Research Article

Fragmentation of the Southern Brown Bandicoot *Isoodon obesulus*: Unraveling Past Climate Change from Vegetation Clearing

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Distribution modeling and vegetation suitability mapping were undertaken to assess (1) the role that past climate change played in fragmenting a subspecies of the endangered southern brown bandicoot *Isoodon obesulus* and (2) the impacts of land cover change on the subspecies following European settlement of Australia. Based on a selection of bioclimatic variables, disjunctions in the broad distribution of *I. obesulus obesulus* were found. Vegetation maps representing the time of European settlement revealed two clear features. First, vegetation that was unsuitable for the subspecies corresponded to climatic disjunctions in its distribution, and, second, substantial additional areas were predicted to have suitable vegetation but not suitable climate. Vegetation mapping showed considerable change over two centuries after European settlement, so that most places that formerly had suitable climate and vegetation were cleared. Our analysis demonstrates that clearing of native vegetation has masked naturally occurring disjunctions in the distribution of *I. o. obesulus*. This finding provides evidence that fragmented, regional-scale populations of *I. o. obesulus* existed prior to European settlement. Implications for conservation planning are discussed.

1. Introduction

Fragmentation has been variously described as either naturally occurring or anthropogenic disruption to habitat continuity that can operate across multiple spatial, temporal, and functional domains [1–3]. Most fragmentation studies focus on the patch scale and biotic effects of relatively recent anthropogenic impacts, for example, loss of habitat through vegetation clearing, increased isolation of remnants, and exposure to edge effects [4–7]. But fragmentation can be considered at much broader spatial and temporal scales including global-scale vicariance events, such as continental drift in the Paleocene-Pliocene, or regional-scale disruption to species distributions during the Pleistocene and Holocene. For example, marsupial evolution and radiation in Australia and South America are largely understood in the context of

the continents' long-term isolation following separation from Gondwana [8], and at a different, finer scale, the distribution of oligostenothermic species such as the mountain pygmy-possum *Burramys parvus* in south-eastern Australia has been fragmented by the change to the thermocline after the last glacial maximum [9]. Scale is a key issue in the present study in which we examine how natural and anthropogenic factors have interacted to fragment the distribution of an endangered species, the southern brown bandicoot *Isoodon obesulus* in south-eastern Australia. Resolution of two modes of fragmentation, long-term natural versus recent anthropogenic change, is important for understanding inter-regional genetic variation in this species and has important implications for planning conservation initiatives, particularly regarding selection of stock for captive breeding and translocation of individuals between wild populations.
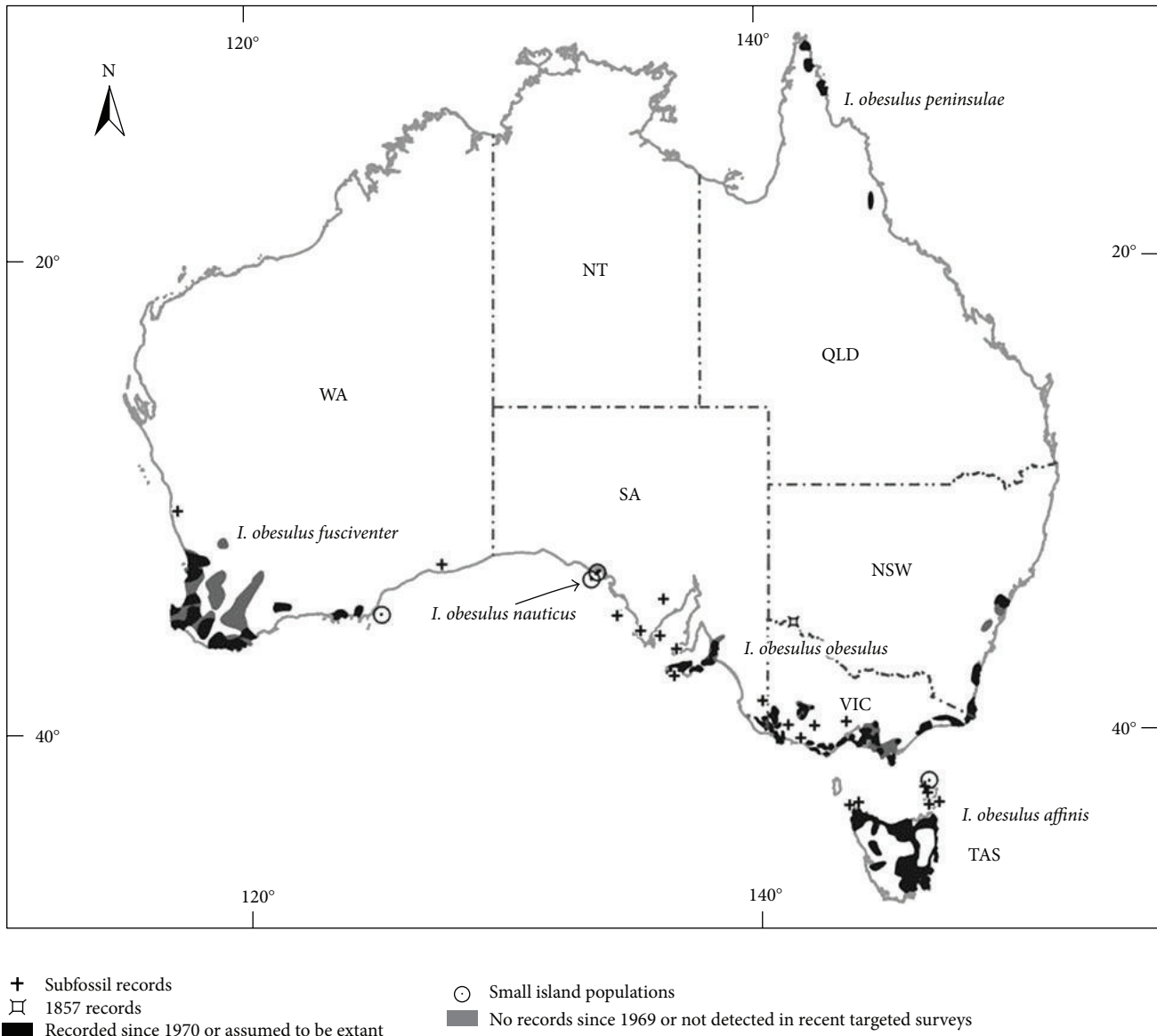
Figure 1: Distribution of *Isoodon obesulus*. Adapted from Rees and Paull [17] and Pope et al. [21]. Originally compiled by Rees and Paull [17] from distribution records published by Ashby et al. [11], Friend [22], Gordon et al. [23], Hocking [24], Kemper [14], Menkhorst and Seebeck [18], and Paull [19]. NSW: New South Wales, NT: Northern Territory, SA: South Australia, TAS: Tasmania, QLD: Queensland, VIC: Victoria, WA: Western Australia.

Isoodon obesulus is a medium-small (~0.5–1.8 kg), omnivorous, ground-dwelling marsupial that has a highly fragmented distribution across the margins of southern and eastern Australia (Figure 1). The total distribution of the species *Isoodon obesulus* in Australia includes five subspecies [10] with the subject of the present study being *Isoodon obesulus obesulus* in the States of South Australia, Victoria, and New South Wales. Its closest relatives are located in the far north of Queensland (*I. o. peninsulae*), in Tasmania (*I. o. affinis*), on islands of Nuyts Archipelago in the Great Australian Bight (*I. o. nauticus*), and in south-western Western Australia (*I. o. fusciventer*). Within the distribution of the subspecies, discrete regional populations exist, and this is the scale of fragmentation we address for *I. o. obesulus*. In the 1800s,

I. o. obesulus was reported to be the most common bandicoot and one of the most abundant mammals in south-eastern Australia [11, 12], but by the 1920s it was extremely rare [13]. Clearing of native vegetation, modification of remnant habitats, introduction of exotic carnivores, and changes to fire regimes have been cited as causes for its decline [14–16]. Because its numbers have been so severely reduced [11, 13, 14, 17–20], it is now listed as endangered under the Australian Commonwealth *Environment Protection and Biodiversity Conservation (EPBC) Act 1999*.

With vast areas of native vegetation having been cleared throughout the range of *I. o. obesulus* [25–28], it is uncertain whether its distribution was already fragmented at the time of European settlement in 1788 by long-standing, naturally

occurring barriers. If past climate change, for example, caused disjunctions within the distribution of *I. o. obesulus*, then some populations that exist today may have been isolated long enough to be substantially genetically distinct. Conversely, if fragmentation was caused by vegetation clearing following European settlement, these distinctions would be less pronounced and perhaps not of consequence for conservation planning.

The explicit aim of this paper is, therefore, to determine if the distribution of *I. o. obesulus* was continuous or fragmented throughout its total range at the time of European settlement of Australia. Specifically, was the fragmented distribution pattern that we see today attributable solely to vegetation change since European settlement in 1788 or to a combination of natural and anthropogenic factors? To clarify this issue, we combined a climate modeling approach with vegetation suitability mapping.

2. Methods

2.1. Distribution Model. The distribution of suitable climate for *I. o. obesulus* was modeled using a combination of climatic data generated with BIOCLIM in ANUCLIM 5.1 [29, 30], generalized additive models (GAMs) [31] in SPLUS (7.0), and ArcView GIS 3.3 (ESRI, Redlands, CA, USA). Species distribution modeling with BIOCLIM has been undertaken for many vertebrate species (see, e.g., [32–36]). Typically, these types of analyses generate statistical profiles of climatic variables at point localities where species have been recorded then apply homocline matching to model potential bioclimatic distributions. For the present study, a modified approach was adopted whereby locality records were used to define sampling areas (not points) within which *I. o. obesulus* has been recorded. Between these known "presence" areas, we established "pseudo-absence" areas where the species has never been recorded. To assume that a species is absent from an area may not be valid when few occurrence records exist [37], but in the case of *I. o. obesulus* there are hundreds of records dating back to the Nineteenth Century. The approach of establishing presence/pseudo-absence data was taken to reduce unknown sampling biases often present in wildlife survey data, for example, where many records are co-located due to biased field survey effort, and it allowed probability estimates to be calculated for each discrete sampling area, thus avoiding the issue of arbitrarily defining a "core" bioclimatic distribution as encountered in other studies (see, e.g., [38, 39]).

Locality records for *I. o. obesulus* were compiled from the South Australian Museum, Museum Victoria, the Australian Museum, the Atlas of Victorian Wildlife database, the New South Wales Wildlife Atlas database, and field survey results of Paull [19] and Rees and Paull [17]. These combined sources totaled 1561 records, of which one-fifth were considered to be unique, accurate, and reliable based on the following criteria: (1) records duplicated between data sources were used only once; (2) records with an estimated positional error >1500 m were excluded from analysis; (3) records of *I. o. obesulus* hairs in predator scats were omitted because scats were collected an unknown distance from where prey was captured;
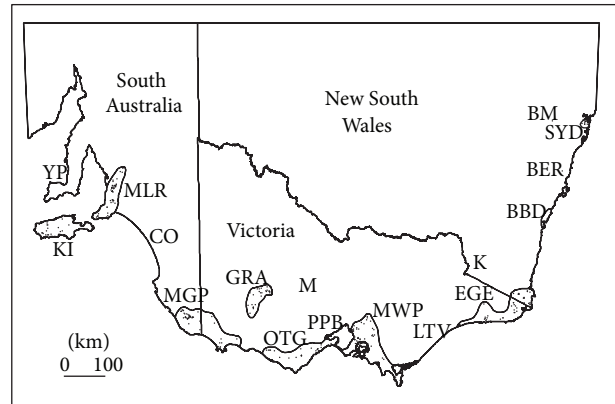

Figure 2: Occurrence records for *Isoodon obesulus obesulus* in south-eastern Australia. BBD: Batemans Bay to Durras region, BER: Berry, BM: Blue Mountains, CO: Coorong lagoon, EGE: East Gippsland to Eden region, GRA: Grampian Ranges, K: Khancoban, KI: Kangaroo Island, LTV: La Trobe Valley, M: Maldon, MGP: Mount Gambier to Portland region, MLR: Mount Lofty Ranges, MWP: Melbourne to Wilsons Promontory region, OTG: Otway Ranges to Geelong region, PPB: Port Phillip Bay, SYD: Sydney region, YP: Yorke Peninsula.

(4) subfossil records from cave deposits were omitted because their age and contemporary climatic conditions were unknown; (5) indirect, potentially unreliable observations of *I. o. obesulus*, including nests and signs of foraging, were excluded; (6) records from Eyre Peninsula in South Australia and from the north of Hawkesbury River in New South Wales were rejected because it is doubtful if they actually refer to *I. o. obesulus* ([19, 40] C. Kemper, personal communication; J. Dixon, personal communication; P. Johnston, personal communication). At the conclusion of the screening process, 338 records were selected for modeling (Figure 2) with an age distribution of 1895–1970 (58 records), 1971–1980 (68 records), 1981–1990 (131 records), and 1991–2000 (81 records).

The selected bandicoot locality records were mapped in ArcView and a hexagonal sampling array with a cell size of 0.25° was overlaid within a 200 km buffer zone from the coast (as guided by the experimental results of VanDerWal et al. [41]) using the DNR sampling tool (V2.1, 22 June 2004). Hexagonal cells in the array were then assigned binary values of "1" for presence (79 cells) or "0" for pseudo-absence (768 cells) (Figure 3). Next, a systematically distributed sample of 19,812 points was established across the hexagonal array, with each point spaced 0.05° apart. An elevation value (m above sea level) was extracted for each point using a digital elevation model (DEM) with a cell size of 0.025° and the ArcView extension Get Grid Value. Values for each of the 35 default BIOCLIM climatic variables [30] were calculated for each of the 19,812 points. The final stage of data preparation was to calculate the arithmetic mean values of the 35 BIOCLIM variables for each hexagonal presence/pseudo-absence cell based on the sampling points that fell within them.

Based on these data, GAMs were developed after first testing for correlation between the climatic variables and choosing those with least correlation for the modeling
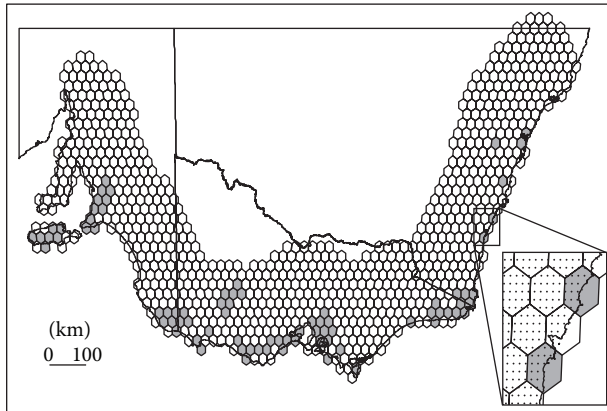
FIGURE 3: Hexagonal sampling scheme used to characterize climate throughout the distribution of *Isoodon obesulus obesulus* in southeastern Australia. Gray hexagons have locality records of *I. o. obesulus* associated with them whereas hollow hexagons have no records and were, therefore, treated as regions where the subspecies is absent. BIOCLIM values were calculated based on overlaid points illustrated in the inset.

process. BIOCLIM variables that were Pearson correlated with any other variables by >0.7 were culled from analysis leaving 11 candidate explanatory climatic variables (annual mean temperature, isothermality, maximum temperature of the warmest period, minimum temperature of the coldest period, annual precipitation, precipitation seasonality, precipitation of coldest quarter, annual mean radiation, radiation seasonality, radiation of wettest quarter, and highest period moisture index). Three GAMs were calculated using backward selection of variables at the significance level of α = 0.05, with each model having progressively fewer explanatory variables to highlight those aspects of climate that had the greatest influence on the distribution of *I. o. obesulus*. Finally, spatial predictions for *I. o. obesulus* were made by mapping probability estimates from the GAMs across the hexagonal array.

2.2. Analysis of Vegetation Change. Throughout southeastern Australia, *I. o. obesulus* has been documented in native vegetation that includes heathland, shrubland, woodland, and forest communities (Table 1). Common attributes are dense ericaceous shrubs in the ground stratum (0-1 m), thought to be associated with predator avoidance [19]. *Isoodon o. obesulus* also makes limited use of some exotic vegetation, for example, blackberry *Rubus* spp. [19], but only where suitable native vegetation exists nearby. Vegetation types that are avoided include wet and closed forests and communities with grassy lower strata. Based on these known habitat relationships, weightings were used to rank the suitability of vegetation types represented in two digitized vegetation maps, namely, Vegetation of Australia 1788 and Vegetation of Australia 1988 [42, 43]. A modified version of Bryan's [44] generic GIS method for mapping habitat suitability (Table 2(a)) was used in ArcView GIS to combine the dominant species of the tallest stratum and the growth form of the lowest stratum, to produce spatial predictions

of vegetation suitable for *I. o. obesulus* (Table 2(b)). These two particular vegetation attributes were selected because they directly related to the structure and floristic composition of *I. o. obesulus* habitats as summarized in Table 1. They covered the entire study area and were the best available representation at this scale of vegetation at the time of European settlement and two centuries later at a nominal scale of 1 : 5,000,000.

3. Results

3.1. Statistical Predictions. Three GAMs were calculated that incorporated BIOCLIM variables relating to precipitation and temperature. They contained six, four, and three significant variables with adjusted D^2 values of 0.518, 0.403, and 0.378, respectively (Figure 4). Temperature annual range (TAR) and precipitation of the driest period (PDP) were inversely related with the probability of *I. o. obesulus* occurring within a hexagonal cell being greatest when values of TAR were low (approximately <20°C) and PDP was high (approximately >15 mm). Other explanatory variables (annual precipitation (AP), precipitation seasonality (PS), isothermality (ISO), and annual mean temperature (AMT)) approximated Gaussian functions, indicating that *I. o. obesulus* was most likely to occur in places where these variables took values intermediate to the ranges provided in Figure 4.

Figure 4 indicates how each variable would respond if the others were held at their mean values. To illustrate the interaction between variables, a three-dimensional representation of the three-variable model (PDP + TAR + AP) is provided in Figure 5. This clearly shows the inverse relationship between TAR and PDP and that the greatest probabilities for *I. o. obesulus* occur when values of TAR are small and values of PDP are large. Figure 5 also shows that when these two variables interact with AP, the probability of *I. o. obesulus* occurring increases above P = 0.5 only if AP exceeds ~500 mm, reaching a maximum of P = 0.94 at AP = 891 mm and PDP = 21.6 mm and TAR 13.6°C before decreasing to P < 0.5 at AP = 1495 mm.

3.2. Spatial Predictions. When the probability estimates from the three GAMs were mapped to the hexagonal sampling units, the spatial predictions matched all known major disjunctions in the distribution of *I. o. obesulus* (Figures 1–3, cf. Figures 6(a)–6(c)). The largest of these gaps occurred at the Coorong lagoon in South Australia (SA), and at Port Phillip Bay and the La Trobe Valley in Victoria (VIC). In terms of areas where *I. o. obesulus* currently exists, all three models predicted the region with the most suitable climate to be from East Gippsland (VIC) to Eden in New South Wales (NSW). The six-variable model (AP + PDP + PS + TAR + ISO + AMT) predicted the Mount Lofty Ranges (SA) to also have highly suitable climate for *I. o. obesulus*, with other noteworthy areas being the western part of Kangaroo Island (SA), the Mount Gambier-Portland region (SA-VIC border), the Otway Ranges-Geelong region (VIC), the Melbourne-Wilsons Promontory region (VIC), and the Batemans Bay-Durras region (NSW). The bioclimatic models

TABLE 1: Vegetation types used by *Isoodon obesulus obesulus* throughout its range.

Region	Vegetation types
Kangaroo Island	*Eucalyptus* woodlands, coastal shrublands, heathlands, and mallee [45]
Mount Lofty Ranges	*Eucalyptus obliqua* open forests and woodlands with heath-associated plants in the shrub and ground layers [45]
South-eastern South Australia	Low and medium *Eucalyptus baxteri* woodlands with sparse shrub and dense heath ground layers [45]
South-western Victoria	Open and low-open forests of *Eucalyptus baxteri* and *Eucalyptus obliqua*, open and closed *Banksia marginata* heathlands, *Melaleuca squarrosa* closed scrubs, coastal shrublands, and coastal heathlands [46, 47]
Grampians	Heathlands [48]
Otway Ranges	*Eucalyptus baxteri* open forests and habitats dominated by *Allocasuarina paludosa*, and *Leptospermum continentale* [49, 50]
Melbourne region	Heathlands and shrublands dominated by *Leptospermum myrsinoides*, *Melaleuca squarrosa*, *Banksia marginata*, *Gahnia sieberiana*, and *Leptospermum continentale* [51–56]
East Gippsland	*Leptospermum myrsinoides* heathlands, *Banksia* woodlands, coastal heathlands, damp sclerophyll forests, and coastal sclerophyll forests [57]
South-eastern New South Wales	Associations dominated by *Eucalyptus sieberi*, *Eucalyptus agglomerata*, *Eucalyptus globoidea*, *Eucalyptus cypellocarpa*, and *Eucalyptus gummifera* (Andrew Claridge pers. obs.)
Sydney region	Open *Eucalyptus* woodlands and heathlands on sandstone ridges. Associations of *Eucalyptus sieberi*, *E. capitellata*, *E. gummifera*, *E. sparsifolia*, *E. racemosa*, *E. piperita*, *E. pilularis,* and *Angophora costata* (Andrew Claridge pers. obs.)

predicted low probabilities of *I. o. obesulus* occurring near Maldon in central Victoria, in the Blue Mountains (NSW), at Khancoban (NSW), and north of Hawkesbury River near Sydney (NSW), all of which are associated with unverified records of the subspecies. Interestingly, two hexagons at the base of Yorke Peninsula (SA) were predicted by each model to have relatively high probabilities of *I. o. obesulus* occurring ($P = 0.41$–0.88), although no input records came from there.

A key feature of the spatial predictions was that having fewer terms incorporated into the GAMs resulted in progressively less fragmentation because having fewer terms reduced the fit of the models. The six-variable model incorporated the greatest number of explanatory terms, most closely reflected the distribution of the input records, and concurred best with the known distribution of *I. o. obesulus* (Figure 1). The four-variable and three-variable models indicated less habitat fragmentation; for example, the Mount Gambier-Portland and Otway Ranges-Geelong regions coalesced in these instances. The six-variable model was the only one that showed the Grampian Ranges (VIC) to be fragmented from its neighbouring regions due to climatic factors.

3.3. Vegetation Suitability in 1788 and 1988. The 1788 vegetation suitability map indicated that the distribution of *I. o. obesulus* was likely fragmented at the time of European settlement with unsuitable plant cover existing immediately to the south-east of the Mount Lofty Ranges, between the Mount Gambier-Portland and Otway-Geelong regions, and to the north of Port Phillip Bay (Figure 7(a)). Based on what is known of habitat use by the subspecies (Table 1), parts of the Sydney region, including the Cumberland Plain, would formerly have had unsuitable lower stratum vegetation dominated by tussocky or tufted grasses on shale substrate,

yet optimal areas of heath did, and still do, exist to the north and south of Sydney on sandstone [59, 60]. Large areas of suboptimal vegetation occurred in 1788 in places between the Mount Gambier-Portland and Otway Ranges-Geelong regions, as well as extending north-eastwards from the Melbourne-Wilsons Promontory region towards Sydney. Substantial areas of optimal vegetation were mapped in places where the climate models predicted low probabilities of *I. o. obesulus* being present, for example, inland from the Coorong lagoon, in Victoria's Central Highlands, and in the Blue Mountains. On Kangaroo Island, vegetation was predicted to be more suitable for the subspecies in the eastern half of the island compared to the western half, which was the reverse direction indicated for suitable climate (Figure 6 c.f. Figure 7).

By 1988, vegetation cover for *I. o. obesulus* had become broadly unsuitable in most of the areas where it was formerly optimal (Figure 7(b)), and this occurred particularly where the species had the greatest probabilities of occurring according to the climate models (Figures 6(a)–6(c)). Of all the regions where *I. o. obesulus* is currently known to exist, only the Grampian Ranges in Victoria appear to have avoided major anthropogenic transformation of formerly optimal vegetation cover.

4. Discussion

4.1. Fragmentation Factors. Our analysis highlights that the distribution of *I. o. obesulus* has been fragmented by a combination of underlying climatic factors, natural vegetation patterns, and subsequent "superimposed" anthropogenic clearing of native vegetation. Major geographic barriers, such as rivers or highlands, are not obvious at the points

TABLE 2: (a) Matrix of vegetation suitability for *Isoodon obesulus obesulus* and (b) suitability classification of the tallest and lower strata for *Isoodon obesulus obesulus*. Specht et al. [58] classes are used in the table for vegetation structural forms.

(a)

| | | Lower stratum | | |
		Optimal	Suboptimal	Unsuitable
Tallest stratum	Optimal	Optimal	Suboptimal	Unsuitable
	Suboptimal	Suboptimal	Suboptimal	Unsuitable
	Unsuitable	Unsuitable	Unsuitable	Unsuitable

(b)

	Assessment criteria
Tallest stratum dominants: structural formation	
Banksia: heathland	Optimal
Casuarina: low woodland, low open woodland	Optimal
Eucalyptus: tall-open forest, open forest, low-open forest, woodland, open woodland, low woodland, low-open woodland, open scrub, tall shrubland, tall-open shrubland	Optimal
Melaleuca: low woodland, low-open woodland	Optimal
Acacia: low-open woodland	Suboptimal
Mixed or other: low woodland, low-open woodland, tall shrubland, tall-open shrubland, heathland, open heathland	Suboptimal
Chenopodiaceae: open heathland, sparse heathland	Unsuitable
Conifers: closed forest, low-open woodland	Unsuitable
Fabaceae: other herbaceous plants	Unsuitable
Graminoids: tussock Grassland	Unsuitable
Myoporum: low-open woodland	Unsuitable
Nothofagus: closed forest	Unsuitable
Other grasses: tussock grassland, other herbaceous plants	Unsuitable
Lower stratum growth form	
Low shrubs <2 m	Optimal
Low trees <10 m	Suboptimal
Tall shrubs >2 m	Suboptimal
Hummock grasses	Unsuitable
Other herbaceous plants	Unsuitable
Tussocky or tufted grasses	Unsuitable
No lower stratum	Unsuitable

of disjunction, but unrecognized physical discontinuities may exist. Broad-scale soil variations, for example, may have contributed to the fragmented distribution of *I. o. obesulus* at the time of European settlement, which would be generally reflected in the vegetation mapping. The models we developed were based on the assumption that the climatic niche of *I. o. obesulus* has not altered since 1788 and that no major changes to regional climate have taken place. This may not, in fact, be realistic as some analysts suggest that rainfall and minimum temperatures in south-eastern Australia have trended slightly upwards over the past century [61]. Regardless, the distribution of optimal vegetation has certainly changed in a radical way throughout the study area due to land clearing for agriculture, establishment of urban areas, and other human land uses. It is difficult to separate the

influence of climate from the influence of vegetation in defining the distribution of *I. o. obesulus*: climate clearly underpins its distribution but the vegetation patterns are strongly related to climate [62]. Comparing the *c.* 1988 map to the *c.* 1788 map of vegetation suitability reveals considerable change over 200 years so any "natural" fragmentation in the distribution of *I. o. obesulus* that formerly existed has been masked by human-induced transformations to land cover. The models indicate where former, natural, and long-standing disjunctions most likely existed and, importantly, highlight that very few places remain where optimal vegetation and suitable climate for *I. o. obesulus* coincide.

The relationship between *I. o. obesulus* and vegetation is reasonably well understood particularly regarding the requirement for dense cover for nesting, foraging, and
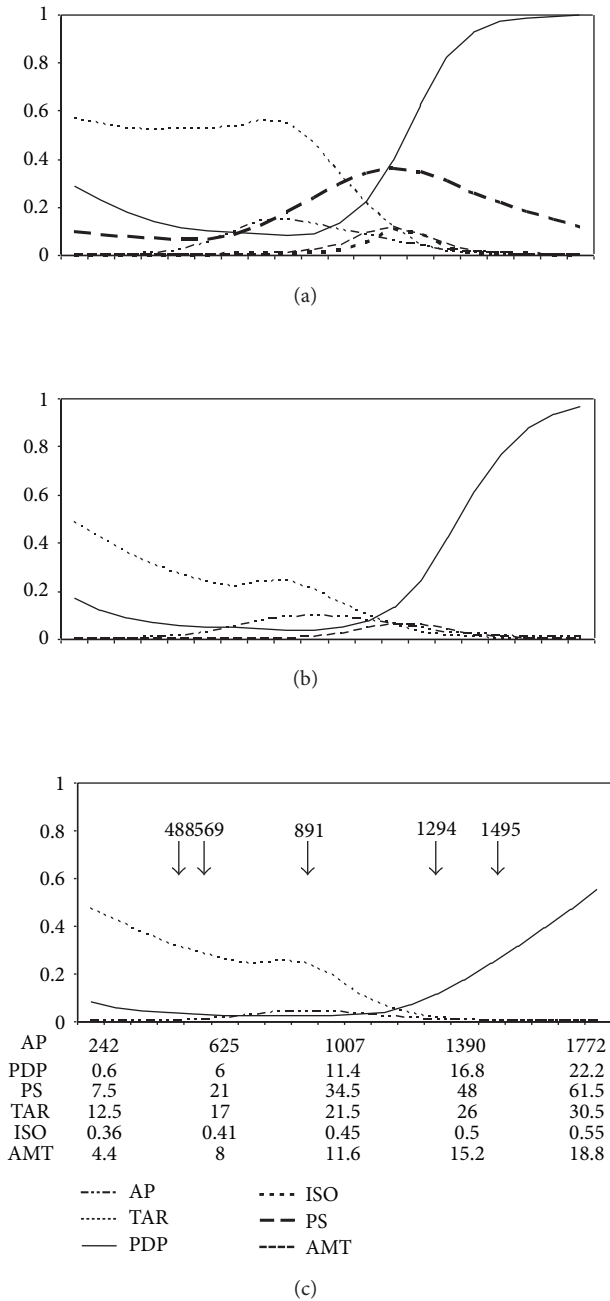
Figure 4: Generalized additive models of the bioclimatic distribution of *Isoodon obesulus obesulus*, based on (a) six variables, (b) four variables, and (c) three variables. *y*-axis: probability of occurrence. *x*-axis: BIOCLIM variables. AP (annual precipitation in mm: sum of all monthly precipitation estimates); PDP (precipitation of the driest period in mm interpolated weeks); PS (precipitation seasonality: Coefficient of Variation, the standard deviation of weekly precipitation estimates expressed as a percentage of the annual mean); TAR (temperature annual range in ˚C: maximum temperature of the warmest week minus minimum temperature of the coldest week); ISO (isothermality: mean diurnal range (weekly maximum minus minimum) divided by temperature annual range); AMT (annual mean temperature in ˚C: mean of all weekly mean temperatures, which are the mean of each week's maximum and minimum temperatures). Arrows and numerals on (c) indicate values of AP illustrated in Figure 5.
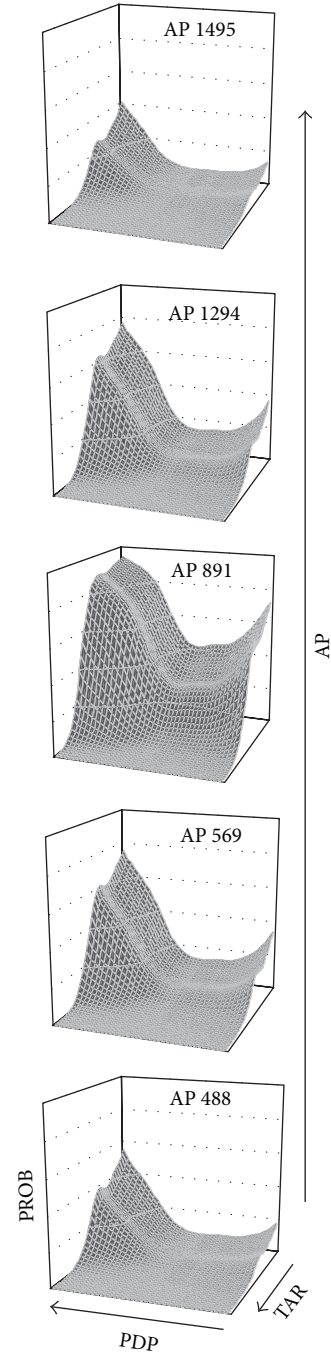
Figure 5: Three-dimensional representation of the three-term model at five values of annual precipitation (AP) in mm. Values on the *x*, *y* and *z*-axes of each graph range between 0 and 21.6 mm for precipitation of the driest period (PDP), 13.6–29.4˚C for temperature annual range (TAR), and 0-1 for probability (PROB).

predator avoidance [10]. Relationships between *I. o. obesulus* and the climatic variables are less easy to interpret although hypotheses developed by Shan et al. [63] regarding soil moisture and the invertebrates eaten by *I. o. obesulus* offer insights. Foraging by *I. o. obesulus* takes place in the top soil, and if the ground is either too wet (waterlogged) or too
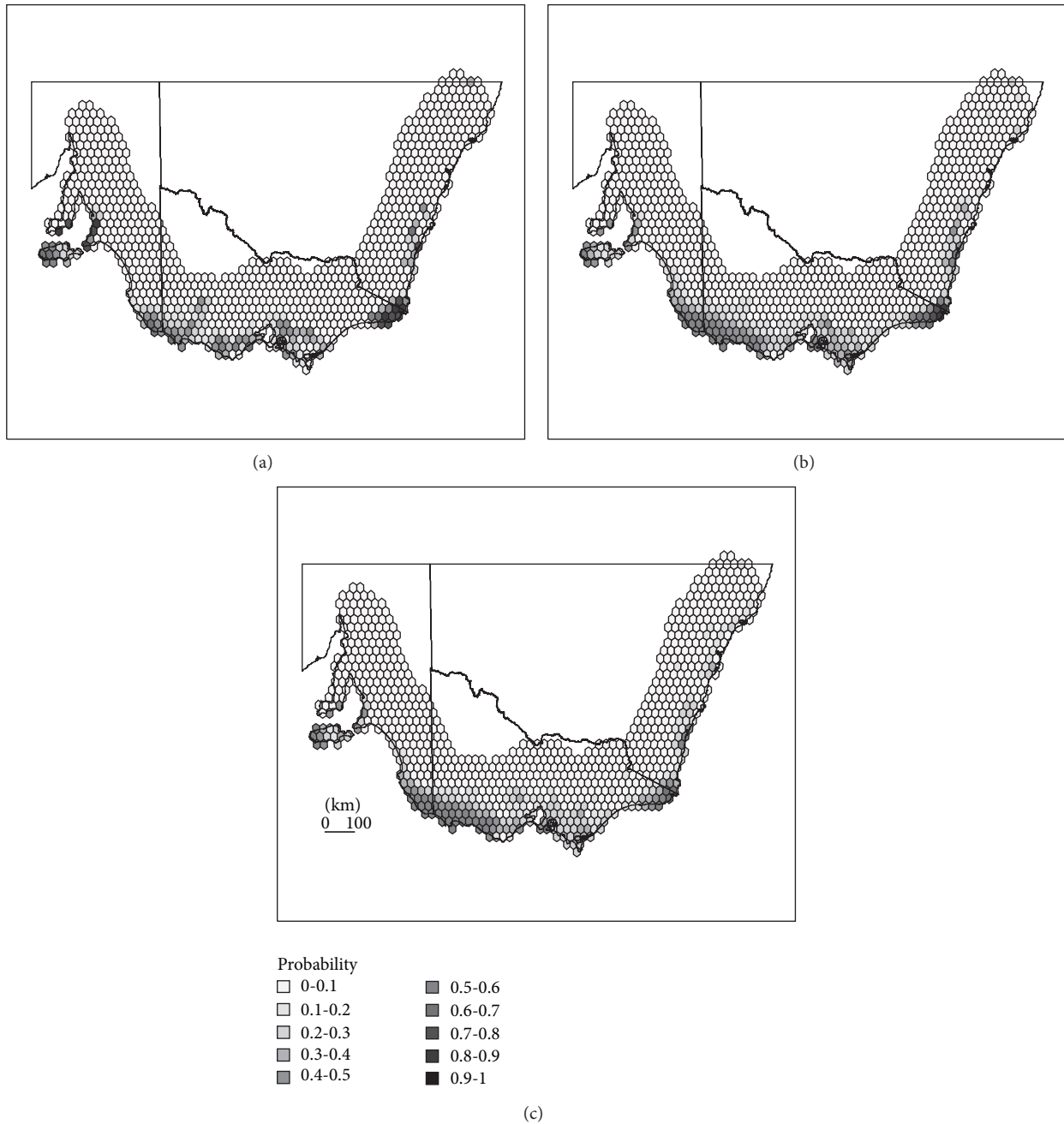
FIGURE 6: Spatial predictions of the distribution of *Isoodon obesulus obesulus* based on the probability estimates from generalized additive models, using (a) six variables, (b) four variables, and (c) three variables.

dry (desiccated), soil-dwelling invertebrate food may not be abundant [48, 55]. Prolonged periods of very dry or very wet conditions may, therefore, detrimentally affect the soil microhabitat of invertebrate food sought by *I. o. obesulus*. The temperature and moisture variables selected in our models would theoretically interact to produce optimal soil moisture regimes for *I. o. obesulus* and its food sources.

4.2. Conservation Implications. The subspecies *I. o. obesulus* is listed as endangered under the *EPBC Act* because it suffered a severe reduction in numbers following European settlement.

It also qualifies to be listed as vulnerable under the same Act because its geographic distribution is restricted and precarious for survival. Its distribution has been fragmented over thousands of years by natural processes that include climate change. Climate will continue to influence the distribution of *I. o. obesulus* in the future as it has in the past, and this has implications for conservation. Brereton et al. [33] modeled the range of *I. o. obesulus* in Victoria under different climate change scenarios and predicted that the distribution could shrink by up to two-thirds in unfavorable circumstances. During the last two centuries, clearing of native vegetation
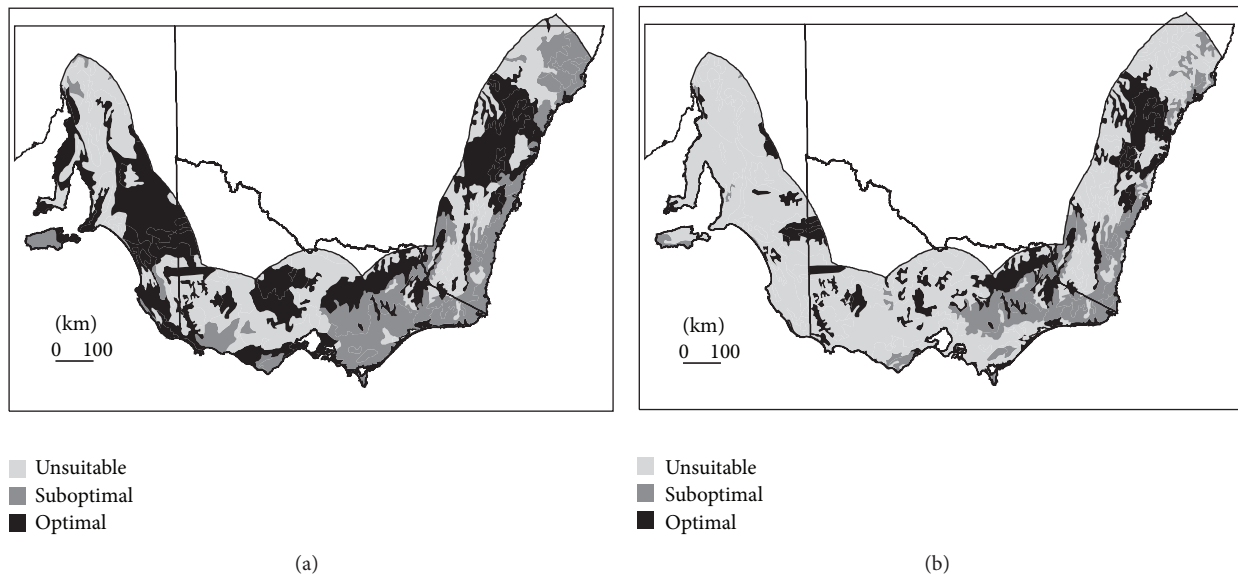
(a)

(b)

FIGURE 7: Suitability of vegetation for *Isoodon obesulus obesulus* (a) *c.* 1788 and (b) *c.* 1988.

by humans has contributed toward a substantial decline in its distribution and abundance. Many other ground-dwelling mammal species are similarly affected, and it is important to recognize this when planning their conservation. We have identified long-standing patterns of fragmentation in the distribution of *I. o. obesulus* that have likely caused genetic isolation and contributed to the speciation process despite these patterns having become masked by anthropogenic influences. We conclude that conservation scenarios that do not consider the "past" as well as more recent environmental history may be unsound.
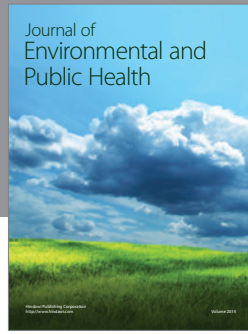
Acknowledgments

References

[1] J. M. Lord and D. A. Norton, "Scale and the spatial concept of fragmentation," *Conservation Biology*, vol. 4, no. 2, pp. 197–202, 1990.

[2] R. T. Forman, *Land Mosaics: The Ecology of Landscapes and Regions*, Cambridge University Press, Cambridge, UK, 1995.

[3] J. C. Bowyer, G. R. Newell, and M. D. B. Eldridge, "Genetic effects of habitat contraction on Lumholtz's tree-kangaroo (Dendrolagus lumholtzi) in the Australian Wet Tropics," *Conservation Genetics*, vol. 3, no. 1, pp. 61–69, 2002.

[4] W. K. Harris, *The Fragmented Forest: Island Biogeographic Theory and the Preservation of Biotic Diversity*, The University of Chicago Press, Chicago, Ill, USA, 1984.

[5] Y. Haila, D. A. Saunders, and R. J. Hobbs, "What do we presently understand about ecosystem fragmentation?" in *Nature Conservation 3: Reconstruction of Fragmented Ecosystems; Global and Regional Perspectives*, D. A. Saunders, R. J. Hobbs, and P. R. Ehrlich, Eds., pp. 45–55, Surrey Beatty and Sons, Chipping Norton, Australia, 1993.

[6] T. R. New, *Conservation Biology: An Introduction for Southern Australia*, Oxford University Press, South Melbourne, Australia, 2000.

[7] Y. Haila, "A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology," *Ecological Applications*, vol. 12, no. 2, pp. 321–334, 2002.

[8] M. Archer, "Earth shattering concepts for historical zoogeography," in *Vertebrate Zoogeography and Evolution in Australasia (Animals in Space and Time)*, M. Archer and G. Clayton, Eds., pp. 45–59, Hesperian Press, Carlisle, Australia, 1984.

[9] L. S. Broome and I. M. Mansergh, "The mountain pygmy possum Burramys parvus (Broom): an alpine endemic," in *The Scientific Significance of the Australian Alps*, R. Good, Ed., pp. 241–264, The Australian Alps National Parks Liaison Committee in association with the Australian Academy of Science, Canberra, Australia, 1989.

[10] D. J. Paull, "Southern brown bandicoot," in *Mammals of Australia*, S. Van Dyke and R. Strahan, Eds., pp. 180–182, Reed New Holland, Sydney, Australia, 3rd edition, 2008.

[11] E. Ashby, D. Lunney, J. Robertshaw, and R. Harden, "Status of bandicoots in New South Wales," in *Bandicoots and Bilbies*, J. H. Seebeck, P. R. Brown, R. L. Wallis, and C. M. Kemper, Eds., pp. 43–50, Surrey Beatty and Sons, Chipping Norton, Australia, 1990.

[12] G. Krefft, "On the vertebrate animals of the Lower Murray and Darling, their habits, economy, and geographical distribution," *Transactions of the Philosophical Society of New South Wales*, pp. 1–33, 1866.

[13] F. W. Jones, *The Mammals of South Australia—Part II*, Government Printer, Adelaide, Australia, 1924.

[14] C. M. Kemper, "Status of bandicoots in South Australia," in *Bandicoots and Bilbies*, J. H. Seebeck, P. R. Brown, R. L. Wallis,

and C. M. Kemper, Eds., pp. 67–72, Surrey Beatty and Sons, Chipping Norton, Australia, 1990.

[15] P. Aitken, "Mammals," in *Natural History of the South East*, M. J. Tyler, C. R. Twidale, J. K. Ling, and J. W. Holmes, Eds., pp. 127–133, Royal Society of South Australia, Adelaide, Australia, 1983.

[16] M. B. Thompson, G. Medlin, R. Hutchinson, and N. West, "Short-term effects of fuel reduction burning on populations of small terrestrial mammals," *Australian Wildlife Research*, vol. 16, no. 2, pp. 117–129, 1989.

[17] M. Rees and D. Paull, "Distribution of the southern brown bandicoot (*Isoodon obesulus*) in the Portland region of south-western Victoria," *Wildlife Research*, vol. 27, no. 5, pp. 539–545, 2000.

[18] P. W. Menkhorst and J. H. Seebeck, "Distribution and conservation status of bandicoots in Victoria," in *Bandicoots and Bilbies*, J. H. Seebeck, P. R. Brown, R. L. Wallis, and C. M. Kemper, Eds., pp. 51–60, Surrey Beatty and Sons, Chipping Norton, Australia, 1990.

[19] D. Paull, "The distribution of the southern brown bandicoot (*Isoodon obesulus obesulus*) in South Australia," *Wildlife Research*, vol. 22, no. 5, pp. 585–600, 1995.

[20] D. Lunney and T. Leary, "The impact on native mammals of land-use changes and exotic species in the Bega district, New South Wales, since settlement," *Australian Journal of Ecology*, vol. 13, no. 1, pp. 67–92, 1988.

[21] L. Pope, D. Storch, M. Adams, C. Moritz, and G. Gordon, "A phylogeny for the genus Isoodon and a range extension for *I. obesulus* peninsulae based on mtDNA control region and morphology," *Australian Journal of Zoology*, vol. 49, no. 4, pp. 411–434, 2001.

[22] J. A. Friend, "Status of bandicoots in Western Australia," in *Bandicoots and Bilbies*, J. H. Seebeck, P. R. Brown, R. L. Wallis, and C. M. Kemper, Eds., p. 84, Surrey Beatty and Sons, Chipping Norton, Australia, 1990.

[23] G. Gordon, L. S. Hall, and R. G. Atherton, "Status of bandicoots in Queensland," in *Bandicoots and Bilbies*, J. H. Seebeck, P. R. Brown, R. L. Wallis, and C. M. Kemper, Eds., pp. 37–42, Surrey Beatty and Sons, Chipping Norton, Australia, 1990.

[24] G. J. Hocking, "Status of bandicoots in Tasmania," in *Bandicoots and Bilbies*, J. H. Seebeck, P. R. Brown, R. L. Wallis, and C. M. Kemper, Eds., pp. 61–66, Surrey Beatty and Sons, Chipping Norton, Australia, 1990.

[25] J. R. Dodson, "The pre-settlement vegetation of the Mount Gambier area, South Australia," *Transactions of the Royal Society of South Australia*, vol. 99, no. 2, pp. 89–92, 1975.

[26] R. T. Lange, "Native vegetation," in *Natural History of the South East*, M. J. Tyler, C. R. Twidale, J. K. Ling, and J. W. Holmes, Eds., pp. 95–113, Royal Society of South Australia, Adelaide, Australia, 1983.

[27] T. Dendy, "South Australian heritage agreement scheme and clearance controls," *South Australian Geographer*, vol. 22, no. 1, pp. 16–26, 1985.

[28] M. A. Burgman and D. B. Lindenmayer, *Conservation Biology for the Australian Environment*, Surrey Beatty and Sons, Chipping Norton, Australia, 1998.

[29] H. Nix, "A biogeographic analysis of Australian elapid snakes," in *Atlas of Elapid Snakes of Australia*, R. Longmore, Ed., vol. 7 of *Australian Flora and Fauna Series*, pp. 4–15, Australian Government Publishing Service, Canberra, Australia, 1986.

[30] D. Houlder, M. Hutchinson, H. Nix, and J. McMahon, *ANU-CLIM USer'S Guide*, Centre for Resource and Environmental Studies, Australian National University, Canberra, Australia, 2000.

[31] T. J. Hastie and R. J. Tibshirani, *Generalized Additive Models*, Chapman and Hall, London, UK, 1990.

[32] D. B. Lindenmayer, H. A. Nix, J. P. McMahon, M. F. Hutchinson, and M. T. Tanton, "The conservation of Leadbeater's possum, *Gymnobelideus leadbeateri* (McCoy): a case study of the use of bioclimatic modelling," *Journal of Biogeography*, vol. 18, no. 4, pp. 371–383, 1991.

[33] R. Brereton, S. Bennett, and I. Mansergh, "Enhanced greenhouse climate change and its potential effect on selected fauna of south-eastern Australia: a trend analysis," *Biological Conservation*, vol. 72, no. 3, pp. 339–354, 1995.

[34] J. Fischer, D. B. Lindenmayer, H. A. Nix, J. L. Stein, and J. A. Stein, "Climate and animal distribution: a climatic analysis of the Australian marsupial *Trichosurus caninus*," *Journal of Biogeography*, vol. 28, no. 3, pp. 293–304, 2001.

[35] P. Olsen and B. Doran, "Climatic modelling of the Australian distribution of the grass owl (*Tyto capensis*): is there an inland population?" *Wildlife Research*, vol. 29, no. 2, pp. 117–125, 2002.

[36] T. D. Penman, M. J. Mahony, A. L. Towerton, and F. L. Lemckert, "Bioclimatic analysis of disjunct populations of the giant burrowing frog, *Heleioporus australiacus*," *Journal of Biogeography*, vol. 32, no. 3, pp. 397–405, 2005.

[37] W. F. Ponder, G. A. Carter, P. Flemons, and R. R. Chapman, "Evaluation of museum collection data for use in biodiversity assessment," *Conservation Biology*, vol. 15, no. 3, pp. 648–657, 2001.

[38] D. B. Lindenmayer, B. G. Mackey, and H. A. Nix, "The bioclimatic domains of four species of commercially important eucalypts from south-eastern Australia," *Australian Forestry*, vol. 59, no. 2, pp. 74–89, 1996.

[39] A. W. Claridge, "Use of bioclimatic analysis to direct survey effort for the long-footed potoroo (*Potorous longipes*), a rare forest-dwelling rat-kangaroo," *Wildlife Research*, vol. 29, no. 2, pp. 193–202, 2002.

[40] J. M. Dixon, "In search of bandicoots on the South Coast," *Forest and Timber*, vol. 14, no. 2, pp. 13–17, 1978.

[41] J. VanDerWal, L. P. Shoo, C. Graham, and S. E. Williams, "Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know?" *Ecological Modelling*, vol. 220, no. 4, pp. 589–594, 2009.

[42] Geoscience Australia, *Vegetation—Pre-European Settlement (1788)*, Geoscience Australia, Canberra, Australia, 2004.

[43] Geoscience Australia, *Vegetation—Post-European Settlement (1988)*, Geoscience Australia, Canberra, Australia, 2004.

[44] B. A. Bryan, "A generic method for identifying regional koala habitat using GIS," *Australian Geographical Studies*, vol. 35, no. 2, pp. 125–139, 1997.

[45] D. J. Paull, *The distribution, ecology and conservation of the Southern Brown Bandicoot in South Australia [M.S. thesis]*, University of Adelaide, Adelaide, Australia, 1993.

[46] P. W. Menkhorst and C. M. Beardsell, "Mammals of southwestern Victoria from the little desert to the coast," *Proceedings of the Royal Society of Victoria*, vol. 94, no. 4, pp. 221–247, 1982.

[47] M. Rees, *Habitat Suitability Mapping for the Southern Brown Bandicoot in South-Western Victoria [BSc (Hons) Thesis]*, University of New South Wales, Canberra, Australia, 1997.

[48] B. Lobert and A. K. Lee, "Reproduction and life history of Isoodon obesulus in Victorian heathland," in *Bandicoots and Bilbies*, J. H. Seebeck, P. R. Brown, R. L. Wallis, and C. M. Kemper, Eds., pp. 311–318, Surrey Beatty and Sons, Chipping Norton, Australia, 1990.

[49] B. A. Wilson, D. Robertson, D. J. Moloney, G. R. Newell, and W. S. Laidlaw, "Factors affecting small mammal distribution and abundance in the eastern Otway Ranges, Victoria," in *Australian Ecosystems: 200 Years of Utilization, Degradation and Reconstruction*, D. A. Saunders, A. J. M. Hopkins, and R. A. How, Eds., vol. 16, Proceedings of the Ecological Society of Australia, pp. 379–394, 1990.

[50] D. Moro, "The distribution of small mammal species in relation to heath vegetation near Cape Otway, Victoria," *Wildlife Research*, vol. 18, no. 5, pp. 605–618, 1991.

[51] R. W. Braithwaite and P. K. Gullan, "Habitat selection by small mammals in a Victorian heathland," *Australian Journal of Ecology*, vol. 3, no. 1, pp. 109–127, 1978.

[52] D. M. Stoddart and R. W. Braithwaite, "A strategy for the utilization of regenerating heathland habitat by the brown bandicoot (*Isoodon obesulus*; Marsupialia, Peramelidae)," *Journal of Animal Ecology*, vol. 48, no. 1, pp. 165–179, 1979.

[53] A. M. Opie, "Habitat selection and the diet of *Isoodon obesulus*," *Bulletin of the Australian Mammal Society*, vol. 6, no. 2, p. 56, 1980.

[54] R. W. Braithwaite, "Southern brown bandicoot," in *The Australian Museum Complete Book of Mammals*, R. Strahan, Ed., pp. 94–95, Angus and Robertson Publishers, Sydney, Australia, 1983.

[55] B. Lobert, *The ecology of the Southern Brown bandicoot in Southeast Australian Heathland [MSc thesis]*, Monash University, Melbourne, Australia, 1985.

[56] B. Lobert and A. Opie, "Habitat preference by Isoodon obesulus in heathland at Cranbourne, Victoria," *Bulletin of the Australian Mammal Society*, vol. 9, no. 1, p. 24, 1986.

[57] A. Opie, P. Gullan, and I. Mansergh, "Prediction of the geographic range and habitat preference of *Isoodon obesulus* and *Perameles nasuta* in Gippsland," in *Bandicoots and Bilbies*, J. H. Seebeck, P. R. Brown, R. L. Wallis, and C. M. Kemper, Eds., pp. 327–334, Surrey Beatty and Sons, Chipping Norton, Australia, 1990.

[58] R. L. Specht, A. Specht, M. B. Whelan, and H. Elywyne, *Conservation Atlas of Plant Communities in Australia*, Centre for Coastal Management and Southern Cross University Press, Lismore, Australia, 1995.

[59] J. S. Benson and P. A. Redpath, "The nature of pre-European native vegetation in south-eastern Australia: a critique of D. G. Ryan, J. R. Ryan, and B. J. Starr, (1995) The Australian Landscape—Observations of Explorers and Early Settlers," *Cunninghamia*, vol. 5, no. 2, pp. 285–328, 1997.

[60] S. J. Hill and K. French, "Potential impacts of fire and grazing in an endangered ecological community: plant composition and shrub and eucalypt regeneration in Cumberland Plain Woodland," *Australian Journal of Botany*, vol. 52, no. 1, pp. 23–29, 2004.

[61] Bureau of Meteorology, *Australian Climate Variability and Change*, 2012, http://www.bom.gov.au/climate/change/auscc .shtml.

[62] M. P. Austin, "Case studies of the use of environmental gradients in vegetation and fauna modelling: theory and practice in Australia and New Zealand," in *Predicting Species Occurrences: Issues of Accuracy and Scale*, J. M. Scott, P. J. Heglund, M. L. Morrison et al., Eds., pp. 73–82, Island Press, Washington, DC, USA, 2002.

[63] Y. Shan, D. Paull, and R. I. McKay, "Machine learning of poorly predictable ecological data," *Ecological Modelling*, vol. 195, no. 1-2, pp. 129–138, 2006.