

# Identifying important environmental variables in the niche partitioning of two keystone ecosystem engineers (*Bettongia gaimardi* and *Potorous tridactylus*) in Tasmania

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## ABSTRACT

**Context.** The eastern bettong (*Bettongia gaimardi*) and the long-nosed potoroo (*Potorous tridactylus*) are mycophagous marsupials regarded as both keystone species and ecosystem engineers. Despite Tasmania being a refuge for these declining species, their niche partitioning is poorly understood.

**Aims.** Our aim was to identify factors that distinguish the distributions of *B. gaimardi* and *P. tridactylus*, and to develop a better explanation of their individual niches. **Methods.** The Department of Primary Industries, Parks, Water and Environment conducted mammal surveys between 1975 and 2019. We used GIS to analyse these data, and geospatial information to identify relationships between *B. gaimardi* and *P. tridactylus* presence/absence and environmental variables. We then developed a model describing the distributions of these species in Tasmania.

**Key results.** Temperature seasonality (s.d.  $\times$  100), precipitation of wettest month (mm), precipitation of the driest month (mm), precipitation seasonality (coefficient of variation), the presence of vegetation dominated by *Eucalyptus amygdalina* and the presence of lowland grassy woodland/forest were the components in the best model for *B. gaimardi*. Our model broadly predicts that the distribution of *B. gaimardi* is restricted to the more fertile eastern half of Tasmania. *P. tridactylus* was associated with very few variables, with the presence of *E. amygdalina*–*Eucalyptus obliqua* damp forest being the only component in a very weak model. Transects with *P. tridactylus* and not *B. gaimardi* were more associated with rainforest and wet forest communities and areas of higher annual and wettest-month precipitation than were those with *B. gaimardi* and not *P. tridactylus*. **Conclusions.** The importance of infertile sites to *B. gaimardi* may have been overstated in the literature, with moderate to high fertility being more characteristic of its range. *B. gaimardi* is adapted to persist in environments of low truffle (food) density, typical of the eastern half of Tasmania, through its ability to adopt a larger home range than for *P. tridactylus*, which requires dense ground vegetation. **Implications.** Sites of high fertility in fragmented landscapes should be considered to be potential habitat for *B. gaimardi*. This challenges previous assumptions that infertile sites are the primary habitat of the species, with fertile sites offering poorer-quality habitat.

**Keywords:** biogeography, conservation, ecological niche, ecology, geographical range, habitat preference, modelling, spatial ecology, threatened species, wildlife management.

## Introduction

Since 1788, Australia has been subject to some of the most rapid extinctions of small mammals in modern history (Woinarski *et al.* 2015). Many of the destructive processes responsible for decline in these species continue (Wintle *et al.* 2019). The protection of remaining populations of a species cannot be achieved without a detailed understanding of their niche (Wiens *et al.* 2010). Without understanding the specific needs of a threatened species, we risk insufficient coverage of their habitats in protected areas (Possingham *et al.* 2006).

The eastern bettong (*Bettongia gaimardi*, Desmarest 1822) and the long-nosed potoroo (*Potorous tridactylus*, Kerr 1792) are nocturnal marsupials, historically restricted to temperate eastern Australia and Tasmania (Rose and Rose 1998; Trent 2015; Frankham *et al.* 2016). Although two subspecies are recognised for *B. gaimardi*, only the Tasmanian subspecies remains extant (Rose and Rose 1998). Three subspecies are recognised for *P. tridactylus*, two on mainland Australia and one in Tasmania, the latter of which occurs in two genetically distinct populations (Frankham *et al.* 2016). *B. gaimardi* and *P. tridactylus* average 1.6–1.8 kg and 0.6–1.64 kg respectively (Rose and Rose 1998; Johnston 2010, p. 95). Sexual dimorphism is pronounced only in *P. tridactylus*, with males larger than females (Norton *et al.* 2010a). Whereas *P. tridactylus* has an average home range of 2–19.4 ha, *B. gaimardi* has an unusually large home range for its size, at 35–149 ha. In both species, males often occupy a larger home range, incorporating those of multiple females (Kitchener 1973; Rose and Rose 1998; Norton *et al.* 2010a; Gardiner *et al.* 2019b). Reproduction in both species occurs year-round (Bennett 1987; Rose and Rose 1998).

*Bettongia gaimardi* and *P. tridactylus* share a largely mycophagous diet. Although non-fungal elements such as seeds, insects, foliage and tree sap may be included in the diet, this material is taken less frequently, or to supplement the diet in times of scarcity (Taylor 1992; Johnson 1994d; Tory *et al.* 1997; Rose and Rose 1998). Most of the diet is made up by the fruiting bodies (hereafter truffles) of ectomycorrhizal fungi, especially those associated with eucalypts, such as the Mesophelliaceae (Claridge *et al.* 1992, 1993; Johnson 1994c; Tory *et al.* 1997; Andren *et al.* 2018). This dietary preference is supported by a well-developed olfactory sense, used to locate truffles, and forelimbs adapted to digging (Donaldson and Stoddart 1994; Rose and Rose 1998; Vernes and Jarman 2014). In addition, the enlarged foregut of *B. gaimardi* may be specifically adapted to optimise digestion of truffles, which are otherwise nutritionally deficient (Rose and Rose 1998). This may explain the positive effect on adult body condition and growth rate in pouch young when truffle consumption is increased (Johnson 1994d).

The habitat of *B. gaimardi* and *P. tridactylus* is very likely to be limited by truffle availability (Taylor 1992; Tory *et al.* 1997; Rose and Rose 1998; Claridge 2002). As the presence and abundance of ectomycorrhizal fungi are influenced by precipitation and soil fertility, *B. gaimardi* and *P. tridactylus* habitat is also predicted by these factors (Slankis 1974; Bougher 1995). However, whereas *B. gaimardi* is common over a wide temperature range and in areas of lower rainfall (Taylor 1993a; Proft *et al.* 2021), *P. tridactylus* is associated with higher rainfall and milder temperatures (Claridge *et al.* 1993, 2019; Claridge and Barry 2000; Robley *et al.* 2014). This means that *B. gaimardi* is recorded largely from dry sclerophyll habitats in Tasmania (Rose and Rose 1998). An open understorey and high tree canopy cover are

associated with foraging by *B. gaimardi* and areas of dense vegetation are important for denning (Gardiner *et al.* 2019a). *P. tridactylus* is associated with a broader range of habitats than is *B. gaimardi*, such as heathy woodland and rainforest (Taylor *et al.* 1985; Andren *et al.* 2013). The dependency of this species on dense ground cover and high tree canopy cover is well documented (Norton *et al.* 2010b; Andren *et al.* 2018; Claridge *et al.* 2019). Furthermore, there is evidence that communities with greater structural heterogeneity support larger populations of *P. tridactylus* (Norton *et al.* 2010b; Andren *et al.* 2018).

*Bettongia gaimardi* and *P. tridactylus* are both keystone species and ecosystem engineers. The symbiotic relationship between plants and ectomycorrhizal fungi is important for the health of forest communities (Claridge 2002). Through depositing viable spores in their faeces, *B. gaimardi* and *P. tridactylus* are important dispersal agents for ectomycorrhizal fungi (Claridge *et al.* 1992; Johnson 1994c). Mesophelliaceae appears particularly dependent on spore dispersal by mammals, which may explain why this is the most common family in both the diet of *B. gaimardi* and in southern dry sclerophyll forests (Johnson 1994c). Additionally, passage through the gut of a mycophagous mammal may be necessary for spore germination in some Mesophelliaceae species (Claridge *et al.* 1992). Some of these ectomycorrhizal fungi significantly increase truffle production after a fire event. This increase in production is followed by immediate population growth (through emigration), and truffle consumption, in *B. gaimardi* and *P. tridactylus* (Claridge *et al.* 1992; Johnson 1995, 1997). An increase in spore production and dispersal ensures that fungi will be spread widely, ready to rapidly inoculate regenerating plants. Finally, *B. gaimardi* and *P. tridactylus* are true ecosystem engineers in their ability to improve soil quality through turn-over, aeration, moderation of soil-surface temperature, and by providing a germination niche for native seedlings (Davies *et al.* 2019; Munro *et al.* 2019; Ross *et al.* 2019, 2020).

*Bettongia gaimardi* is extinct on mainland Australia and the Tasmanian population has reduced genetic diversity (Rose and Rose 1998; Proft *et al.* 2021). Although still extant, the decline of *P. tridactylus* on mainland Australia is well documented (i.e. Andren *et al.* 2013, 2018) and populations have become genetically isolated since European settlement (Frankham *et al.* 2016). Both species fall within the 450–5000 g weight range on which fox (*Vulpes vulpes*, Linnaeus 1758) predation is suggested to be substantial (Dickman 1996; Rose and Rose 1998; Robley *et al.* 2014; Norton *et al.* 2015). Other contributors to decline include predation by the feral cat (*Felis catus*, Linnaeus 1758) and dog (*Canis lupus*, Linnaeus 1758), habitat loss and fragmentation, inappropriate fire regime and drought (Dickman 1996; Johnson 1997; Rose and Rose 1998; Norton *et al.* 2010b, 2015; Andren *et al.* 2013, 2018; Gardiner *et al.* 2019b; Proft *et al.* 2021). The mainland subspecies, *P. tridactylus*

*tridactylus*, is listed as Vulnerable under the *Environmental Protection and Biodiversity Conservation Act 1999*, whereas *B. gaimardi* is listed as Vulnerable on the Mammal Action Plan and Near Threatened on the IUCN Red List (Woinarski *et al.* 2015).

While Tasmania is considered a refuge for *B. gaimardi* and *P. tridactylus*, precisely how their respective niches differ there is unclear. In the present study, we use a long-standing mammal data set and open-source geospatial information to improve understanding of the possible causes of distributions of these species. We aim to (1) identify a set of macro-scale vegetation, geology and climate variables for each species that best describe their distributions, and (2) use this information to better explain their individual niches.

## Materials and methods

### Study area

The present study was conducted on the main island of Tasmania. Tasmania has a temperate maritime climate. Average annual rainfall exceeds 1000 mm in the west, whereas rainfall in the eastern half of the island is lower and less reliable. Mean monthly daily maximum temperatures ranges from 18°C to 23°C in summer and from 9°C to 14°C in winter. Siliceous rocks dominate in the west. Basalt and limestone are common in the north-west. Dolerite dominates in the eastern and the central highlands with sedimentary rocks, recent sediments, Quaternary deposits, sandstone, and siltstone in places. Consequently, soil fertility is low in the west and low to high in the north-west, centre and east. A strong west to east vegetation gradient is present with moorland, wet eucalypt forest and rainforest in the west, dry forests and grassy woodland in the east and alpine and subalpine vegetation in the central highlands (Kitchener and Harris 2013).

### The data set

The data for *B. gaimardi* and *P. tridactylus* was sourced from the 'spotlight survey' data set of the Department of Primary Industries, Parks, Water and Environment (DPIPWE). Surveys began in 1975 and, currently, 173 transects are surveyed annually on the main island of Tasmania (DPIPWE 2010). Transects are placed in strategic locations, which sought to inform wildlife management actions. Wildlife management for the control of herbivore impacts on primary industries is the present stated purpose of the survey. All transects occur along permanent sealed, gravel or forestry service roads, but avoid main roads and highways. The survey undersamples in the south-western third of the state, where there are fewer roads and therefore limited access to establish transect routes. This region of the state has a

concentration of low-fertility soils and high rainfall; therefore, survey data are biased towards fertile dry areas of the state. Nevertheless, the data set covers most Tasmanian terrestrial environments.

Surveys are conducted between the third week in November and the end of December 40 min after sunset, avoiding conditions of high winds, rain, or fog. A driver, whose head is approximately 1.6 m from the ground, makes observations and operates a roof-mounted 100 W sealed beam spotlight, from a vehicle travelling 20 km/h. A passenger records all non-domestic mammal and nocturnal bird observations made by the driver, as well as weather condition, moon phase and traffic volume (DPIPWE 2010). Transects are approximately 10 km long. Mammal observations are attributed to a given transect only, rather than to a specific point location along a transect. Data from this long-term survey were provided in the form of a Microsoft Access database, which contained *B. gaimardi* and *P. tridactylus* presence records as well as coordinates of the approximate central point for each transect. A file with line features representing all transects was provided by DPIPWE.

This survey style was developed targeting the detection and enumeration of mid-sized Tasmanian native and introduced mammals such as kangaroo, wallaby and deer; however, all mammal observations are recorded and *B. gaimardi* and *P. tridactylus* sightings do consistently occur. Owing to their small size and the sometimes-dense nature of roadside vegetation, this method is not particularly efficacious for sightings and identification of these two species, especially *P. tridactylus*, of which the females can be mistaken for *Isodon obesulus* and the males for *Thylogale billardierii* (Michael Driessen and Robbie Gaffney, pers. comm., 14 June 2020).

### Vegetation, geology and climate data sets

We used the open source TASVEG 4.0 geospatial vegetation data set released in 2020 by DPIPWE (2020). This digital state-wide vegetation map comprises 157 mapping units (vegetation communities). It is interpreted from aerial photographs (Michaels 2006). TASVEG 4.0 data are provided as an Esri Shapefile. Detailed descriptions of vegetation communities can be found in the TASVEG companion manual (Kitchener and Harris 2013).

Geology was determined using the open-source Geology of Tasmania 1:250 000 scale geospatial data set provided by Mineral Resources Tasmania ([https://www.mrt.tas.gov.au/products/digital\\_data](https://www.mrt.tas.gov.au/products/digital_data)). This state-wide data package is supplied as an ESRI Shapefile and is compiled from several sources. We used the 'description' field for our analysis, which provides a text description of the geological mapping units (Department of Energy Infrastructure and Resources 2014).

The Worldclim open-source database (Fick and Hijmans 2017) was used to determine climate values. Eight measurements of temperature and rainfall were used, following

previous work on *B. gaimardi* climate range conducted by Proft *et al.* (2021). These were mean annual temperature, temperature seasonality (s.d.  $\times$  100), maximum temperature of the warmest month, minimum temperature of the coolest month, annual precipitation, precipitation seasonality, precipitation of the wettest month and precipitation of the driest month. The 2.5 min spatial resolution version of this data set was used, because this was determined to be an acceptable tradeoff between precision and file size.

## Sampling approach

Spotlight survey data for *B. gaimardi* and *P. tridactylus* were taken from the Microsoft Access database and transferred to Microsoft Excel for manipulation. The number of records for each species was extracted from these data.

Data collection for environmental variables was achieved using Arc GIS Pro by Esri. The file containing all transect line features was loaded as well as vegetation, geology and climate geospatial data files. A polygon feature was created around each transect using the 'buffer' tool in Arc GIS Pro at 1 km for *B. gaimardi* and 0.5 km for *P. tridactylus*. These distances best represent the radii of the home ranges of these two species (Kitchener 1973; Rose and Rose 1998; Gardiner *et al.* 2019b). These polygons were then used to extract presence or absence of all vegetation and geological classes from the TASVEG 4.0 and Geology of Tasmania 1:250 000 spatial data sets by using the 'summarise within' tool in Arc GIS Pro. Presence or absence for each environmental variable within transect polygons was recorded in Excel for all transects, for both *B. gaimardi* and *P. tridactylus*.

The central point provided for each transect in the DPIPWE spotlight survey data set were used as the location at which climate variables were extracted. The 'Zonal Statistics as Table' tool was used to sample data from each of the eight Worldclim geospatial data sets for each transect. These data were stored in Excel and were used for both *B. gaimardi* and *P. tridactylus* analyses, because factoring in home range size was not necessary for climate data, given that the scale of grid cells within the Worldclim data set was larger than the two home-range sizes.

## Data analysis

After examination of histograms, the data for *B. gaimardi* were converted to classes of record number (0, 1–2, >2), as was that for *P. tridactylus* (0, 1, >1). A variable was created to compare the distributions of the two species. The four classes of this variable were as follows: neither species; only *P. tridactylus*; only *B. gaimardi*; both species. The relationship of these four classes to each of the climate variables was determined using one-way ANOVA followed by Tukey's multiple-range test in R (R Core Team 2020). Chi-squared analyses determined the relationships of these classes with each of the vegetation and geological types from the TASVEG and

Geology of Tasmania data sets with sufficient data for the test in R (R Core Team 2020). Given the strong associations detected between *B. gaimardi* and *Eucalyptus amygdalina* communities and with lowland grassy woodland and forest communities, these TASVEG communities were consolidated into the following two aggregate groups: *E. amygdalina* forest and woodland (all) and lowland grassy woodland and forest (all). Where the overall chi-squared value was significant, the transects with only *P. tridactylus* were compared with those with only *B. gaimardi*, to gain insights into differences in their distributions.

## Model fitting and selection

Ordinal logistic regression in the software package Minitab 16™ using default settings was used to reduce the variables to a best predictive model for each species, by successively removing the least significant component, until all slopes were significant

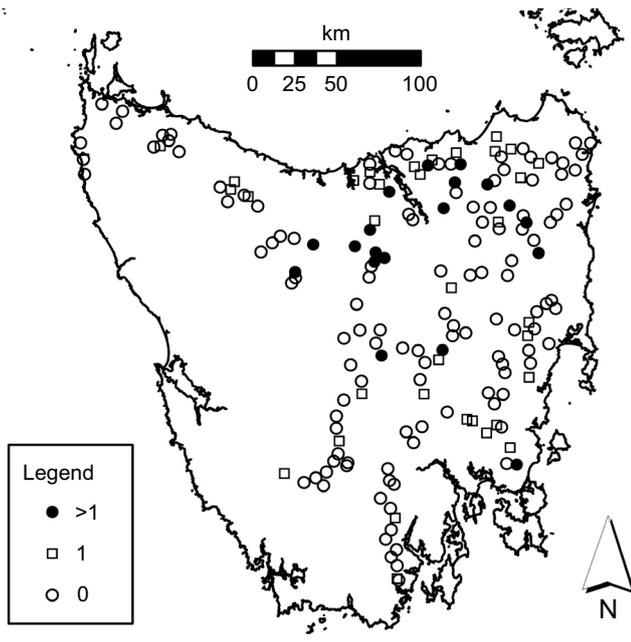
## Results

### *P. tridactylus*

Transects with at least one *P. tridactylus* record were distributed evenly, with a slight concentration around the Tamar River (Fig. 1). A model of very low explanatory power (37.6% concordant, 53.4% ties) consisted of only *E. amygdalina*–*E. obliqua* damp sclerophyll forest (Table 1).

### *B. gaimardi*

The majority of transects with at least one observation of *B. gaimardi* occurred in the eastern half of the state, with the highest proportion of presence transects occurring in the Central Highlands and on the north-eastern coast (Fig. 2). The ordinal regression model was concordant in its predictions in 77.5% of cases and tied in 0.4%. The most significant components in the model were precipitation in the wettest month and rainfall seasonality, but the model also included rainfall in the driest month, temperature seasonality, *E. amygdalina* forest and woodland and lowland grassy woodland and forest (Table 1). In climate space (e.g. Fig. 3), there were eight transects with only one observation of the species mixed with the absences, all in high-rainfall areas in which there were no other observations of the species. These may be observation errors. In contrast, with the puzzling exception of the Deddington transects, the absences mixed with the presences in the graphs were from 12 areas where the species had been observed several times on other transects. The thresholds for more than two observations for the climatic variables in the model were <136 mm for precipitation of the wettest month, <34 for precipitation seasonality, >306 for temperature seasonality and <68 for



**Fig. 1.** Spotlight survey transect locations, showing transects with zero *P. tridactylus* observations, transects with one *P. tridactylus* observation, and transects with >1 *P. tridactylus* observations.

precipitation of the driest month. The two vegetation types were positively associated with *B. gaimardi*.

### Comparison of the distributions of the two species

The two species were discriminated in their climatic ranges by mean annual precipitation and precipitation in the wettest month, with *P. tridactylus* occurring in areas of higher

rainfall than for *B. gaimardi*, but with major overlap of ranges in the lower-rainfall areas (Table 2). The standard deviations for climatic variables that are significantly different among the four classes are consistently higher for *P. tridactylus* by itself than for *B. gaimardi* by itself or the two species together (Table 2). *P. tridactylus* occurred at a higher percentage frequency than did *B. gaimardi* in many rainforest and wet eucalypt communities (Table 3), whereas the reverse pertained for eastern riparian scrub (Table 3).

### Discussion

The association we identified between *B. gaimardi* presence and lowland dry eucalypt communities either dominated by *E. amygdalina* and/or with grassy understories is well established in the literature (Rose and Rose 1998; Davies *et al.* 2019; Gardiner *et al.* 2019a; Proft *et al.* 2021). The preference of *B. gaimardi* for tree-dominated vegetation with open understories (Johnson 1994a, 1997; Davies *et al.* 2019) is consistent with these associations.

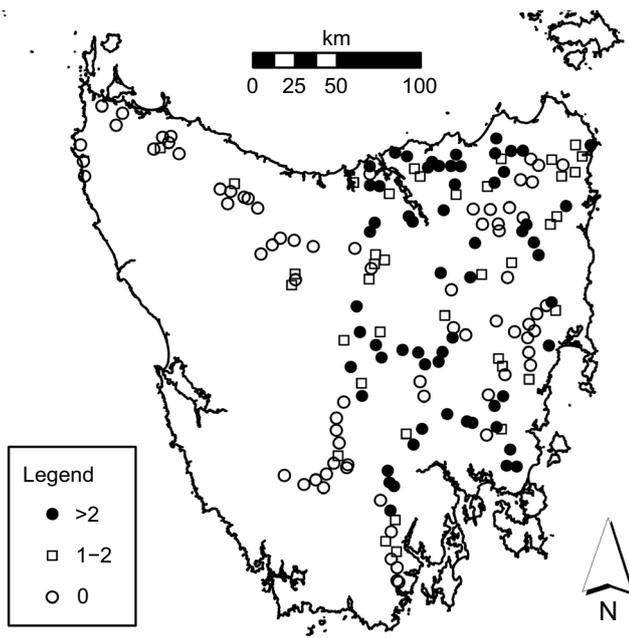
Surprisingly, none of the dry eucalypt communities that we identified to be positively associated with *B. gaimardi* presence was noted to contain *E. tenuiramis*, despite *B. gaimardi* being previously observed in *E. tenuiramis* forests in Tasmania (Johnson 1994a, 1994b, 1994c, 1994d, 1997; Davies *et al.* 2019).

Gardiner *et al.* (2019a, 2019b) demonstrated that *B. gaimardi* adapts to disturbed landscapes so long as its resource needs are met. Therefore, where *B. gaimardi* habitat is replaced by disturbance-related communities, it may be that *B. gaimardi* is able to persist by adjusting its home range accordingly. We speculate that the ability of *B. gaimardi* to persist in disturbed landscapes may exist on

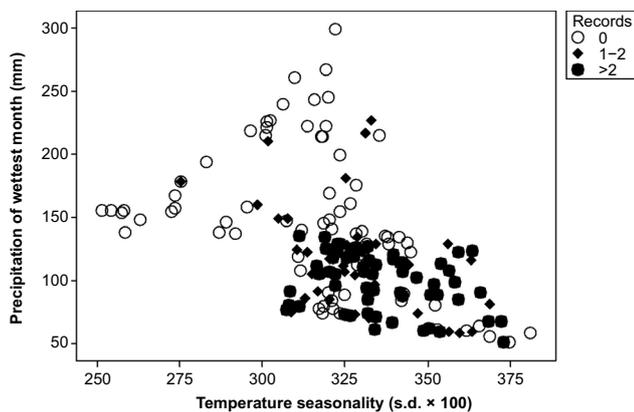
**Table 1.** Most explanatory models.

Predictor	Coefficient	s.e. coefficient	Z	P
<i>Potorous tridactylus</i>				
Constant (1)	1.24184	0.208887	5.95	<0.001
Constant (2)	2.6468	0.294927	8.97	<0.001
<i>Eucalyptus amygdalina</i> – <i>E. obliqua</i> damp forest	1.59602	0.360022	4.43	<0.001
<i>Bettongia gaimardi</i>				
Constant (1)	9.1683	3.30693	2.77	0.006
Constant (2)	10.4013	3.33243	3.12	0.002
Temperature seasonality	0.0191938	0.0080029	2.4	0.016
Precipitation of wettest month	0.0830558	0.0203282	4.09	<0.001
Precipitation of driest month	0.119978	0.0385744	3.11	0.002
Precipitation seasonality	0.299873	0.0749288	4	<0.001
<i>Eucalyptus amygdalina</i> forest and woodland (all)	1.21926	0.496529	2.46	0.014
Lowland grassy woodland and forest (all)	0.95251	0.442135	2.15	0.031

Most explanatory ordinal logistic regression models for *Potorous tridactylus* and *Bettongia gaimardi*.



**Fig. 2.** Spotlight survey transect locations, showing transects with zero *B. gaimardi* observations, transects with 1–2 *B. gaimardi* observations, and transects with >2 *B. gaimardi* observations.



**Fig. 3.** *Bettongia gaimardi* records in climate space with the most significant rainfall variable, precipitation of wettest month plotted against the significant temperature variable, Temperature seasonality. Transects with >2 *B. gaimardi* records are indicated by black circles, transects with 1–2 *B. gaimardi* records are indicated by black diamonds and transects with no *B. gaimardi* records are indicated by white circles.

a spectrum with an upper limit on the proportion of disturbed land to natural habitat that the species will tolerate.

Our results supported the consensus that *B. gaimardi* seldom occurs in wetter habitats (Rose and Rose 1998; Davies *et al.* 2019), unlike *P. tridactylus*. We identified a preference for dry and damp eucalypt communities by *P. tridactylus*. Eastern riparian scrub was preferred by *B. gaimardi* but not by *P. tridactylus*. This community

usually occurs as linear vegetation in open or cleared areas. *P. tridactylus* avoids areas with low or no cover (Claridge *et al.* 1992, 2019; Norton *et al.* 2010b; Trent 2015; Andren *et al.* 2018). *B. gaimardi* may be able to utilise disturbed landscapes, whereas *P. tridactylus* may not (Gardiner *et al.* 2019a, 2019b). Our results confirmed that *P. tridactylus* is able to utilise a broader range of vegetation communities than is *B. gaimardi*, including vegetation types in areas of high rainfall (Rose and Rose 1998), such as rainforest (Taylor *et al.* 1985).

*Eucalyptus ovata* forest and woodland is listed as a threatened community under the *Nature Conservation Act 2002*. We found the two species to be associated with this community, emphasising the need to conserve the remaining fragments of *E. ovata* forest and woodland.

An association between *B. gaimardi* and sand or sandstone geology is recorded in the literature (Taylor 1993a; Johnson 1994a, 1994b, 1994c). The association between *B. gaimardi* and sand or sandstone geology and associated sandy soils has been explained by higher densities of ectomycorrhizal fungi on infertile sites (Slankis 1974), especially species in the family Mesophelliaceae, which disproportionately contribute to the diet of *B. gaimardi* (Johnson 1994c). Yet, two-third of the transects with *B. gaimardi* were at least partially underlain by Jurassic dolerite, with transects containing only the species having the highest concentration of this argillaceous rock. *B. gaimardi* is thus associated with a wide range of soil fertility.

Our results indicated that the distribution of *B. gaimardi* is strongly influenced by climate. There is a disparity between our work and that of Proft *et al.* (2021), who found precipitation in the driest quarter, minimum temperature of the coldest month and annual precipitation to be most associated with *B. gaimardi* occurrence. However, we did find precipitation of the driest month to be comparable to precipitation in the driest quarter reported by Proft *et al.* (2021). The higher number (254) and more varied sources of *B. gaimardi* records used by Proft *et al.* (2021) in constructing their Species Distribution Model (SDM) is likely to be the reason for any discrepancies. Examples from the literature support our modelled *B. gaimardi* climate range (Taylor 1992; Davies *et al.* 2019; Ross *et al.* 2019).

We identified no statistically significant relationships between *P. tridactylus* presence and any climate variables. This is contrary to work by Trent (2015), who found that habitat suitability was negatively correlated with mean annual temperature and positively correlated with mean annual precipitation and that these were the best predictors of presence, along with two environmental predictors. These environmental predictors, potential habitat within 1 km and undergrowth cover, were positively correlated with *P. tridactylus* habitat suitability. The difference from our results may reflect a greater range of annual precipitation at sites in Victoria and New South Wales from which

**Table 2.** Variation in climatic variables among transect classes.

Climate variable	Neither species		<i>P. tridactylus</i> only		<i>B. gaimardi</i> only		<i>B. gaimardi</i> and <i>P. tridactylus</i>		F	P
	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.		
Temperature seasonality (s.d. × 100)	313B	30	326AB	22	336A	19	327A	15	9.8	<0.001
Mean annual temperature (°C)	10.0A	1.5	10.1A	1.2	10.4A	1.9	10.9A	1.5	2.3	0.078
Mean daily maximum temperature, warmest month (°C)	19.6B	1.3	19.9AB	1.7	20.7A	1.6	20.7A	1.3	7	<0.001
Mean daily minimum temperature, coldest month (°C)	2.2A	1.8	2.0A	1.1	1.9A	1.7	2.6A	1.5	1.7	0.175
Mean annual precipitation (mm)	1263A	444	1172AB	451	916C	254	941BC	239	12.2	<0.001
Mean precipitation wettest month (mm)	150A	59	138AB	59	103C	32	112BC	35	11.9	<0.001
Mean precipitation driest month (mm)	58A	22	54AB	22	45B	12	43B	9	9.3	<0.001
Precipitation seasonality (coefficient of variation)	26A	8	25AB	7	22B	5	26A	7	4.8	0.003

Variation in means and standard deviations of climatic variables among transects without *B. gaimardi* or *P. tridactylus* ( $n = 57$ ), those with *P. tridactylus* only ( $n = 17$ ), those with *B. gaimardi* only ( $n = 63$ ) and those with both species ( $n = 36$ ). One-way ANOVA with Tukey's *post hoc* test. Means with the same letter are identical at  $P > 0.05$ .

*P. tridactylus* is reported (Claridge *et al.* 1993; Robley *et al.* 2014), than at our sites. It may be that *P. tridactylus* distribution is not easily predicted by climate in Tasmania within the climatic range of the observations we used.

Mycorrhizal fungi are known to achieve maximum infection and sporulation in soils of low fertility and high water availability (Slankis 1974). In Australia, the mycorrhizal fungi most common in both eucalypt communities and mycophagous mammal diets, Mesophelliaceae, show the same pattern of higher biomass in infertile wet environments and lower biomass in fertile dry environments (Taylor 1992; Johnson 1994b, 1994c; Bougher 1995). However, this ectomycorrhizal family is known to tolerate a wide range of conditions. Therefore, in most cases, suboptimal conditions will simply result in low abundance of Mesophelliaceae, rather than complete absence.

Over the past three decades, much of the work undertaken on *B. gaimardi* in Tasmania has been disproportionately focused on populations in areas with infertile soils, where truffle density, and therefore *B. gaimardi* density, is high (Johnson 1994a, 1994d, 1995; Rose and Rose 1998; Claridge and Barry 2000). Furthermore, many of these studies have been conducted at the same infertile site near Colebrook Tasmania. Most of these works refer to Taylor (1993a), who came to the conclusion that, although *B. gaimardi* distribution is extensive across the eastern half of the state, densities are highest on infertile sites. We believe that the emphasis in the literature on *B. gaimardi* density being higher on infertile sites does not accurately describe the breadth of the niche which *B. gaimardi* fills in the Tasmanian landscape.

Although *B. gaimardi* may take advantage of high food availability on infertile sites by increasing its own population density, our results suggest that these sites are not representative of the species' habitat across the full extent of its distribution. Modelling by Taylor (1993a), Proft *et al.* (2021), and our own work, has amply demonstrated that *B. gaimardi* is widespread on fertile soils. The eastern half

of Tasmania has higher soil fertility and lower rainfall than does the western half of the state, where *B. gaimardi* is largely absent, implying that *B. gaimardi* is broadly associated with areas of low truffle density.

Gardiner *et al.* (2019a, 2019b) showed that *B. gaimardi* has the ability to expand its home range in fragmented landscapes, so as to meet its resource requirements. *B. gaimardi* is also known to have a much larger home range than for many other small mammals of a similar size (Taylor 1993b; Rose and Rose 1998). Therefore, we postulate that the ability of *B. gaimardi* to adopt a larger home range to meet its resource requirements is indicative of the species niche. That is, *B. gaimardi* is adapted to persist in habitats of low truffle density where other mycophagous specialists are not, through its ability to travel large distances and its willingness to traverse unsuitable habitats in search of food.

Evidence in support of this hypothesis can be seen in the physiognomy of the species. Heavily muscled hind limbs with long tibiae and fibulae and elongated feet enable rapid movement over large distances (Rose and Rose 1998). These features may be particularly useful in open habitats, typical of the vegetation communities in eastern Tasmania. Conversely, these features may make moving through dense vegetation difficult. Therefore, dense habitats may favour *P. tridactylus* rather than *B. gaimardi*, such as at the Peter Murrell Reserves, south of Hobart (Driessen and Jarman 2014; Driessen *et al.* 2021). Furthermore, the smaller home range of *P. tridactylus* and unwillingness to go far from dense vegetation, makes it more suited than *B. gaimardi* to the wet and infertile western half of the state where truffle density is likely to be higher.

## Conclusions

We have used a novel GIS approach to analyse a long-standing data set in a new way. *B. gaimardi* habitat in Tasmania can

**Table 3.** Variation in vegetation and geologic variables among transect classes.

Variable	Neither species	<i>P. tridactylus</i> only	<i>B. gaimardi</i> only	<i>B. gaimardi</i> and <i>P. tridactylus</i>	Chi <sup>2</sup>	P
<i>Nothofagus</i> – <i>Atherosperma</i> rainforest	<b>61.40</b>	47.06	31.75	41.67	10.9	0.013 (n.s.)
<i>Nothofagus</i> – <i>Phyllocladus</i> rainforest	<b>54.39</b>	47.06	11.11	16.67	32.2	<0.001 (0.002)
<i>Eucalyptus obliqua</i> wet forest	<b>54.39</b>	29.41	19.05	25.00	18.5	<0.001 (n.s.)
<i>Eucalyptus delegatensis</i> wet forest	<b>43.86</b>	35.29	9.52	8.33	26.2	<0.001 (0.016)
<i>Leptospermum lanigerum</i> scrub	<b>38.60</b>	35.29	31.75	11.11	8.4	0.038 (n.s.)
Western wet scrub	<b>35.09</b>	11.76	3.17	2.78	30.2	<0.001 (n.s.)
<i>Leptospermum lanigerum</i> forest	<b>29.82</b>	11.76	6.35	8.33	14.9	0.002 (n.s.)
<i>Eucalyptus delegatensis</i> wet forest	<b>28.07</b>	17.65	6.35	2.78	16.5	0.001 (n.s.)
<i>Eucalyptus nitida</i> wet forest	<b>26.32</b>	17.65	1.59	2.78	21.6	<0.001 (0.029)
<i>Eucalyptus nitida</i> dry forest	<b>22.81</b>	5.88	1.59	2.78	18.9	<0.001 (n.s.)
Western buttongrass moorland	<b>19.30</b>	5.88	0.00	2.78	17.7	<0.001 (n.s.)
<i>Eucalyptus nitida</i> wet forest	<b>19.30</b>	11.76	4.76	2.78	9.7	0.021 (n.s.)
<i>Nothofagus</i> rainforest	<b>19.30</b>	11.76	3.17	2.78	11.6	0.009 (n.s.)
Shallow marine sandstone–mudstone	<b>17.54</b>	11.76	1.59	5.56	10.3	0.016 (n.s.)
<i>Eucalyptus nitida</i> wet forest	<b>15.79</b>	11.76	0.00	2.78	13.2	0.004 (0.043)
<i>Leptospermum</i> with rainforest	22.81	<b>29.41</b>	3.17	2.78	18.5	<0.001 (0.004)
Shallow marine limestone sequences	14.04	<b>17.65</b>	1.59	2.78	10.3	0.016 (0.029)
Dolerite	36.84	47.06	<b>63.49</b>	52.78	8.7	0.034 (n.s.)
<i>Eucalyptus viminalis</i> grassy woodland	14.04	35.29	<b>41.27</b>	27.78	11.2	0.011 (n.s.)
<i>Bursaria</i> – <i>Acacia</i> woodland	8.77	11.76	<b>28.57</b>	25.00	8.8	0.033 (n.s.)
Eastern riparian scrub	3.51	0.00	<b>22.22</b>	8.33	13.8	0.003 (0.033)
Agricultural land	66.67	76.47	79.37	<b>97.22</b>	12.3	0.006 (n.s.)
<i>Eucalyptus amygdalina</i> forest and woodland (all)	36.84	64.71	73.02	<b>86.11</b>	27.7	<0.001 (n.s.)
Lowland grassy woodland and forest (all)	36.84	58.82	57.14	<b>72.22</b>	11.9	0.008 (n.s.)
<i>Eucalyptus ovata</i> forest and woodland	24.56	35.29	39.68	<b>55.56</b>	9.2	0.026 (n.s.)
<i>Eucalyptus amygdalina</i> – <i>E. obliqua</i> damp forest	7.02	23.53	23.81	<b>52.78</b>	25.2	<0.001 (n.s.)
<i>Eucalyptus amygdalina</i> coastal forest	8.77	35.29	36.51	<b>38.89</b>	15.4	0.002 (n.s.)
Dominantly non-marine sediments	12.28	35.29	30.16	<b>38.89</b>	9.8	0.02 (n.s.)
Upper glaciomarine sequences	14.04	5.88	36.51	<b>38.89</b>	14.3	0.003 (0.016)
<i>Eucalyptus amygdalina</i> forest on mudstone	10.53	5.88	14.29	<b>30.56</b>	8.5	0.036 (n.s.)

Variation in percentage frequencies of significantly varying (chi-squared) vegetation and geologic variables among transects without *B. gaimardi* or *P. tridactylus* ( $n = 57$ ), those with *P. tridactylus* only ( $n = 17$ ), those with *B. gaimardi* only ( $n = 63$ ) and those with both species ( $n = 36$ ). In parentheses, to the right of the  $P$ -value, is the significance of the difference between *B. gaimardi* only and *P. tridactylus* by using only Fisher's exact test. Numbers in bold indicate the transect class with the highest percentage frequency for each variable.

n.s., not significant.

generally be described as open dry sclerophyll in the eastern half of the state. *B. gaimardi* is associated with fertile soils across the majority of its distribution. On the basis of these findings we suggest that *B. gaimardi* is adapted to persist in environments of low truffle density where other mycophagous mammals cannot, through its ability to adopt a larger home range. This is where the niche of *B. gaimardi* differs from that of *P. tridactylus*, which appears to favour wet and infertile environments where groundcover and truffle density are likely to be higher, meaning that *P. tridactylus* can meet its

food requirements over a smaller home range. Although the overemphasis in the literature on *B. gaimardi* populations in infertile areas does highlight the importance of high-quality *B. gaimardi* habitat, care should be taken by land managers to avoid discounting fertile sites that represent the majority of its distribution. Furthermore, we found that *E. ovata* forest and woodland constitutes habitat for both species. Because this vegetation community is listed as threatened under the *Nature Conservation Act 2002*, our work emphasises the importance of conserving remaining fragments.

## References

- Andren M, Milledge D, Scotts D, Smith J (2013) The distribution of long-nosed potoroo *Potorous tridactylus tridactylus* habitat on the far north coast of New South Wales. *Australian Zoologist* **36**, 494–506. doi:10.7882/AZ.2013.015
- Andren M, Milledge D, Scotts D, Smith J (2018) The decline of the northern long-nosed Potoroo *Potorous tridactylus tridactylus* on the far north coast of New South Wales. *Australian Zoologist* **39**, 414–423. doi:10.7882/AZ.2018.010
- Bennett AF (1987) Conservation of mammals within a fragmented forest environment: the contributions of insular biogeography and autecology. In 'Nature conservation: the role of remnants of native vegetation'. (Eds DA Saunders, GW Arnold, AA Burbidge, AJ Hopkins) pp. 41–52. (Surrey Beatty: Sydney, NSW, Australia)
- Bougher NL (1995) Diversity of ectomycorrhizal fungi associated with eucalypts in Australia. In 'Ectomycorrhizal research for forestry in Asia'. (Eds M Brundrett, B Dell, N Malajczuk, M Gong) pp. 8–15. (Australian Centre for International Agricultural Research: Canberra, ACT, Australia)
- Claridge AW (2002) Ecological role of hypogeous ectomycorrhizal fungi in Australian forests and woodlands. *Plant and Soil* **244**, 291–305. doi:10.1023/A:1020262317539
- Claridge AW, Barry SC (2000) Factors influencing the distribution of medium-sized ground-dwelling mammals in southeastern mainland Australia. *Austral Ecology* **25**, 676–688. doi:10.1111/j.1442-9993.2000.tb00074.x
- Claridge AW, Tanton MT, Seebeck JH, Cork SJ, Cunningham RB (1992) Establishment of ectomycorrhizae on the roots of two species of *Eucalyptus* from fungal spores contained in the faeces of the long-nosed potoroo (*Potorous tridactylus*). *Australian Journal of Ecology* **17**, 207–217. doi:10.1111/j.1442-9993.1992.tb00799.x
- Claridge AW, Cunningham RB, Tanton MT (1993) Foraging patterns of the long-nosed potoroo (*Potorous tridactylus*) for hypogeous fungi in mixed-species and regrowth eucalypt forest stands in southeastern Australia. *Forest Ecology and Management* **61**, 75–90. doi:10.1016/0378-1127(93)90191-0
- Claridge AW, Paull DJ, Welbourne DJ (2019) Elucidating patterns in the occurrence of threatened ground-dwelling marsupials using camera-traps. *Animals* **9**, 913. doi:10.3390/ani9110913
- Davies GTO, Kirkpatrick JB, Cameron EZ, Carver S, Johnson CN (2019) Ecosystem engineering by digging mammals: effects on soil fertility and condition in Tasmanian temperate woodland. *Royal Society Open Science* **6**, 180621. doi:10.1098/rsos.180621
- Department of Energy, Infrastructure and Resources (2014) 'Structure of datasets. Mineral resources Tasmania.' (Department of Energy, Infrastructure and Resources)
- DPIPWE (2010) 'Spotlight survey manual.' (Department of Primary Industries, Parks, Water and Environment)
- DPIPWE (2020) 'TASVEG 4.0.' (Tasmanian Vegetation Monitoring and Mapping Program, Natural and Cultural Heritage Division, Department of Primary Industries, Parks, Water and Environment)
- Dickman CR (1996) Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology* **2**, 185–195. doi:10.2981/wlb.1996.018
- Donaldson R, Stoddart M (1994) Detection of hypogeous fungi by Tasmanian bettong (*Bettongia gaimardi*: Marsupialia; Macropodoidea). *Journal of Chemical Ecology* **20**, 1201–1207. doi:10.1007/BF02059754
- Driessen MM, Jarman PJ (2014) Comparison of camera trapping and live trapping of mammals in Tasmanian coastal woodland and heath-land. In 'Camera trapping: wildlife management and research'. (Eds PD Meek, PJS Flemming, G Ballard, P Banks, AW Claridge, J Sanderson, D Swann) pp. 253–262. (CSIRO Publishing: Melbourne, Vic., Australia)
- Driessen MM, Jarman PJ, Visoiu M, Dewar E (2021) Mammal responses to moderate-intensity planned burning in a small, isolated woodland reserve. *Wildlife Research* **48**, 561–576. doi:10.1071/WR20165
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**, 4302–4315. doi:10.1002/joc.5086
- Frankham GJ, Handasyde KA, Eldridge MDB (2016) Evolutionary and contemporary responses to habitat fragmentation detected in a mesic zone marsupial, the long-nosed potoroo (*Potorous tridactylus*) in south-eastern Australia. *Journal of Biogeography* **43**, 653–665. doi:10.1111/jbi.12659
- Gardiner R, Hamer R, Leos-Barajas V, Peñaherrera-Palma C, Jones ME, Johnson C (2019a) State-space modeling reveals habitat perception of a small terrestrial mammal in a fragmented landscape. *Ecology and Evolution* **9**, 9804–9814. doi:10.1002/ece3.5519
- Gardiner R, Proft K, Comte S, Jones M, Johnson CN (2019b) Home range size scales to habitat amount and increasing fragmentation in a mobile woodland specialist. *Ecology and Evolution* **9**, 14005–14014. doi:10.1002/ece3.5837
- Johnson CN (1994a) Distribution of feeding activity of the Tasmanian bettong (*Bettongia gaimardi*) in relation to vegetation patterns. *Wildlife Research* **21**, 249–255. doi:10.1071/WR9940249
- Johnson C (1994b) Fruiting of hypogeous fungi in dry sclerophyll forest in Tasmania, Australia: seasonal variation and annual production. *Mycological Research* **98**, 1173–1182. doi:10.1016/S0953-7562(09)80201-3
- Johnson CN (1994c) Mycophagy and spore dispersal by a rat-kangaroo: consumption of ectomycorrhizal taxa in relation to their abundance. *Functional Ecology* **8**, 464–468. doi:10.2307/2390070
- Johnson CN (1994d) Nutritional ecology of a mycophagous marsupial in relation to production of hypogeous fungi. *Ecology* **75**, 2015–2021. doi:10.2307/1941606
- Johnson CN (1995) Interactions between fire, mycophagous mammals, and dispersal of ectomycorrhizal fungi in *Eucalyptus* forests. *Oecologia* **104**, 467–475. doi:10.1007/BF00341344
- Johnson CN (1997) Fire and habitat management for a mycophagous marsupial, the Tasmanian bettong *Bettongia gaimardi*. *Australian Journal of Ecology* **22**, 101–105. doi:10.1111/j.1442-9993.1997.tb00645.x
- Johnston PG (2010) Long-nosed potoroo. In 'Field companion to the mammals of Australia'. (Eds S VanDyck, I Gynther, A Baker) pp. 95. (Reed New Holland: Sydney, NSW, Australia)
- Kitchener DJ (1973) Notes on the home range and movement in two small macropods, the Potoroo (*Potorous apicalis*) and the Quokka (*Setonix brachyurus*). *Mammalia* **37**, 231–240. doi:10.1515/mamm.1973.37.2.231
- Kitchener A, Harris S (2013) 'From forest to fjældmark: descriptions of Tasmania's vegetation.' 2nd edn. (Department of Primary Industries, Parks, Water and Environment: Tas., Australia)
- Michaels K (2006) 'A manual for assessing vegetation condition in Tasmania. Version 1.' (Resource Management and Conservation, Department of Primary Industries, Water and Environment: Hobart, Tas., Australia)
- Munro NT, McIntyre S, Macdonald B, Cunningham SA, Gordon IJ, Cunningham RB, Manning AD (2019) Returning a lost process by reintroducing a locally extinct digging marsupial. *PeerJ* **7**, e6622. doi:10.7717/peerj.6622
- Norton MA, Claridge AW, French K, Prentice A (2010a) Population biology of the long-nosed potoroo (*Potorous tridactylus*) in the southern highlands of New South Wales. *Australian Journal of Zoology* **58**, 362–368. doi:10.1071/ZO10075
- Norton MA, French K, Claridge AW (2010b) Habitat associations of the long-nosed potoroo (*Potorous tridactylus*) at multiple spatial scales. *Australian Journal of Zoology* **58**, 303–316. doi:10.1071/ZO10042
- Norton MA, Prentice A, Dingle J, French K, Claridge AW (2015) Population characteristics and management of the long-nosed potoroo (*Potorous tridactylus*) in high-quality habitat in the Southern Highlands of New South Wales. *Australian Mammalogy* **37**, 67–74. doi:10.1071/AM14026
- Possingham HP, Wilson KA, Andelman SJ, Vynne CH (2006) Protected areas: goals, limitations, and design. In 'Principles of conservation biology'. (Eds MJ Groom, GK Meefe, CR Carroll) pp. 516–519. (Sinauer Associates, Inc.: Sunderland, MA, USA)
- Proft KM, Bateman BL, Johnson CN, Jones ME, Pauza M, Burrige CP (2021) The effects of weather variability on patterns of genetic diversity in Tasmanian bettongs. *Molecular Ecology* **30**, 1777–1790. doi:10.1111/mec.15847
- R Core Team (2020) 'R: a language and environment for statistical computing.' (R Foundation for Statistical Computing: Vienna, Austria). Available at <https://www.R-project.org/>
- Robley A, Gormley AM, Forsyth DM, Triggs B (2014) Long-term and large-scale control of the introduced red fox increases native

- mammal occupancy in Australian forests. *Biological Conservation* **180**, 262–269. doi:10.1016/j.biocon.2014.10.017
- Rose RW, Rose RK (1998) *Bettongia gaimardi*. *Mammalian Species* **584**, 1–6. doi:10.2307/3504399
- Ross CE, Munro NT, Barton PS, Evans MJ, Gillen J, Macdonald BCT, McIntyre S, Cunningham SA, Manning AD (2019) Effects of digging by a native and introduced ecosystem engineer on soil physical and chemical properties in temperate grassy woodland. *PeerJ* **7**, e7506. doi:10.7717/peerj.7506
- Ross CE, McIntyre S, Barton PS, Evans MJ, Cunningham SA, Manning AD (2020) A reintroduced ecosystem engineer provides a germination niche for native plant species. *Biodiversity and Conservation* **29**, 817–837. doi:10.1007/s10531-019-01911-8
- Slankis V (1974) Soil factors influencing formation of mycorrhizae. *Annual Review of Phytopathology* **12**, 437–457. doi:10.1146/annurev.py.12.090174.002253
- Taylor RJ (1992) Seasonal changes in the diet of the Tasmanian bettong (*Bettongia gaimardi*), a mycophagous marsupial. *Journal of Mammalogy* **73**, 408–414. doi:10.2307/1382076
- Taylor RJ (1993a) Habitat requirements of the Tasmanian bettong (*Bettongia gaimardi*), a mycophagous marsupial. *Wildlife Research* **20**, 699–710. doi:10.1071/WR9930699
- Taylor RJ (1993b) Home range, nest use and activity of the Tasmanian bettong, *Bettongia gaimardi*. *Wildlife Research* **20**, 87–95. doi:10.1071/WR9930087
- Taylor RJ, Bryant SL, Pemberton D, Norton TW (1985) Mammals of the Upper Henty River region, Western Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **119**, 7–14. doi:10.26749/rstpp.119.7
- Tory MK, May TW, Keane PJ, Bennett AF (1997) Mycophagy in small mammals: a comparison of the occurrence and diversity of hypogean fungi in the diet of the long-nosed potoroo *Potorous tridactylus* and the bush rat *Rattus fuscipes* from southwestern Victoria, Australia. *Australian Journal of Ecology* **22**, 460–470. doi:10.1111/j.1442-9993.1997.tb00697.x
- Trent SW (2015) Assessment of habitat factors and development of a species distribution model for the long nosed potoroo (*Potorous tridactylus tridactylus*) in SEQ. Master's thesis, University of Southern Queensland, Toowoomba, Qld, Australia.
- Vernes K, Jarman P (2014) Long-nosed potoroo (*Potorous tridactylus*) behaviour and handling times when foraging for buried truffles. *Australian Mammalogy* **36**, 128–130. doi:10.1071/AM13037
- Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes J-A, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**, 1310–1324. doi:10.1111/j.1461-0248.2010.01515.x
- Wintle BA, Cadenhead NCR, Morgain RA, Legge SM, Bekessy SA, Cantele M, Possingham HP, Watson JEM, Maron M, Keith DA, Garnett ST, Woinarski JCZ, Lindenmayer DB (2019) Spending to save: what will it cost to halt Australia's extinction crisis?. *Conservation Letters* **12**, e12682. doi:10.1111/conl.12682
- Woinarski JCZ, Burbidge AA, Harrison PL (2015) A review of the conservation status of Australian mammals. *Therya* **6**, 155–166. doi:10.12933/therya-15-237

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