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Modeling the thermal zones and biodiversity on the high mountains of Meganesia: the importance of local differences

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Abstract

Alpine areas in Meganesia occur on maritime and continental mountains, and range from tropical to warm and cool temperate. At their current treelines, we measured soil temperatures, which were found to be within the bounds for treeline temperatures worldwide. We modeled areas above these alpine treelines using (1) a growing season mean synoptic temperature of 6.4 °C at treeline and (2) monthly temperature extremes. It was possible to adjust the threshold temperatures of the growing season model until predicted areas approximated observed alpine areas for New Guinea, the Australian mainland Snowy Mountains, and Tasmania, but meaningful predictions could not be made for the unknown alpine area of the Victorian Alps. The temperature extreme model was unsuitable for New Guinea and Tasmania but gave better predictive results for the Victorian Alps. We correctly predicted a strong relationship between alpine area and number of alpine vascular plant species and between regional area and number of terrestrial vertebrate species. However, there was no clear relationship between alpine area and alpine terrestrial vertebrate richness. Differences among the mountains were better explained by climatic extremes and insolation. If local explanations are required to model alpine vertebrate fauna, it is difficult to build robust global models and consequently make general predictions of climate change impacts.

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Introduction

With mountain regions being particularly susceptible to impacts of climate change, computer modeling is commonly being used to predict trends in the distribution of high elevation ecosystems and species (Brereton et al., 1995; Bugmann et al., 2007; Green et al., 2008). Such modeling relies on projections of physical parameters such as temperature lapse rates or downscaling of global climate models (Beniston, 2003; Bugmann et al., 2007). Central to this is an understanding of how elevation affects mountain thermal zones and how modeling biotic responses to these thermal zones can best be achieved. Complex studies across disparate mountain areas work because of adherence to pre-existing sampling protocols and geographical definitions, as is the case with GLORIA (A Global Observation Research Initiative in Alpine Environments) (Grabherr et al., 2000; Gottfried et al., 2012). However, where comparisons are attempted among unrelated studies this is compromised where terminology is not standardized, *alpine* and *treeline* being cases in point (Körner, 2012).

Attempts to formulate a quantitative, generalized scientific definition of a mountain based on elevation and slope have evolved to a relief-based definition of ruggedness (Körner et al., 2011). A key parameter in comparing mountain areas and future biotic responses to climate change is the climatic belt in which a mountain area lies, the combination essentially of elevation and latitude that determines the local climate and hence vegetation. According to Körner et al. (2011), the main thermal reference line on mountains is the climatic treeline, the limit to tree growth where plants are still sufficiently tall to become uncoupled from ground-level thermal conditions and are instead coupled to the circulating atmosphere and hence can be defined from weather station data (Körner, 2007). Some mountain regions may not contain tree species that are sufficiently cold-adapted to achieve this limit to tree growth, or human actions have removed

trees from the local flora so that they do not reach their potential maximum elevation (Körner, 2012, p. 21). However, this line, the lower limit of the alpine zone, can be defined by a growing season mean temperature of 6.4 °C (Körner et al., 2011). The growing season mean shaded soil temperature at 10 cm depth is virtually identical to the seasonal mean treeline air temperature (Körner, 2012, p. 36). Körner et al. (2011) defined seven mountain thermal belts with four thermal zones below the climatic treeline and three above.

A region suitable for testing this model is Meganesia, the continent of Australia–New Guinea (Filewood, 1984), also known as Sahul (Ballard, 1993), which refers to the area on the same continental shelf that was joined as a single landmass until ca. 8000 years ago, and stretches from the equator to 44°S in a similar longitudinal belt. Its areas share a similar history of 20 million years of isolation as it drifted north through about 30° of latitude (Crook, 1981), after the breakup of Gondwana, until it collided with southeast Asia. During this period, there were few faunal inputs from elsewhere. Consequently, Australia–New Guinea had a shared biota for at least 10 million years (Heinsohn and Hope, 2006), with evolution essentially in situ (Heatwole, 1987). New Guinea, however, was a series of low islands during the Tertiary and probably docked with several Asian islands since the mid- to late Tertiary (Heinsohn and Hope, 2006). There were subsequent waves of immigration from Asia, penetrating well into southern Meganesia. The floras across Meganesia differ, particularly the alpine flora which has greater inputs from Himalayan sources into New Guinea than into the Australian mountains (Hope, 2014).

The alpine areas of Meganesia are small but extend from 3°S to 43°30'S, forming a diverse transect along which questions can be examined concerning the relationship of plant and animal richness to thermal zones on mountains. The main objective of our study was to determine whether the area of alpine habitat in these

mountain ranges could be determined by a single model such as that of Körner et al. (2011). A second objective was to examine if the richness of the flora and fauna of the alpine zones could be easily modeled. We chose a simple approach for our analysis, which included three mountain areas across three climatic zones (equatorial, warm temperate, and cool temperate), and we used two biological groups, vascular plants and terrestrial vertebrates. Some alpine areas will not fall within the worldwide generalization of an alpine temperature threshold of 6.4 °C used within the model of Körner et al. (2011) because there is probably some climatic heterogeneity in the alpine synoptic temperature similar to that of the empirically derived 6.4 ± 0.7 °C (SD) for soil temperature (Körner and Paulsen, 2004; Körner, 2012). We therefore ask how much the model threshold needs to be altered to fit local alpine conditions. We also explore an empirically derived model for the Snowy Mountains of New South Wales (NSW) (Costin, 1954) and examine its applicability. We further ask whether the area of the alpine zone of a region determines the richness of flora and fauna, or if other factors explain biotic richness.

Methods

DEFINING THE ALPINE AND SUBALPINE ZONES

In an attempt to determine whether the current treeline elevation is the climatic treeline, temperatures were measured at 10 cm soil depth in permanently shaded microsites using temperature loggers (Gemini Data Loggers, Chichester, England) in New Guinea, mainland Australia in the Snowy Mountains and Victorian Alps, and in the island of Tasmania. A 3.2 °C threshold at this depth corresponds to a 0 °C weekly mean temperature at canopy level and was used to determine the commencement and end of the growing season (Körner and Paulsen, 2004). We initially deployed temperature loggers for a three-year period. However, owing to misplacement or loss of loggers and logger malfunctions there was no single year of synchronous temperature records across all mountain areas.

The alpine area of West Papua is 3125 km² and Papua New Guinea (PNG) 225 km² (Hope, 2014). Based on mapping from a traverse of the treeline by foot and helicopter in summer 2007/2008, the alpine area of the Snowy Mountains was calculated as 135 km² (Green, 2009). The alpine area of the Victorian Alps has never, to our knowledge, been mapped. The exact area of alpine vegetation in Tasmania is difficult to determine because of the lack of a clearly demarcated treeline but is given as 1135 km² (Kirkpatrick, 1997).

We also determined the area of subalpine mainland Australia. Costin (1957) defined the Australian subalpine as those areas with continuous snow cover lying for at least one month. Körner (2012) suggested a “logical definition” of the subalpine zone as that area between the timberline (the upper limit of closed montane forest) at its lower limit and the alpine treeline at the upper limit. In summer 2012/2013 a road-based circuit was made of the upper elevational limits of stands of the timber tree *Eucalyptus delegatensis* in the Snowy Mountains (six sites) and the northern Victorian Alps (nine sites) and elevations were measured using a handheld Global Positioning System (GPS) unit and corrected to the nearest site with a known elevation. The area above timberline was then calculated. For the Baw Baw plateau, where road access to timberline was limited, Ecological Vegetation Class mapping by the Victorian Department of Environment and Primary Industries was used to delimit the timberline as the boundary between forest and subalpine grassland, shrubland, and woodland. The area delimited above timberline was measured using a planimeter.

THE MODELS

We modeled mountain thermal zones for the Australian mainland and Tasmania using two temperature-based methods, those of Körner et al. (2011) and Costin (1954), henceforward referred to as the Körner and Costin models. The Körner model was also applied to PNG, the only political division of New Guinea for which climate surfaces were available. Using the same climate surfaces, we also calculated the area of land above the isotherm representing a mean temperature of 10 °C in the warmest month for Tasmania, the Australian mainland, and PNG.

The Körner model uses thresholds to delineate thermal belt zones, with a mean temperature over the growing season of <6.4 °C defining Alpine, 10 °C Upper Montane, and 15 °C Lower Montane. The thermal zones can further be confined to mountain terrain defined by a ruggedness threshold, with the central cell of a 3 × 3 grid of 30 second resolution classified as mountain terrain if there is a minimum vertical rise of 200 m between the lowest and highest cells (Körner et al., 2011). We used the national 9 second digital elevation model (DEM) (Hutchinson et al., 2008) for Australia, so each grid cell was analyzed using a 10 × 10 cell neighborhood to retain the 200 m relief threshold and the same vertical to horizontal ratio. Similarly, the 18 second DEM of Papua New Guinea (Nix et al., 2000) was analyzed using a 5 × 5 cell neighborhood. Growing season length was calculated at each grid cell by using estimates of its long-term monthly mean maximum and minimum air temperatures. Climate surfaces for two periods available from the ANUCLIM package (Xu and Hutchinson, 2013) were investigated for Australia: 1921–1995 and 1976–2005. In New Guinea, climate surfaces were available only for the PNG region for the period 1921–1991 (Nix et al., 2000). In all cases, growing season was defined as the period between monthly mean temperature exceeding 0.9 °C then falling below 0.9 °C (Körner et al., 2011).

Costin (1954) identified mountain thermal zones by the number of months with temperatures below defined thresholds: alpine and subalpine zones required below-freezing mean monthly minimum temperatures for 6–8 months per year, with 0–6 months for montane. Further, alpine was delineated by mean monthly temperature falling below freezing for 4–6 months and subalpine for 1–4 months. Both available periods of long-term mean temperature surfaces for Australia (including Tasmania) were used for modeling, with temperatures between 0 and +2 °C (ground frost) investigated as thresholds for freezing.

We ran the models in an iterative way separately for Tasmania, mainland Australia, and PNG to determine the temperature threshold required to match the alpine area previously calculated for each mountain area.

FLORA AND FAUNA

We plotted the number of species of vascular plants and vertebrates against the alpine area. Within Meganesia, the numbers of species within the alpine floras were taken from Kirkpatrick (1997) for Tasmania, Costin et al. (2000) for the Snowy Mountains, and van Royen (1980–1983) for New Guinea. The flora and alpine areas of five other regions (Southern Alps of New Zealand, Hokkaido, Swiss Alps, Afro Alpine, and the Sierra Nevada in U.S.A.) were also plotted. With the vertebrate fauna, we were stringent in our definition of alpine species and omitted vagrants. There were three stages in the compilation of the faunal lists: lists were compiled initially from the literature; these lists were submitted to experts

TABLE 1

Treeline temperature relative to the permanently located soil temperature logger at South Ramshead (1950 m, Snowy Mountains) in years where data were synchronous between South Ramshead and four mountains in Papua New Guinea (PNG), Victorian Alps (Vic), and Tasmania (Tas).

Mountain location	Temperature (°C)	Temperature relative to South Ramshead	Growing season
Mount Wilhelm (PNG)	7.21	+0.21	2008/2009
Mount Bogong (Vic)	7.9	+0.21	2011/2012
Mount Hotham (Vic)	9.01	+2.01	2008/2009
Mount Field (Tas)	6.74	-1.28	2012/2013

in the field for comment; all alpine zones were then visited for ground-truthing by Ken Green.

The regional vertebrate terrestrial faunas were taken from regional field guides to determine the approximate availability of animals at lower elevations as a source for alpine species. For Tasmania, the regional area was considered to be the whole island (area 67,800 km²). For the Snowy Mountains the boundaries were from the east coast of Australia west to the upper Murray River and from East Gippsland north to just south of Sydney, an area of 114,192 km². This area was chosen for its proximity to the Snowy Mountains and the ease of interpreting and extracting distribution data from maps in regional faunas. For New Guinea as a whole, the mainland area of 831,390 km² was used and for Papua New Guinea the mainland area of PNG (418,606 km²) was used.

Results

DEFINING THE ALPINE AND SUBALPINE ZONES IN THE FIELD

Length of Growing Season

Growing season lengths based on definitions from Körner and Paulsen (2004) were 365 days (2008/2009) on Mount Wilhelm (PNG); 230 days (2008/2009), 205 days (2011/2012), and 199 days (2012/2013) on South Ramshead (Snowy Mountains); 221 days (2011/2012) on Mount Bogong; and 247 days (2008/2009) on Mount Hotham (both Victorian Alps) and 236 days (2012/2013) on Mount Field (Tasmania). South Ramshead had the shortest growing season. For overlapping years, relative to South Ramshead growing seasons were longer on Mount Wilhelm by 135 days, Mount Hotham by 17 days, Mount Bogong by 16 days, and Mount Field by 37 days.

THE ALPINE ZONE

At treeline on South Ramshead (1950 m) the growing season mean soil temperature in 2008/2009 was 7.00 °C, while at treeline (3960 m) on Mount Wilhelm (summit 4509 m) the period 2008/2009 yielded two growing seasons with a mean of 7.21 °C (Table 1). The temperature at treeline (1750 m) on Mount Hotham (summit 1861 m) averaged 9.01 °C in 2008/2009 and at treeline (1862 m) on Mount Bogong (summit 1986 m) averaged 7.9 °C in 2011/2012. At the same time, South Ramshead recorded 7.7 °C. Data were available from Mount Field for the season 2012/2013 with a treeline temperature (1245 m) of 6.74 °C, while the South Ramshead temperature over the same period was 8.02 °C.

THE SUBALPINE ZONE

Based on Körner's (2012) definition, and using data from the timberline survey, the lower limits of the subalpine zone were calculated as 1506 ± 26.7 m for the Snowy Mountains and 1454 ± 40.0 m for the northern Victorian Alps with timberline on the Baw Baw Plateau mapped at about 1300 m. This gives areas above timberline (including alpine as well as subalpine) of 1310 km² in the Snowy Mountains and 859 km² in the Victorian Alps.

THE MODELS

Alpine

For PNG, the Körner model using temperature data from 1921 to 1991 with a threshold of 6.4 °C gave an alpine area of 41 km². A threshold of 7.35 °C, which is close to our measurement of 7.2 °C from soil temperature loggers, was required to approximate the previously calculated alpine area of 225 km².

The threshold of 6.4 °C applied to temperatures from the period 1976–2005 underestimated alpine areas for mainland Australia with only 8 km² identified, and overestimated those for Tasmania with 2651 km² identified. To approximate the empirically measured area of 135 km² for the Snowy Mountains, a threshold of 7.15 °C was required to achieve 132 km² (Table 2). This threshold is close to our 2008/2009 temperature logger measurement of 7.00 °C. The 7.15 °C threshold gave 44 km² of alpine area in the Victorian Alps and a large overestimate of 5051 km² in Tasmania. An upper threshold of 5.85 °C was required in the model to reduce the calculated alpine land area in Tasmania to 1132 km², which approximates the 1135 km² calculated by Kirkpatrick (1983). None of the modeled 44 km² of alpine area in the Victorian Alps was located in the main northern Victorian Alps, which lie inland of a line through Mounts Arnold, Reynard, Phipps, and Nunniong, with the majority (93%) on the Mount Baw Baw plateau, an area that is subalpine rather than alpine (Fig. 1).

When the model was run using temperatures from the period 1921–1995, the 6.4 °C threshold yielded a smaller underestimate of 31 km² for mainland Australia but a larger overestimate of 4606 km² for Tasmania. The required threshold temperature to achieve 133 km² in the Snowy Mountains was 6.65 °C and to attain 1124 km² in Tasmania the threshold needed to drop to 5.44 °C. The 6.65 °C threshold gave 23 km² of alpine area in the Victorian Alps, with 85% on the subalpine Mount Baw Baw plateau.

When running the Costin model, a minimum threshold of 0 °C was found to be too low, and underestimated alpine areas for the Snowy Mountains over both time periods. For the period 1921–1995, 0.5 °C was required for a good fit of alpine areas in the Snowy Mountains with the threshold at 1.0 °C to attain a similar

TABLE 2

Areas modeled as alpine and upper montane using Körner et al. (2011) with data from two time periods for Tasmania (Tas) and Australian mainland mountains and one time period for Papua New Guinea (PNG). On the mainland, alpine conditions occur in the Victorian Alps (Vic) and the Snowy Mountains in New South Wales (NSW), but upper montane extensions to the Snowy Mountains extend into the Australian Capital Territory (ACT). Areas modeled are km² and figures in bold show the nearest approximations to those arrived at by on-ground mapping.

Time period:	1921–1995				1976–2005				1921–1991	
Alpine growing season temperature (°C)	5.44	6.4	6.65	6.77	5.85	6.4	7.15	7.18	6.4	7.35
Alpine (NSW)	0	31	133	207	0	8	132	144		
Alpine (Vic)	0	4	23	52	0	0	44	51		
Alpine (Tas)	1124	4606	5516	5989	1132	2651	5051	5143		
Alpine (PNG)									41	223
Upper Montane (NSW/ACT)	15,270	15,238	15,137	15,063	8503	8495	8371	8359		
Upper montane (Vic)	14,174	14,170	14,151	14,122	7973	7973	7929	7922		
Upper montane (Tas)	33,597	30,115	29,205	28,732	24,050	22,531	20,131	20,039		
Upper montane (PNG)									1477	1295

result for the period 1976–2005 (Table 3). For the Snowy Mountains, the geographic area mapped in the Costin model was similar to that in the Körner model, but the alpine area was more clearly delineated (Fig. 2). However, in the Victorian Alps, the Mount Baw Baw plateau was not mapped as alpine (Fig. 2). The Costin model yielded alpine areas of 2–5 km² for the Victorian Alps with the majority occurring on Mount Bogong, Mount Nelse, Mount Feather-top, and in the Mount Hotham area (Fig. 2). All thresholds were too restrictive for Tasmania, and in PNG no alpine areas were delineated using the Costin model. For the subalpine zone, the models again provided underestimates, and for the period 1921–1995, 1–1.5 °C were required to approximate the area above timberline (subalpine and alpine combined) in the Snowy Mountains (1310 km²) and Victorian Alps (821 km²) with 2.0 °C for the period 1976–2005 (Table 3). As with Tasmania, the Costin model was probably too restrictive for the Baw Baw plateau, and much of the area predicted as “alpine” in the Körner model (Fig. 1) was not even predicted as subalpine by the Costin model (Fig. 2). Figure 2 contains the alpine zone modeled at a threshold of 1.0 °C with the subalpine modeled at 2.0 °C, which shows an overestimate for the Snowy Mountains (1525 km² cf. 1310 km²) and an underestimate for the Victorian Alps (611 km² cf. 821 km²) that can only partially be corrected by adding in the subalpine area of the Baw Baw plateau (63 km²) that was not modeled.

The use of an alpine boundary based on a temperature in the warmest month of ≤10 °C (Daubenmire, 1954) for the time period closest to that publication (1921–1995) gave an underestimate of alpine area for New South Wales (NSW) by 64%, and an overestimate for alpine Tasmania of 113%, and for PNG the 1921–1991 time period gave an overestimate of alpine area of 1391% (Table 4). The climate surface for the time period 1976–2005 gave underestimates of alpine area for both NSW and alpine Tasmania.

FLORA AND FAUNA

The richness of the alpine flora on the worldwide comparison, including the three areas in Meganesia, was strongly correlated ($R^2 = 0.935$) with the log of the alpine area (Fig. 3, part a). The regional fauna also showed a strong relationship with the log

of regional area (Fig. 3, part b). However, this was not the case with the alpine fauna for which there was no apparent relationship with alpine area (Fig. 3, part c). Tasmania had the highest number of alpine vertebrate species and these constituted a higher proportion of the regional fauna than in the Snowy Mountains with the total alpine area of New Guinea showing slightly more species (for a much larger area) but fewer species in PNG than the Snowy Mountains despite nearly twice the alpine area. The alpine fauna of both PNG and New Guinea as a whole was a smaller proportion of the regional fauna than either the Snowy Mountains or Tasmania (Fig. 3, part c).

Discussion

ALPINE/SUBALPINE

The use of in-ground temperature loggers has established that treelines in major alpine areas of Meganesia fall in the range of true alpine treelines worldwide (Körner, 2012). However, for single-year records anomalous temperatures could be expected. The 2008/2009 summer could be termed a “normal” summer; at the permanent meteorological site at Thredbo Top Station (1957 m) in the Snowy Mountains, temperature records equaled the long-term mean minimum and were just 0.1 °C above the mean maximum; additionally, precipitation closely approximated the long-term mean (Bureau of Meteorology, 2009). In the same period at the nearby permanent monitoring site on South Ramshead, the mean growing season soil temperature was 7.00 °C. In the 2011/2012 growing season, soil temperature at South Ramshead was 7.7 °C with 7.9 °C recorded on Mount Bogong in the Victorian Alps. These higher temperatures may reflect the La Niña that was associated with the unusual temperature trend in southeastern Australia of the coolest summer on record in the north to the third warmest in the south. The Snowy Mountains and Victorian Alps lie in a zone along this gradation with Victoria recording an anomaly from the long-term average of +0.34 °C in maximum temperature and +1.00 °C in minimum temperature (Bureau of Meteorology, 2013a, 2013b). In 2012/2013 the average growing season temperature at treeline on South Ramshead reached its highest recorded value of 8.02 °C, during the hottest 12 month period in Australian records when the

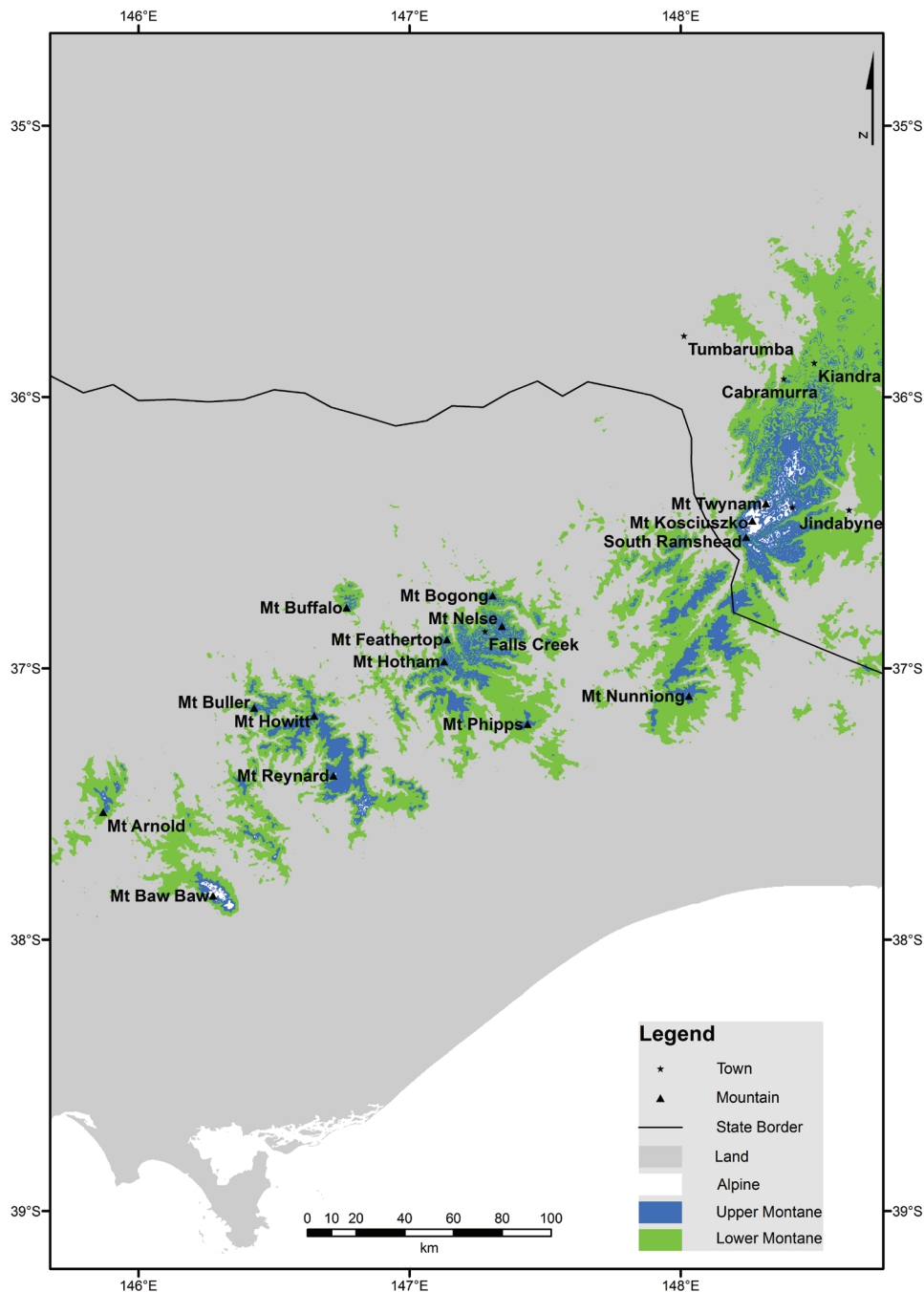


FIGURE 1. Modeled thermal zones for mountains of southeast mainland Australia based on a mean temperature in the growing season of 7.15 °C to define alpine, modified from Körner et al. (2011) and using temperature data for the period 1976–2005. The map shows the southeastern corner of mainland Australia from 35° to 39°S and 145.8° to 148.8°E

mean temperature from October 2012 to September 2013 was 1.25 °C above the long-term average (Bureau of Meteorology, 2014). Hence a key message for using treeline temperatures to determine whether an area is true alpine is the imperative to consider the years in which data were collected with regard to long-term records.

High temperatures at some treelines, however, suggest that they do not represent a true alpine treeline. Data for 2008/2009 at treeline on Mount Hotham (Victorian Alps) gave a mean of 9.01 °C, 2 °C higher than at treeline (1950 m) on South Ramshead (Snowy Mountains) and 1.8 °C higher than on Mount Wilhelm PNG. Given that the treeline at the Mount Bogong site (southern aspect) was 1862 m, it is quite likely that the nearby summit of Mount Hotham (1861 m) is not alpine. McDougall and Walsh

(2007) reported treeline at 1600 m on Mount Howitt (37°10'S), but there is a 0.43° difference in latitude between Mount Bogong and Mount Howitt, giving an expected lowering of the treeline of only 48 m, rather than the reported difference of 262 m. The Mount Howitt treeline and others of similar elevation in the Victorian Alps are therefore not true alpine treelines and are probably the result of summit syndrome (Körner, 2012): no matter how warm a summit is it will remain treeless through combinations of small area, wind effects, substrate, and poor seed transport. Hence, very few of the summits in the Victorian Alps, apart from Mount Bogong, Mount Nelse, and Mount Feathertop are truly alpine.

The subalpine zone is a useful delineation for ecological studies. Both the upper boundary (alpine treeline) and lower boundary

TABLE 3

Areas modeled as alpine and subalpine for Tasmania (Tas) and Australian mainland mountains based on Costin (1954) using data from two time periods. On the mainland, alpine conditions occur in the Victorian Alps and the Snowy Mountains in New South Wales (NSW), but subalpine extensions to the Snowy Mountains extend into the Australian Capital Territory (ACT). Areas modeled are km², and figures in bold show the nearest approximations to those arrived at by on-ground mapping.

Time period:	1921–1995					1976–2005				
Minimum temperature threshold (°C)	0	0.5	1	1.5	2	0	0.5	1	1.5	2
Alpine (NSW)	73	144	252	388	539	39	88	168	290	432
Alpine (Victoria)	0	2	12	57	160	0	1	5	25	73
Alpine (Tasmania)	0	6	28	112	318	0	0	3	26	109
Subalpine (NSW/ACT)	178	428	850	1981	3919	112	283	466	658	1093
Subalpine (Victoria)	5	54	283	789	1838	0	2	27	188	611
Subalpine (Tasmania)	70	385	1281	2421	3907	0	106	796	1873	3142

(the timberline) of the subalpine zone (Körner, 2012) are easily identified on the ground on the Australian mainland, and it is also defined on the basis of the duration of snow pack (Costin, 1957). However, for mountain areas elsewhere it may be of less use. Of the three areas studied here, Tasmania, mainland Australia, and New Guinea, the delineation of the subalpine zone only has practical ecological usefulness on mainland Australia and then only because of the coincidence of the tree form and species change from *E. pauciflora* to *E. delegatensis* with temperatures that determine snow pack longevity.

THE MODELS

Previous, largely 19th century, attempts to set the elevation of treelines thermally worldwide resulted in the much quoted temperature in the warmest month of “roughly” 10 °C (Daubenmire, 1954). This was largely a temperate zone perspective and has been used with limited success elsewhere (see discussion in Körner, 2003, pp. 81–82). Our data support this assessment (see our data graphed for equatorial New Guinea in Fig. 4.7 of Körner, 2012, p. 45), and even using the data from the older data set 1921–1995 in temperate areas failed to approximate mapped alpine areas and gave opposing results with the exaggeration of the extent of the Tasmanian alpine and underestimation of the Snowy Mountains (Table 4). The warmest month mean temperature at treeline varies by about 5 °C between tropical and temperate zones, whereas the mean temperature over the growing season varies by only about 1 °C (Körner, 2012, p. 83) and therefore could be seen as a better basis for modeling alpine areas.

However, the Körner model, when run across Meganesia in its original form virtually eliminates recognition of the Australian mainland alpine zone and severely reduces that in PNG. To approximate the known alpine area of 225 km² for PNG, a threshold of 7.35 °C is required. Similarly, to approximate the alpine area of 135 km² for the Snowy Mountains for 1976–2005 and 1921–1995 requires thresholds of 7.15 °C and 6.65 °C, which are, respectively, just outside and well inside the 6.4 ± 0.7 °C found for alpine tree-line soil temperatures worldwide, bearing in mind that the mean shaded soil temperature at 10 cm depth is virtually identical to the seasonal mean treeline air temperature (Körner and Paulsen, 2004; Körner, 2012). By contrast, the 6.4 °C threshold greatly overestimates the 1135 km² of Tasmanian alpine areas generating 2651 km² and 4606 km² for the two temperature periods, with a similar

figure calculated independently by Körner (personal communication) using Worldclim temperature data. The Körner model incorrectly attributes nearly all of the alpine area of the Victorian Alps to the subalpine Baw Baw plateau, which suggests that the model does not perform well in maritime environments. Of the 23–44 km² of Victorian alpine zone modeled, at least 85%–93% was subalpine being attributed to the Baw Baw plateau, which, like Tasmania, has higher humidities and greater cloudiness than other Victorian subalpine mountains and supports a number of typically Tasmanian plant species (Costin, 1957).

A mean growing season soil temperature from Mount Field (Tasmania) 1.28 °C lower than that recorded at the permanent site on South Ramshead (Snowy Mountains) confirms the low treeline temperature in Tasmania. The temperature threshold required to approximate the calculated alpine land area in Tasmania was 5.85 °C, which is within the ±0.7 error bars found by Körner and Paulsen (2004) for soil temperature, which suggests the 6.4 °C threshold for synoptic temperature is not invariable and there is some climatic heterogeneity in alpine treelines. Ignoring the incorrectly attributed alpine status of the Baw Baw plateau, both the Körner and Costin models reveal less than 5 km² of alpine area occurring in the Victorian Alps. With most botanical papers conflating alpine and treeless subalpine regardless of the location of the alpine tree-line, there is, as yet, no other published figure for the alpine area in Victoria.

Earlier temperature data may more closely reflect conditions when observed treelines were becoming established. In fact, the Costin model came from empirical observations published in 1954, and using the 1921–1995 data set required increasing the freezing threshold from 0.0 to 0.5 °C to model a good fit of alpine areas in the Snowy Mountains, with a further increase to approximately 1.0 °C in both the Costin and Körner models to 1976–2005 (Tables 2 and 3). Temperature loggers in situ at treeline in recent years are a measure of the current climate, whereas the treelines reflect a past climate. The effect of global warming cannot be ignored and will have substantial implications for modeling. Assuming treeline advance lags at least 50 years behind the rate expected from the 20th century mean global temperature rise of approximately 0.7 °C, the true temperature threshold for treeline would be close to 6.0 °C (Körner, 2012). There are, however, worldwide differences in climatic warming and a higher rate of change at higher elevations (Hennessy et al., 2003). In Australia, Gallagher et al. (2009) calculated a rise of 0.74 °C in mean annual temperature at elevations

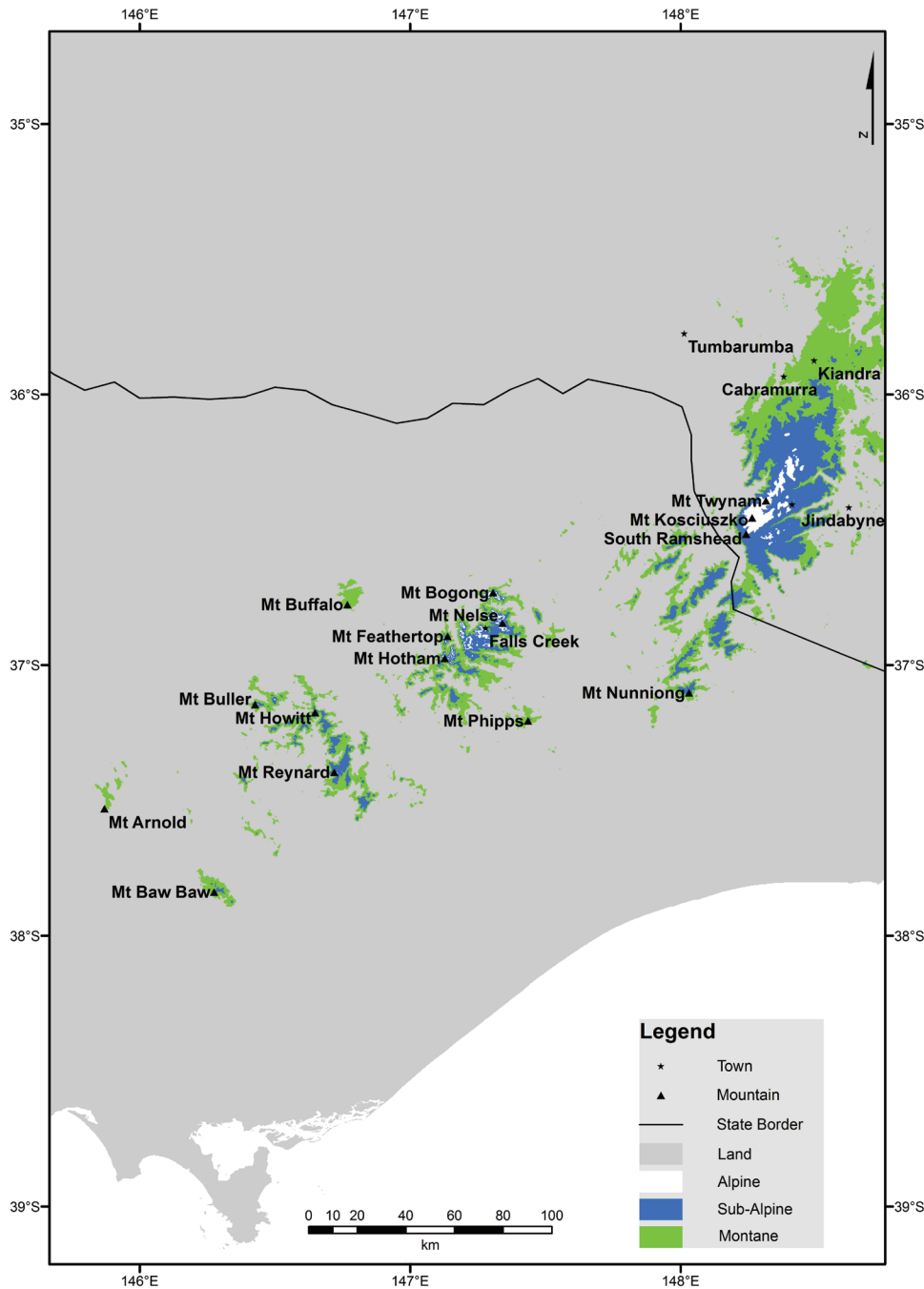


FIGURE 2. Modeled thermal zones for mountains of southeast mainland Australia based on temperature extremes modified from Costin (1954) and using temperature data for the period 1976–2005. The map shows the southeastern corner of mainland Australia from 35° to 39°S and 145.8° to 148.8°E. The estimated alpine boundary was derived with the minimum threshold for freezing of +1 °C, whereas subalpine and montane boundaries were derived with a minimum threshold of +2 °C.

above 1500 m during the period 1950 to 2007. Accounting for this difference, the 7.15 °C required for the Körner model in the period 1976–2005 data gives a treeline temperature within the confidence limits of the newly estimated threshold of ~6.0 °C (Körner, 2012) (presumably also ± 0.7 °C). Similarly, this rise would help explain the better fit of a temperature threshold above 0 °C for the Costin model. For Tasmania, the difference in thresholds between the two temperature periods of 0.41 °C reflects Tasmania’s warming rate in the second half of the 20th century, which was only 60% of the national average (ACE CRC, 2010).

Costin (1954) differentiated three zones of increasing harshness with elevation, with the highest two, alpine and sub-alpine, separated from montane by the winter snowline. Taking

a relatively central point from the Snowy Mountains (Mount Twynam, 36°23.6’S) and a decrease in treeline elevation of 110 m for each degree increase in latitude (Costin et al., 2000), then in the Victorian Alps at Mount Bogong (36°44’S) the treeline should be 51 m lower (our site was actually 88 m lower). If timberlines are similarly set by thermal thresholds and given the timberline elevation of 1506 \pm 26.7 m for the Snowy Mountains, then the 1454 \pm 40.0 m for the Victorian Alps, 52 m lower, is approximately correct.

Given that the timberline in the Snowy Mountains lies at about 1500 m and the alpine treeline at about 1950 m, both on the Perisher Range (Costin, 1957) and the South Ramshead, the growing season lapse rate of 9.1 °C per 1000 m (Green, 2014) would

TABLE 4

Areas modeled as alpine (km²) on the basis of an average temperature in the warmest month of $\leq 10^{\circ}\text{C}$.

Time period:	1921–1995	1976–2005	1921–1991	Measured area
Alpine (NSW)	48	6		135
Alpine (Victoria)	0	0		?
Alpine (Tasmania)	2420	637		1135
Alpine (PNG)			3354	225

NSW = New South Wales, PNG = Papua New Guinea.

mean that the timberline sits at a temperature threshold of about 11°C . This gives a thermal “depth” to the subalpine zone of approximately 4°C , which is similar to the 3.6°C thermal depth for Upper Montane (Körner et al., 2011) and means that the Snowy Mountains subalpine should be virtually equivalent as a zone to Körner’s Upper Montane (compare Figs. 1 and 2).

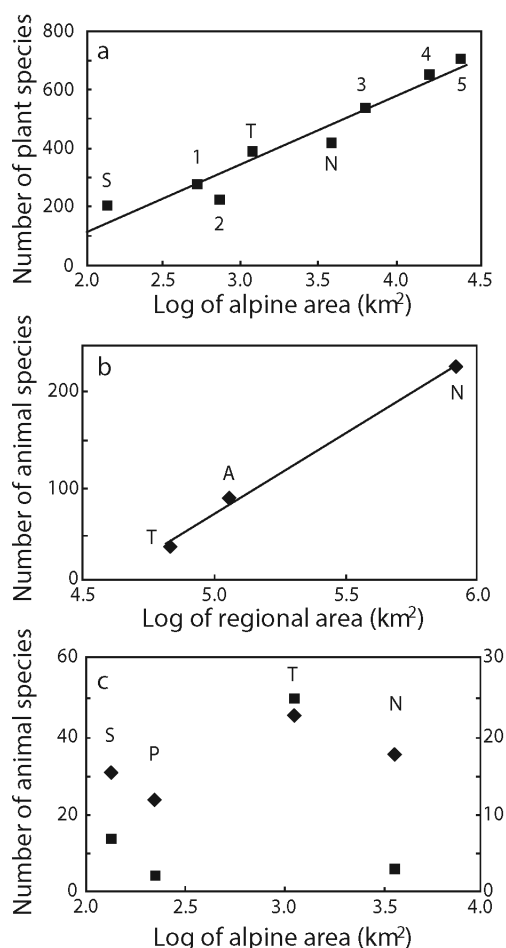


FIGURE 3. The relationship between land area and the diversity of species for (a) alpine vascular plants (S = Snowy Mountains, T = Tasmania, N = New Guinea, 1 = Afro-alpine, 2 = Hokkaido, 3 = Sierra Nevada [U.S.A.], 4 = Swiss Alps, and 5 = Southern Alps [New Zealand]), (b) regional vertebrate fauna (T = Tasmania, A = Australian mainland, N = New Guinea), and (c) alpine vertebrate fauna (diamonds left axis) and alpine fauna as a percentage of the regional fauna (squares right axis) (S = Snowy Mountains, P = PNG only, T = Tasmania, N = whole of New Guinea).

We have not been able to calibrate the Körner model for the whole of Meganesia, so it has proved difficult to examine specific mountain areas because of the need to adjust the temperature used within the error margin either upward (Australian mainland and New Guinea) or downward (Tasmania). Hence, unless the alpine area is known, or data exist for treeline temperature, the model may be difficult to use other than on a very broad scale. However, even when calibrated against the Snowy Mountains, it failed to model a believable figure for the Victorian Alps because of its tendency to over-estimate alpine areas in maritime climates as shown on the subalpine Baw Baw plateau and in Tasmania. Using the Costin model of winter temperature extremes rather than growing season averages for modeling also proved unproductive for both the Tasmanian and New Guinea alpine zones and, because of climate warming, temperatures had to be adjusted upward to get a reasonable approximation of the alpine area of the Snowy Mountains. It proved to be a better model in predictive mapping for the Victorian Alps, in that it mapped the expected alpine areas rather than the subalpine Baw Baw plateau. However, on a regional scale, ground-truthing with in-ground temperature loggers may be the only solution to determining alpine areas.

FLORA AND FAUNA

The existence of very different alpine zones within Meganesia makes for an interesting comparison of the biodiversity among these zones. Within Tasmania there is a significant relationship between area of alpine “islands” and the number of plant species, with many plant species restricted to certain “islands” and an increase in the number of local endemics from east to west and south (Kirkpatrick, 2002). Across Meganesia as a whole the number of vascular plant species in the alpine zones increases predictably from the smallest alpine area to the largest in line with a worldwide trend. However, this is not the case with the alpine fauna, where the highest richness occurs in Tasmania. The high vertebrate richness in Tasmania is not a function of regional faunal availability, which, like the alpine plants, also increases with increasing land area. Both the numbers of vertebrate species in the alpine zone and the proportion of the regional fauna occurring in the alpine zone are highest in Tasmania. The proportion of the regional fauna occurring in the alpine zone of New Guinea is lower than in the Snowy Mountains, with the number of species in the alpine zone not much higher (and in fact being lower in PNG despite having nearly twice the alpine area of the Snowy Mountains).

Given the similarities in the fauna available to colonize the alpine zones in Meganesia, factors other than the area of the alpine zone must be examined to explain the richness of the alpine fauna. Pleistocene glaciation in Meganesia was restricted to the mountains (Hope, 2014) and should not have directly removed source

populations from areas below the mountain regions. However, adaptations to a generally colder climate, as experienced in Tasmania during widespread glaciation, might have led to more species being pre-adapted to colonize alpine areas once glaciers retreated. The alpine mountains of New Guinea are much younger than those of Australia (Hill and Hall, 2003; Costin et al., 2000), which may contribute to under-utilization of some vertebrate niches (Heinsohn and Hope, 2006). Animals, however, can react quickly to unoccupied niches, and the European hare (*Lepus europaeus*), which generally does not extend to the higher mountains in its native range, spread quickly into southern hemisphere alpine zones when introduced (Green et al., 2013). Also, the younger age of the mountains does not appear to have affected the alpine plant richness of New Guinea adversely and the alpine zone has a flora commensurate with its area. So time does not seem to have led to differential colonization by plant species across Meganesia and probably had little impact on faunal differences.

In defining the lower limit of the alpine zone, Körner (2012) concluded that the alpine treeline is a result of the thermal environment occurring in summer and stated that no understanding of its global nature could be gained from winter climatic extremes. This statement could, by extension, be applied to the occurrence of many plant species in the alpine zone. Once an alpine area is defined, the vegetation can to a large degree be inferred, with the likely presence of characteristic alpine life forms such as those of short stature, including graminoids mainly as tussocks, herbaceous perennials, and cushion plants (Körner 2003). However, our study shows that while Meganesian alpine zones from the tropics to cool temperate zone are similar in their growing season mean temperatures, they differ in their temperature extremes, and so for many alpine areas there is no way of understanding the make-up of the fauna *except* by examining climatic extremes. Climatic extremes may select both for and against certain animal groups, but it would require a larger data set than presented here to explore fully all the processes determining vertebrate presence in the alpine zone, so we examine just two that appear to explain a large proportion of the differences in alpine vertebrate richness among Meganesian mountain ranges.

COLD EXTREMES

Many animals have an “active season” rather than a “growing season,” and in a seasonally cold alpine environment, the only faunas whose active season is linked to the growing season are migrants and hibernators, limiting the extent to which the vertebrate fauna can be modeled using growing season climatic data. Although most plants and many animals beneath the snow are quiescent in winter, many vertebrates must actively forage (Green, 1998).

Tasmania and the Snowy Mountains share a number of species within their respective regional faunas. However, seven vertebrate species found only up to subalpine elevations in the Snowy Mountains extend into the alpine zone in Tasmania (Green and Osborne, 2012). Among these, macropods (kangaroos and wallabies) are excluded from the alpine zone of the Snowy Mountains because of the regular seasonal snowpack that both reduces the access to foraging and severely impedes locomotion (Kirkpatrick, 1989). Macropods, however, occur in the alpine zone in New Guinea and Tasmania, areas that receive, respectively, virtually no snow or no regular deep seasonal snowpack. Alpine Tasmania does experience winter snow, but not the depth nor duration of the seasonal snowpack of the mainland, and in years of deep snow, mortality

among Tasmanian alpine wallabies may be high (Kirkpatrick, personal communication). Hence, winter harshness partially explains faunal distribution in these alpine areas.

SOLAR RADIATION

The Tasmanian alpine has nine species of reptiles, the Snowy Mountains alpine has eight, but the alpine areas of PNG have none. All Snowy Mountains alpine reptiles and seven of those from Tasmania are viviparous (live bearing). Viviparity is the major form of reproduction at high elevations because reptiles can maintain their developing embryos at temperatures in excess of ambient by basking in the sun to optimize development time (Green and Osborne, 2012). This requires a minimum amount of solar radiation, and adaptations to overcome low ambient temperatures such as sun-basking will be of little use under cloudy conditions. Pindaunde on Mount Wilhelm receives less than 25% of the possible hours of sunshine because of almost permanent cloud (Hnatiuk et al., 1976) and in the same area alpine plants receive only one-third of the solar radiation of plants in the lowlands (Körner, 2012). This cloudiness rather than temperature is a major factor in alpine distribution of reptiles. New Guinea has few alpine reptiles despite the occurrence of skinks up to treeline (Hope, personal communication) and the fact that all the alpine/subalpine families in Australia—the Agamidae, Scincidae, and Elapidae—arrived via New Guinea (Heatwole, 1987).

It appears the interactions of the fauna with the alpine environment are far more complex than the simple relationships with the flora. However, to obtain a better understanding of the causes of alpine vertebrate diversity a larger worldwide study is needed to assess vertebrate species richness of alpine areas in relation to land area and the composition of the regional fauna, as examined here, as well as elevation, latitude, continentality, cloudiness, and duration of snow cover.

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