions that occurred towards the lower edge of the bell curve (within the decreasing slope of the graph) for precipitation of the driest quarter (61–121 mm) (Fig. 5b). The range for annual mean temperature was 19.1–20.5°C, towards the hotter portion of the gradient in the decreasing slope of probability of occurrence for this food resource (Fig. 5c).

On the SRE, sites that had higher truffle availability experienced lower maximum temperatures in the warmest period, lower annual mean temperatures, and more precipitation in the driest quarter than the sites with lower truffle availability (Table 2). This is consistent with higher probabilities of occurrences on the regional scale throughout the Wet Tropics, including the stable RC region, although still on the lower end for probability of occurrence of truffles.
lack of a site effect on truffle density in analysis that included rainfall indicated that the main difference between truffle availability in the two regions was due to rainfall.

Although truffles were less abundant on the SRE in comparison with the RC, truffle biomass was relatively high (although not significantly higher) on the SRE (44.61 g ha\(^{-1}\)). This was due to patches having few but large truffles. The most common truffles found in the SRE were from the family Mesophelliaeae, including Mesophelium and Castoreum spp. These taxa tend to be large and have thick shell-like peridia. They are considered fire adapted and tolerant to desiccation (Claridge et al. 2009). In contrast, the RC had more taxa that produce smaller and more abundant fruit bodies with thin peridia (Abell-Davis 2008). Truffles from the Mesophelliaeae, including Castoreum, Mesophelium, Malajzuka and Gummiglobus, made up only 6.8% of the total density and 30% of the total biomass in the RC. More genera overall were found in the RC (25) than in the SRE (10). This means that 21 of the 25 genera that were collected in the RC were those that had relatively thin peridia. The SRE has been shown to be more susceptible to severe drought, as well as variable temperature (Bateman et al. 2011), which is consistent with the observation that truffles on the SRE are predominantly from taxa adapted to withstand dry conditions. Additionally, truffle biomass did not respond in a similar manner to precipitation between the SRE and RC, with truffles on the SRE responding to lower levels of rainfall to yield higher biomass levels.

As truffles within the SRE are already at their upper summer temperature limits and lower dry-season precipitation limits, any further pressure from drought could significantly reduce truffle availability. In tropical Australia, truffle production has been linked most strongly with precipitation, which is reduced in the late dry season or times of drought (Abell et al. 2006). No fungal survey was conducted in the SRE in this study during the late dry season (September). However, surveys conducted under conditions of below-average precipitation in the preceding month had significantly lower truffle density. In addition, precipitation events one month before the surveys were positively related to truffle density and biomass. This is consistent with previous studies that have also found truffle availability to be positively correlated with precipitation lagged by one or two months (Abell-Davis 2008; North 2002). Therefore, years with below-average precipitation may entail low truffle availability (Meyer and North 2005; Abell-Davis 2008). This effect could be confounded by hotter temperatures, as truffle availability declines with high temperatures (above 30°C) (Fogel 1976) and is governed by an interaction between moisture and temperature (Fogel 1976; Claridge et al. 1993; Jumpponen et al. 2004).

These findings confirm the vulnerability of animal species that use truffles as a food resource, including *B. tropica*, to drought events (Abell et al. 2006). This restricts such species to suitable truffle-producing habitat types that are closer to the rainforest edge, with higher or more regular precipitation (Johnson and McIlwee 1997; Abell et al. 2006). The recent failure to detect *B. tropica* on the climatically more seasonal SRE may be linked to declines in truffle availability in association with recent drought conditions and fluctuations in suitable weather conditions that were experienced in this region (Bateman et al. 2011). Where food resources are abundant, specialisation, like that of *B. tropica*

**Discussion**

Truffle availability differed between the core and southern extremity of the range of *B. tropica*, and climate and weather factors evidently contributed to this difference. Lower densities of truffles on the SRE could explain why *B. tropica* is also less abundant there. Truffle density showed the same response to precipitation on the SRE and RC, but precipitation and, accordingly, truffle densities were lower at the range edge. The

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**Fig. 5.** Response curve of truffles (probability of presence) to (a) maximum temperature of the warmest period (°C), (b) precipitation of the driest quarter (mm), and (c) annual mean temperature (°C) in the Australian Wet Tropics. This figure is adapted from the Maxent model output response curve plots. Response curves represent how the predicted suitability (probability of presence) is dependent on the variable selected.
on truffles, can provide a competitive advantage (Rosenzweig and Lomolino 1997; Ritchie et al. 2009) which can be lost if food availability is reduced. In the SRE a generalist competitor species, the rufous bettong (Aepyprymnus rufescens) replaces the northern bettong during times of drought (Bateman et al. 2011). As truffles are less abundant and their distribution is patchier (fewer patches of large, drought-resistant truffles) in the SRE B. tropica would lose its competitive edge and need to contract its range to areas where truffle availability is more consistent in the landscape.

Drought has already been implicated in local extinctions of several bettong species, which as a genus are highly mycophagous, although declines were attributed to the confounding effect of drought in combination with other factors such as stock overgrazing, competition with introduced rabbits (Oryctolagus cuniculus) and, in particular, predation by the introduced red fox (Vulpes vulpes) (Short 1998). Bettong species such as the brush-tailed bettong (Bettongia penicillata), the rufous bettong, the burrowing bettong (Bettongia lesueuri), and the eastern bettong (Bettongia gaimardi), have experienced large range contractions towards areas with higher rainfall, with the latter two species now extinct on the mainland (Short and Turner 1993; Johnson et al. 2006). In these instances, it is likely that predation by foxes may have made it more difficult for rat-kangaroos to recover from drought-caused declines in dry areas. B. tropica has also declined elsewhere, with contraction of populations from south to north and west to east towards higher-rainfall areas (Winter 1992; Winter 1997a; Winter 1997b; Abell et al. 2006). Although foxes are not a significant threat to B. tropica in the tropical north of Australia (Johnson et al. 2007), other factors such as land clearing (Accad et al. 2006), vegetation changes relating to fire intervals (Harrington and Sanderson 1994), competition with feral pigs (Sus scrofa) and the rufous bettong, restriction to upland habitat, and changes in fire regime (Environmental Protection Agency 2007) could make recovery from droughts more difficult here.

Increasing temperatures, more seasonal precipitation, and extended and more severe dry seasons predicted for the region as a result of climate change (Walsh and Ryan 2000; Hughes 2003) could have dramatic detrimental impacts on truffle availability. It is likely that climate change, through reduced truffle availability, will marginalise more of the range of B. tropica, placing pressure on a species already endangered and restricted in its distribution. Many other mammals also use truffles as a food resource (Claridge and May 1994), making it imperative that similar studies into fluctuations in rainfall and other climate factors need to be assessed, particularly at species range edges.

The recent focus on species range shifts solely in terms of increasing global temperature trends may underestimate climate change impacts where other climate factors beyond increasing temperature influence species survival, and could already be causing detrimental alterations to species distributions.

### Acknowledgements

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### References


### Table 2. Truffle availability and climate data by sites with highest availability and lowest availability on the SRE

Presented are the average density and biomass data and average climate data for the top Maxent variables, between the sites with higher truffle availability (top four sites) and lower truffle availability (bottom four sites). Standard deviations are included. Sites represent: Top Four: Sites 2, 3, 6 and 7; Bottom Four: Sites 1, 4, 5 and 8. Codes are as follows: MTDQ is maximum temperature of the warmest period, AMT is annual mean temperatures, and PDQ is precipitation in the driest quarter.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Density (truffles/m²)</th>
<th>Biomass (g/m²)</th>
<th>MTDQ (°C)</th>
<th>AMT (°C)</th>
<th>PDQ (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top Four</td>
<td>7.5 (4.51)</td>
<td>10.12 (3.61)</td>
<td>28.72 (0.22)</td>
<td>19.38 (0.28)</td>
<td>109.5 (12.18)</td>
</tr>
<tr>
<td>Bottom Four</td>
<td>3.5 (2.89)</td>
<td>1.86 (0.56)</td>
<td>29.33 (0.30)</td>
<td>20.07 (0.31)</td>
<td>78.0 (14.47)</td>
</tr>
</tbody>
</table>

Density is measured in number of sporocarps.


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