Austral
ECOLOGY A Journal of ecology in the Southern Hemisphere

*Austral Ecology* (2021) **46**, 8–19

# Decline in lizard species diversity, abundance and ectoparasite load across an elevational gradient in the Australian alps

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**Abstract** The rapid changes in altitude, and associated habitat, of mountain ecosystems make them ideal natural laboratories for testing the effect of environmental heterogeneity on species assemblage. Our understanding of the sensitivity of Australian reptiles to elevational clines is limited. We examined lizard distribution across three elevation zones (montane, subalpine and alpine), spanning from 900 to 1840 m above sea level, in the Australian alps. We aimed to examine how elevation influences species diversity and abundance, and ectoparasite load, and whether species alter their habitat use amongst different elevational zones. Active searches were conducted across the elevation zones to identify lizard community structure (at least 16 species) across elevational zones, along with skink habitat preferences and the ectoparasite load. Skink diversity and abundance were negatively correlated with increased elevation. The alpine zone had significantly lower diversity and abundance of skinks. Habitat use differed amongst both elevations and species. Ectoparasite prevalence was also significantly diminished in the alpine zone. Ectoparasites only infected a subset of the skink community, with ectoparasite load increasing as the active season progressed. This study provides evidence of the complex interplay between elevation and species diversity, as well as the differences in ectoparasite pressure along elevational gradients in the Australian alps.

**Key words:** alpine zone, altitudinal cline, community ecology, Kosciuszko National Park, skink.

## INTRODUCTION

Both species diversity and abundance often exhibit latitudinal or elevational clines (Willig *et al.* 2003; Gaston 2008). The mechanisms underlying these patterns have been attributed to steep changes in the physical environment, including temperature, atmospheric pressure, season length, sunlight hours and geology (Lomolino 2001; Abbott & Brennan, 2014). Mountains represent around 25% of global terrestrial land area and support at least one third of the Earths' terrestrial plant species, including many endemic species (Korner 2007). The strong relationship between altitude and changes in temperature, precipitation and vegetation structure has been well studied (Korner 2007; Abbott & Brennan, 2014), and often correlated to rapid shifts in species diversity over a relatively short distance (Kevin 2000). Evolutionary adaptations of both flora and fauna can be examined over short spatial scales as elevational gradients give rise to rapid transitions in local conditions. Elevational clines can be used to test important ecological concepts relating to patterns of species diversity over manageable geographical distances (Korner 2007).

Adaptations to different climatic conditions are a key determinate of an ectotherm's geographic range (Monasterio *et al.* 2016). Present day alpine endemics are generally restricted to 'sky islands' of suitable alpine habitat and may have physiological adaptations to cold climates (Koumoundouros *et al.* 2009). Differences in climatic tolerance between species, and poor dispersal, can shape community structure in this group. For instance, the rock lizard (*Iberolacerta cyreni*) is restricted to alpine regions due to the low thermal quality and lack of refuges in a pine forest belt which separated the alpine habitat from lower elevations (Monasterio *et al.* 2009). However, a range of other factors in addition to climate can influence the geographic distribution of ectotherms.

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Accepted for publication August 2020.

doi:10.1111/aec.12951

Whilst the ecophysiological requirements of a species restrict its persistence to regions that meet its basic requirements, both intra- and inter-species competition also play a significant role in niche occupation and affect community structure (Schöb *et al.* 2012). This is particularly important in the context of species inhabiting alpine regions. For example, Melville (2002) found evidence for competitive exclusion in two closely related species of high-elevation skink, the northern snow skink (*Carinascincus greeni*) and southern snow skink (*C. microlepidotus*). In allopatric populations, the southern snow skink occupied both heath habitats and boulder fields, but was found to shift its habitat use to exclusively occupying heath habitat when occurring in sympatric populations. The southern snow skink was also smaller and less competitive than the northern snow skink, excluding it from preferable habitat when the two species co-occurred (Melville 2002). Variation in community structure can provide significant insight into the effect that inter- and intraspecies interactions can exert on resource access.

Although not typically examined as a mechanism of species assemblage, ectoparasite load (ectoparasites per host) is another factor that can influence community dynamics (Bower *et al.* 2019). For instance, parasite load has inherent links to both species diversity and abundance in a range of host systems (Main & Bull 2000; Godfrey 2013; Gómez & Nichols 2013). The spatial and social construction of a population provides opportunities for a myriad of direct or indirect transmission of parasites (Lumbad *et al.* 2011; Turgeona *et al.* 2018). For instance, network connectivity, by way of refuge sharing in sleepy lizards (*Tiliqua rugosa*), has been demonstrated to facilitate the indirect transmission of an ectoparasitic tick (*Amblyomma limbatum*; Leu *et al.* 2010). Species that occur in high densities may therefore experience higher parasite load, which can influence species ecology. Parasite interactions with host biota can have significant effects on host behaviour and habitat usage, which, in turn, may affect community structure (Main & Bull 2000; Biaggini *et al.* 2009; Gómez & Nichols 2013; Bozick & Real 2015). However, we have relatively little information on how ectoparasite diversity varies across elevation. Ecological studies have demonstrated that reptile ectoparasites (e.g. ticks and mites) are highly sensitive to temperature, moisture, vegetation type and soil type (e.g. Smyth 1973; Chilton *et al.* 2000), and therefore elevational clines in both species richness and abundance may be expected. Green and Slatyer (2020) reported that free-living mites were the most common arthropod found in snowmelt areas in the Mt Kosciuszko region, but it is unknown whether ectoparasitic species are common in the high-elevation regions of the Australian alps.

Australia is home to ~12% of the world's lizard species (Wilson & Swan 2017; Uetz *et al.* 2019); however, the vast majority of studies on the community structure and ecology of species have focused on the hyperdiverse arid regions of the continent (Pianka 1986). Relatively few studies have investigated the community ecology of Australian lizards across elevations in high-elevation regions (McCain 2010; Kutt *et al.* 2011), and only one above 1100 m (Fischer & Lindenmayer 2005). Thus, high-elevation communities of Australian lizards remain poorly understood (Green & Osborne 2012). We aim to address this knowledge gap by investigating the community structure of montane and alpine lizards (above 900 m) in south-eastern Australia. Approximately 20 lizard species have previously been reported from the mainland Australian alpine zone, including *Acritoscincus duperreyi*, *Cyclodomorphus praealtus*, *Lampropholis guichenoti* and multiple species of *Pseudemoia*, *Eulamprus*, *Liopholis* and *Egernia* (Green & Osborne 2012; Wilson & Swan 2017).

The Australian alpine ecosystem occupies a very small proportion of the continent, in the Snowy Mountains between New South Wales (NSW) and Victoria, and parts of Tasmania (approximately 0.15% of the terrestrial land space; Williams & Costin 1994). As such, Australian high-elevation lizards exist in relatively isolated, extreme environments. Changes in the thermal quality of the environment may affect dispersal, predation and resource availability, as reported in the alpine she-oak skink (*C. praealtus*) and Guthega skink (*Liopholis guthega*; Sato *et al.* 2014a). These species are alpine endemics, confined to two main regions within the Australian mainland alps (Koumoundouros *et al.* 2009; Atkins *et al.* 2020). The isolation of the high-elevation environment in Australia has facilitated high rates of endemism within this region, and several species are listed as Threatened (e.g. *C. praealtus*, Clemann *et al.* 2018a; *L. guthega*; and Clemann *et al.* 2018b). Climate change, along with changes to land use and fire regimes in the Australian sub-alpine–alpine region, has been identified as key threats for this community (Sato *et al.* 2014a,b; Atkins *et al.* 2015; Clemann 2015). A better understanding of the current community structure of Australian high-elevation skinks is imperative to predict and protect their future.

Here, we aim to characterise lizard diversity, and the mechanisms driving this diversity, across an elevational cline in Kosciuszko National Park, NSW, Australia. Specifically, we investigated the following questions:

1. How do lizard communities vary temporally and spatially with respect to elevation?
2. What aspects of the habitat are most important to each species, and how does habitat usage change with elevation?

doi:10.1111/aec.12951

3. Do morphological traits vary according to elevation and habitat use?
4. How does ectoparasite diversity and load vary in relation to both elevation and lizard density?

To address these questions, data were collected *in situ* on native lizards in montane, subalpine and alpine regions between 900 and 1840 m. We predicted that low- to mid-elevation zones would support higher species diversity and abundance, and that parasite load would be greatest in species and sites of high lizard abundance. In addition, we predicted that the ecomorphology of species would be strongly related to habitat use, irrespective of elevation.

## MATERIALS AND METHODS

### Study region

Lizard communities were sampled across an elevational gradient (900–1840 m) from Jindabyne to Mt Kosciuszko, NSW, Australia (Table S1, Fig. S1). The region contains Australia's highest mountain (Mt Kosciuszko, 2228 m), and we investigated three broad elevational zones: montane (900–1400 m), subalpine (1500–1650 m) and alpine (1650+ m) (Green & Osborne 2012). Climate and vegetation communities vary across each of these zones. The alpine zone occurs above tree line and consists of a wide variety of habitats, including exposed ridgelines, rocky outcrops, herbfields, grasslands and bogs (Green & Osborne 2012). The subalpine zone is comprised of a diverse array of habitat types, but primarily Snow Gum (*Eucalyptus pauciflora*) woodlands with herbfield, grassland and/or heathland understories (Green & Osborne 2012). The montane zone is generally characterised by dry, open forests and experiences temporary snow cover (Green & Osborne 2012).

### Field sampling

Sampling occurred within each of the three elevational zones between November 2017 and January 2018. Two sites, each with three replicate 100 m transects (with the area 5 m either side searched), were sampled in each of the three elevational zone (total sites: $n = 6$; total transects: $n = 18$). All sites were sampled between two and four times across the study period to account for variation across the active season. Montane transects were sampled in November, December and January, whereas subalpine and alpine sites were sampled in December and January due to snow cover in the early part of the active season making these sites inaccessible. Only one site was sampled per day, but all three transects within the site were sampled on the same day (in randomised order). Sampling only occurred on days that were sunny, or partly cloudy. Each sampling session/block was conducted over a period of approximately one week. During each sampling session, two to four experienced observers (typically two) walked each transect at a consistent pace. Lizards were captured by hand or using a noose, visually identified, sexed (through the eversion of hemipenes in males) and their positions at time of observation marked for microhabitat assessment. For each captured lizard, morphological measurements and the presence and number of ectoparasites were recorded. Morphological measurements (to the nearest mm) included snout–vent length (SVL), head length and width, interlimb length, pelvic width, and fore- and hindlimb length and evidence of tail loss (regenerated tail or partial tail). A descriptive summary of the weather conditions at the time of capture was also noted. We ensured that lizards were not recaptured within a sampling session (released lizards were marked with a dot of non-toxic white-out at the base of their tails), or counted twice. The time taken to complete each transect depended on the number of lizards caught. Capture data were used to assess lizard abundance (defined as the number of lizards caught) and species richness (defined as the number of species) across elevational zones.

### Microhabitat characterisation

Habitat assessments were conducted on the location where each lizard was collected. A 1 $m^2$ quadrat was positioned around the location that each lizard was first observed (Fig. S2). Within the quadrat, per cent canopy closure as well as understory vegetation height (cm) was estimated. Canopy cover was calculated using a photograph taken from the middle of the quadrate looking up. This took into account the canopy relevant for the skink that was observed at that location and incorporated shrubbery cover. Substrate was characterised by estimating the per cent cover of rocks, leaf litter and bare soil. The distance to water was measured for water bodies within 10 m of the quadrat. The temperature of the spot the skink was observed was recorded using a pocket laser digital temperature (DIGITECH QM-7218; accuracy ± 1.0°C, Chukwuka *et al.* 2019; Drummond *et al.* 2020).

### Parasite load

The ectoparasite load was assessed for each captured lizard. The number of ticks and clusters of mites was counted and recorded. A representative sample of each tick and mite species was collected and sent to Dr Di Barton (School of Animal & Vet Science, Charles Sturt University) and Dr R. B. Halliday (Research Fellow Acarology, Australian National Insect Collection) for identification.

### Statistical analysis

All data were analysed using the statistical programme R 3.50 (R Development Core Team 2016). Statistical significance was assigned at $\alpha = 0.05$ using diagnostic plots, Shapiro–Wilk test of normality and Bartlett's tests of equal variances. Where assumptions were not met, the data were transformed or non-parametric equivalent tests were used.

doi:10.1111/aec.12951

### *Lizard abundance and species richness across elevation*

Generalised linear models ('MASS' package) with a binomial distribution were used to test for clinal variation in the presence of each lizard species captured. Elevational zone, number of observers and sampling period were specified as fixed effects. Variation in lizard abundance and species richness across elevational zones was assessed using linear mixed effects models ('lme4' package). Either lizard abundance or richness was the response variables and elevational zone, the number of observers, sampling period and number of samples per transect were included as fixed factors. Transect ID nested within site was included as a random effect. Differences in abundance and richness between sites within each zone were examined using linear mixed effects models. In each of these models, site, the number of observers, sampling period and number of samples per transect were included as fixed factors whilst transect ID was assigned as a random effect. Where significant differences amongst elevational zones or site were identified, post hoc analyses were performed ('lsmeans' package) to identify which paired comparisons were significant.

### *Microhabitat use*

A principal component analysis (PCA) with varimax rotation was applied to reduce the dimensionality of data and determine the important environmental variables for each species across the elevational cline. All measured microhabitat variables within each 1-m$^2$ quadrat were used in the analyses, including per cent canopy closure, vegetation height, proximity to water and substrate composition (rock, leaf litter and bare soil). All variables were scaled and centred. Two PC components were retained based on the Kaiser–Guttman criterion (eigenvalues >1) and used for further analyses. Linear mixed effects models were used to evaluate variation in habitat use between elevational zones. Each of the two PC components was used as separate response variables with elevational zone, weather conditions, and sampling period as fixed effects and transect ID nested within site included as a random factor. Linear mixed effects models were also used to evaluate variation in habitat use between sites. These models had site, weather and sampling period included as fixed effects along with the random effect of transect ID. Where significant differences amongst elevational zones or site were identified, post hoc analyses were performed to identify which paired comparisons were significant.

### *Ecomorphology and tail loss*

A PCA with varimax rotation was used to describe morphological variation by elevational zone. Morphological variables included the following: SVL, head length, head width, interlimb length, pelvic width, upper and lower forearm length, forefoot length, upper and lower hindlimb length, hindfoot length and tail length. All variables were scaled and centred. Two PC components were retained based on the Kaiser–Guttman criterion (eigenvalues >1) and used as separate response variables in linear models. Elevational zone and species were included as fixed effects. The first component was log-transformed to meet the assumption of normality. Linear models were also used to evaluate morphological variation in terms of habitat used by each species with habitat PC components, species and their interaction as fixed effects. Differences in the incidence of tail loss across elevational zones were assessed using generalised linear models with a binomial distribution. Tail loss (yes/no) was included as the response variable and zone as a fixed factor.

### *Ectoparasites*

Clinal variation in the presence and number of ectoparasites was modelled using random intercept models. All models included elevational zone and sampling period as fixed factors. Transect ID nested within site was included as the random term for models assessing differences in presence and abundance across zones. Differences in the abundance of each type of ectoparasite, mites and ticks, across zones were evaluated using separate generalised linear models with elevational zone and sampling period as fixed factors. Presence was modelled with a Poisson distribution whilst a binomial distribution was used for modelling abundance.

Ectoparasite presence and abundance were also modelled as a function of sex and site using random intercept models. For all models having ectoparasite presence as a response variable, a binomial distribution was used whereas those models having ectoparasite abundance as the response variable used a Poisson distribution. Site ID and sampling period were included as fixed factors and transect ID as a random factor for models assessing variation between sites. Analyses of variation between males and females included sex and sampling period as fixed factors and transect ID as a random factor. Finally, generalised linear models with a Poisson distribution were used to model if mites and ticks preferentially parasitised particular lizard host species. Post hoc analyses were performed for all models having significant differences between fixed factors.

## RESULTS

A total of 527 lizards, from 16 different species, were captured (Table 1). It was generally difficult to identify *Pseudemoia* species accurately; therefore, they were considered as *Pseudemoia* spp. The presence or absence of each species was not affected by elevation, except for *Eulamprus tympanum*, whose occurrence varied between the alpine and subalpine zones (Dunnet-corrected comparison, $Z = 2.74$, $P = 0.02$), with abundance higher in the subalpine zone. Detectability differences amongst sampling periods were also demonstrated in *Egernia cunninghami*. This species had higher occurrence in November than during July (Dunnet-corrected comparison, $Z = 2.03$, $P = 0.04$). The number of observers also had an effect on detectability for two species, *E. cunninghami* and for *L. guthega*. The number of individuals detected was higher when the number of observers was four rather than two for *E. cunninghami* (Dunnet-corrected

doi:10.1111/aec.12951

comparison, $Z = 2.75$, $P = 0.01$) whilst *L. guthega* was observed at a higher rate with three rather than two observers (Dunnet-corrected comparison, $Z = 2.85$, $P = 0.01$). Species richness decreased with elevation, with the montane zone having significantly higher species richness than both the subalpine (Dunnet-corrected comparison, $t = -2.82$, $P = 0.03$) and alpine zones (Dunnet-corrected comparison, $t = -3.95$, $P = 0.004$; Fig. 1a). Lizard abundance followed a similar pattern of decreasing number of lizards with increasing elevation (Fig. 1b) and was influenced by the number of observers (estimate = 4.70 ± 1.54, $P = 0.005$). Sites within elevational zones did not differ in species richness (Montane: Dunnet-corrected comparison, $t = 3.14$, $P = 0.08$; Subalpine: Dunnet-corrected comparison, $t = -1.37$, $P = 0.76$; Alpine: Dunnet-corrected comparison, $t = 0.73$, $P = 0.98$; Fig. 1b). By contrast, abundance did differ between sites within the montane zone (Dunnet-corrected comparison, $t = 7.94$, $P < 0.001$; Fig. 2b). The number of observers also influenced the abundance at both the zone and site levels. Abundance was highest with four observers compared to when it was two (Dunnet-corrected comparison, $t = 4.42$, $P = 0.0003$; Dunnet-corrected comparison, $t = 4.91$, $P = 0.0001$; respectively) or three (Dunnet-corrected comparison, $t = 3.92$, $P = 0.001$; Dunnet-corrected comparison, $t = 4.46$, $P = 0.0002$; respectively).

## Habitat

The PCA revealed that the first principal component, explaining 26.28% of the variation in microhabitat, described low canopy closure as well as a substrate having higher rock than soil/leaf litter cover (Table 2). The second principal component explained an additional 22.26% of the variation, and was characterised by high proximity to water and low vegetation height. Habitat varied in PC1 between alpine and subalpine zones (Dunnet-corrected comparison, $t = -0.92$, $P = 0.02$), as well as between subalpine and montane zones (Dunnet-corrected comparison, $t = 1.52$, $P = 0.002$) indicating that canopy closure was lowest and rock cover highest in the alpine zone whereas the opposite pattern was observed in the montane zone. Species also differed in their use of microhabitat for PC1 ($F_{13} = 17.76$, $P < 0.001$; Fig. S3) and PC2 ($F_{13} = 15.09$, $P < 0.001$).

## Ecomorphology

The two principal components explained a total of 72.49% of the variation in morphology amongst captured lizards (Table 3). The first component characterised long and wide bodies, long and wide heads, and long limbs and feet. Pelvic width loaded strongly and negatively on PC2 along with high positive loadings of lower hindlimb length. This component can be interpreted as lizards having narrow pelvic widths also having long lower limbs. No variation in morphology was found across elevation for either PC1 or PC2 ($F_1 = 2.02$, $P = 0.16$; $F_2 = 0.37$, $P = 0.70$; respectively). Similarly, morphology did not differ according to used habitat ($F_1 = 0.44$, $P = 0.84$; $F_1 = 0.22$, $P = 0.88$; $F_1 = 0.12$, $P = 0.73$; $F_1 = 0.66$, $P = 0.42$, respectively). Incidence of tail loss was

**Table 1.** Total number of individuals of each species captured within the three elevational zone sampled within Kosciuszko National Park, NSW, Australia, during November 2017 to January 2018. Straight line distance between sampling sites across the montane and alpine zones measured 27.15 km

| Species name | Common name | Montane zone (900–1200 m) | Subalpine zone (1200–1660 m) | Alpine zone (1660–1840 m) |
|---|---|---|---|---|
| *Acritoscinus platynotum* | Red-throated skink | 11 | 0 | 0 |
| *Ctenotus taeniolatus* | Copper-tailed skink | 67 | 0 | 0 |
| *Cyclodomorphus praealtus* | Alpine she-oak skink | 0 | 0 | 1 |
| *Egernia cunninghami* | Cunningham's skink | 33 | 7 | 0 |
| *Eulamprus heatwolei* | Yellow-bellied water skink | 18 | 0 | 0 |
| *Eulamprus kosciuskoi* | Alpine water skink | 0 | 0 | 1 |
| *Eulamprus tympanum* | Southern water skink | 0 | 18 | 17 |
| *Lampropholis guichenoti* | Common garden skink | 86 | 19 | 0 |
| *Liopholis guthega* | Guthega skink | 0 | 0 | 62 |
| *Liopholis montana* | Tan-backed skink | 0 | 11 | 0 |
| *Liopholis whitii* | White's skink | 112 | 0 | 0 |
| *Pseudemoia* spp[†] | n/a | 2 | 54 | 1 |
| *Rankinia diemensis* | Mountain dragon | 5 | 0 | 0 |
| *Tiliqua nigrolutea* | Blotched blue-tongue skink | 2 | 0 | 0 |

[†] *Pseudemoia entrecasteauxii*, *P. pagenstecheri* and *P. rawlinsoni* were not easily discernible from field markings and thus were treated as a single group.

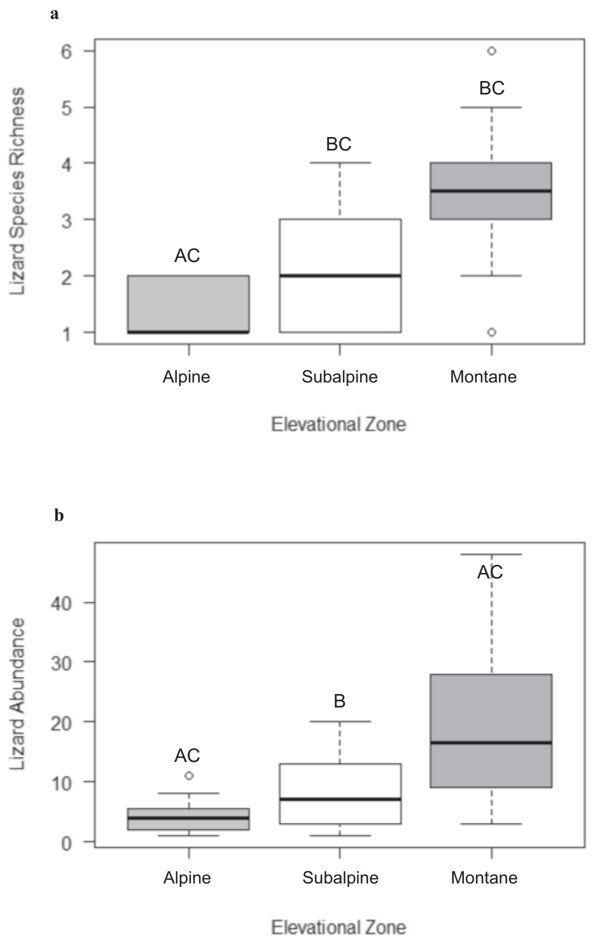

**Fig. 1.** Lizard species richness (a) and abundance (b) across elevational zones of Mount Kosciuszko, NSW, Australia. Letters indicate whether significant differences in mean richness are present.

similar across elevational zones ($X_2^2 = 1.93$, $P = 0.55$; Fig. S4).

## Ectoparasites prevalence

Only six of the 16 species caught across the study had ectoparasites (Fig. S5). One ectoparasite appeared to represent an undescribed species of mite from the family Trombiculidae and was found across all elevations. Two species of tick (Acari: Ixodida) were identified within the montane zone, with no lizards being parasitised by ticks at either of the two higher elevation zones. Both types of ectoparasites were found infecting the same species where they co-occurred. Both types of ectoparasites were non-host specific and infected multiple species within the community. Clinal variation was detected in the presence of ectoparasites. The number of lizards with ectoparasites was less in the alpine zone compared to that within the subalpine (Dunnet-corrected comparison, $Z = -0.06$, $P = 0.01$) and montane zones (Dunnet-corrected comparison, $Z = -2.42$, $P = 0.04$). Presence did not differ between the subalpine and montane zones (Dunnet-corrected comparison, $Z = 0.98$, $P = 0.62$). Sampling period was also found to influence the presence of ectoparasites across zones. The occurrence of ticks and mites decreased from December to January (Dunnet-corrected comparison, $Z = -2.47$, $P = 0.04$). Similarly, clinal and temporal variation in the abundance of ectoparasites was also found. The number of ticks and mites was higher in

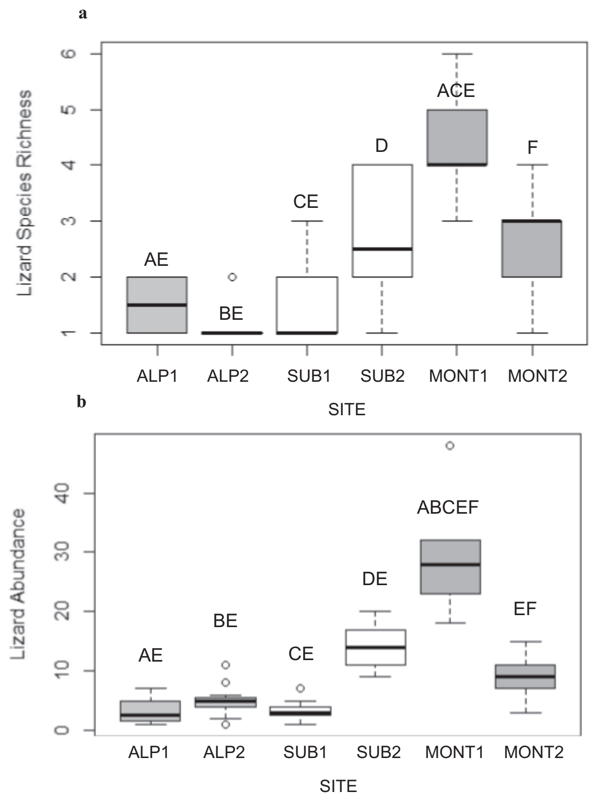

**Fig. 2.** Lizard species richness (a) and abundance (b) across sites sampled at Mount Kosciuszko, NSW, Australia. Letters indicate whether significant differences in mean richness are present.

**Table 2.** Component loadings and per cent variance of two orthogonally rotated principle components describing microhabitat characteristics within 1 $m^2$ quadrats around captured lizards. Loadings of at least 0.3 (indicated in bold) were considered to contribute to a component

| Habitat variable | PC1 | PC2 |
|---|---|---|
| Canopy closure | **−0.56** | 0.29 |
| Distance to water | −0.16 | **0.70** |
| Rock | **0.55** | 0.27 |
| Soil and leaf litter | **−0.58** | **−0.32** |
| Understory veg height | 0.12 | **−0.50** |
| Cumulative variance (%) | 26.28 | 48.54 |

doi:10.1111/aec.12951

**Table 3.** Component loadings and per cent variance of two orthogonally rotated principle components describing morphological characteristics of captured lizards. Loadings of at least 0.3 (indicated in bold) were considered to contribute to a component

| Morphological variable | PC1 | PC2 |
|---|---|---|
| Snout-vent length | **0.33** | −0.19 |
| Head length | **0.32** | −0.13 |
| Head width | **0.34** | 0.02 |
| Interlimb length | 0.29 | −0.25 |
| Pelvic width | 0.13 | **−0.64** |
| Upper forlimb length | 0.29 | −0.09 |
| Lower forlimb length | **0.31** | 0.18 |
| Front foot length | **0.33** | −0.09 |
| Upper hindlimb length | **0.31** | 0.23 |
| Lower hindlimb length | 0.23 | **0.58** |
| Hind foot length | 0.28 | 0.17 |
| Tail length | 0.25 | 0.00 |
| Cumulative variance (%) | 63.93 | 72.49 |

Loadings of at least 0.3 were considered to contribute to a component.

the montane and subalpine zones relative to the alpine zone (Dunnet-corrected comparison, $Z = 3.03$, $P = 0.01$; Dunnet-corrected comparison, $Z = 3.37$, $P < 0.001$; respectively). Additionally, ectoparasite abundance varied between sampling periods with the number of ticks and mites being higher in January than December (Dunnet-corrected comparison, $Z = 3.21$, $P = 0.003$) as well as November (Dunnet-corrected comparison, $Z = 4.76$, $P < 0.001$). Abundance did not differ between November and December (Dunnet-corrected comparison, $Z = 2.02$, $P = 0.11$). Elevational zones did not vary in the number of mites ($Z = 0.02$, $P = 0.99$) or ticks ($Z = 0.01$, $P = 0.99$) present.

Both the presence and abundance of ectoparasites varied across field sites, and this pattern even occurred within the same elevational zone. Presence was higher in site MID2 relative to sites HIGH1 (Dunnet-corrected comparison, $Z = 3.16$, $P = 0.02$) and LOW1 (Dunnet-corrected comparison, $Z = 3.53$, $P = 0.01$). Similarly, the presence of ectoparasites was found to be greater in site LOW2 compared to that of LOW2 (Dunnet-corrected comparison, $Z = 3.67$, $P = 0.003$). With respect to the number of ectoparasites, MID2 had greater abundance than LOW1 (Dunnet-corrected comparison, $Z = 5.10$, $P < 0.001$) and LOW2 had greater abundance than site HIGH1 (Dunnet-corrected comparison, $Z = 3.08$, $P = 0.03$). Temporal variation amongst sites in ectoparasite abundance was also detected. The greatest number of ectoparasites on captured lizards occurred in January (December: Dunnet-corrected comparison, $Z = 2.85$, $P = 0.01$: November: Dunnet-corrected comparison, $Z = 4.78$, $P < 0.001$). By contrast, sex differences in either the presence ($Z = 0.18$, $P = 0.86$) or abundance ($Z = -0.08$, $P = 0.93$) were not detected. Nor did the abundance of mites or ticks vary between parasitised lizard species (Table S2).

## DISCUSSION

Our study represents the most detailed examination of the influence of elevation on reptile community structure and diversity in the Australian alps. Our findings fit broadly with reptile diversity trends across elevations globally (McCain 2010; Malonza 2015). The potential for range shifts in lower elevation species with climate change is widely accepted (Pearman *et al.* 2010). A deeper understanding of what mechanisms shape community structure under present environmental conditions is therefore imperative for protecting and monitoring change into the future. This study has highlighted the current patterns of skink species distribution across three elevational zones in the Australian alpine region. Many of the species were found to overlap in their habitat requirements and preference for specific habitat structures. Ectoparasites were present on around half the species caught throughout the study. We documented differences in the parasite load across the active season and prevalence across elevational zones.

### The effect of elevation on community structure

Lizard diversity in Kosciuszko NP was inversely related to elevation. This decrease in species diversity within higher elevations is consistent with observations across a wide range of taxon (Birds: Ding *et al.* 2005; Reptiles: Fischer & Lindenmayer 2005; Mammals: McCain 2005; Insects: Slatyer & Schoville 2016). Notability, Kutt *et al.* (2011) found that reptile diversity was highest at the montane zone (600–900 m). Although not directly measured in this study, climatic changes across an altitudinal gradient such as changes in temperature, precipitation, partial pressure of atmospheric gases, wind speed and radiation are well established and recognised to be highly interactive (Barry 1992). Extreme climatic conditions (including air pressure) associated with high elevation, in particular, temperature, pose particular challenges on a species physiological capacity to function and have been associated with a decrease in the number of species capable of surviving in high elevations. The present study found only two species within the highest elevational zone that also persisted at lower elevations. This suggests significant specialisation in adaptations required to survive in the alpine zone. The structural complexity of the floral habitat typically decreases with increased elevation (Korner 2007). A decrease in resource availability, coupled with the evolution of adaptations to harsh conditions,

doi:10.1111/aec.12951

is likely to be influencing the significant drop in skink diversity and abundance in the alpine zone.

Lizard diversity similarly decreased with increases in elevation. Consistent with this finding, Malonza (2015) found that more species occur in the low and mid elevations, whilst only a select few were found in the high-elevation zone. Given that the Australian alpine region is lower altitude than alpine regions in other parts of the world, much of the Australian elevational range investigated in this study may lie within a climatic envelope that is still suitable for a broad range of species (Green & Osborne 2012). The alpine region sits just above the upper range limit for many species (Green & Osborne 2012). Our results suggest that elevation zones differ substantially in their capacity to support reptile abundance, although this study did not document continuous distributions across the entire elevational gradient (0–2228 m). The spatial variation in thermal conditions across elevations (e.g. Senior *et al.* 2019) is likely to drive large-scale patterns in the diversity and abundance of lizards. Interestingly, Fischer and Lindenmayer (2005) found that a difference of as little as 50 m in elevation was sufficient to change the composition of skink species at a given site. Variation in the aspect and structural complexity of individual sites is likely to be influential in the environmental temperature directly experienced by lizards.

## Do skinks differ in their habitat selection?

Microhabitat preference was relatively similar amongst most species, irrespective of species elevational range. Most of the lizard species were found to reside in habitats with a combination of both rock and groundcover vegetation, which is unsurprising as this is a community of sympatric species with common resource requirements, in terms of thermoregulation and diet. Australian alpine reptile studies within the same study area (Kosciuszko National Park, NSW) have indicated that structural complexity in the environment can dramatically affect ground temperatures and reptile occurrence in these areas (Sato *et al.* 2014c). Aside from creating suboptimal thermal environments, reduced complexity in the habitat can also increase predation risk to lizards and reduce foraging success (Webb & Whiting 2005). This may explain the higher density of species in complex habitats. Some species demonstrated individual preferences for various habitat types, potentially indicating resource partitioning within the community. For instance, *Pseudemoia* sp., *C. praealtus* and *L. guthega* were found to have distinct preference for habitat dominated by groundcover vegetation and leaf litter, whilst *Eulamprus* species were found in habitats incorporating water and rock. Rock-dominated habitats were largely occupied by species such as *E. cunninghami*, *E. tympanum*, *L. whitii* and *L. montana*. Strong overlap in habitat requirements, particularly in dense populations, is likely to drive competition for resources both within and between species. The divergence in microhabitat preference between species is a strong indicator of competition mediated population dynamics in this community.

Selection for habitat variables was evident across species and elevations, which may indicate differences in resource availability and niche differentiation as a mechanism for facilitating species coexistence (Melville *et al.* 2001). Despite being found in similar, and at times, the same microhabitat, many species preferred distinct substrates. *Ctenotus taeniolatus*, for example, was found to actively select soil and leaf litter substrates. Interestingly, *L. guichenoti* and *Pseudemoia* sp. differed in their habitat selection (compared to their conspecifics at other sites). At the higher of the subalpine sites (‘subalpine2’), both species indicate a preference for rock substrate. This may represent differences in resource availability between the sites (e.g. Atkins *et al.* 2018); however, rock was a relatively common feature of all subalpine and montane sites. Alternatively, changes in a species’ use of a resource may alter in response to competition with sympatric species. Niche differentiation has been proposed as a mechanism for competing species to coexist (Dayan & Simberloff 2005). Differences in activity time, diet and habitat preference enable species to separate into niches, reducing competition and facilitating coexistence with a variety of other species (Morin 2011). The abundance of *L. montana* or *L. whitii* across these sites may have altered competition pressure on *L. guichenoti* and *Pseudemoia* sp., possibly resulting in the use of what could be considered suboptimal habitat types. Both *Liopholis* skink species are medium-sized and demonstrated a preference for rock-dominated habitat. *Liopholis whitii* exclusively inhabited montane zone in high abundance, whilst *L. montana* persisted exclusively in the subalpine zone in far lower abundance (Senior *et al.* 2019). Both skinks are significantly larger in body size than either *L. guichenoti* or *Pseudemoia* sp., perhaps enabling them to outcompete these smaller species. Indeed, body size has been found to be tightly linked with interspecific competition in Australian montane skinks, and so this is a strong indicator that *Liopholis* skinks could be excluding smaller skinks from preferred habitat when they themselves persist in relatively high densities (Langkilde & Shine 2004).

## Ectoparasites of high-elevation lizards in south-eastern Australia

Ectoparasite abundance exhibited a negative correlation with increased elevation. Only one individual

doi:10.1111/aec.12951

skink within the alpine zone had ectoparasites (*E. tympanum*). However, ectoparasites were prevalent across both the subalpine and montane skink communities. Godfrey *et al.* (2011) examined the microhabitat preferences of reptile ticks, finding that they preferred microhabitats that reduced the risk of desiccation and increased opportunities to encounter the lizard host. This suggests that ectoparasites may be more abundant in lizard populations where the local conditions are most favourable for the free-living stage of the ectoparasite lifecycle (e.g. Chilton *et al.* 2000). The harsh conditions of the alpine region in Australia may pose thermoregulatory restrictions on ectoparasites. With temperatures sustained below zero for many months at a time, cold temperatures are likely to have a strong influence in shaping host/parasite relationships in montane to alpine regions. Low temperature is likely to affect not only host/parasite survival, but also shape a parasites' lifecycle. A shift in the elevational range of parasitic species as a result of anthropogenic climate change is predicted. This may enable parasites to persist in regions currently above their thermal range. *Eulamprus tympanum* had ectoparasites in montane elevational zones, but were almost devoid of parasites in subalpine and alpine regions. *Liopholis guthega*, an alpine endemic, were not found to have any ectoparasites at the time of survey. However, their closest relatives (*L. montana* and *L. whitii*) in the subalpine and montane regions were parasitised by mites, and at the lowest montane site, both mites and ticks. Conditions are predicted to become more favourable under climate change for lower elevation species. Range expansions of lower elevation species are likely to increase interspecific competition experienced by high-elevation species. Additionally, ectoparasites may be brought up by lower elevation species. Warmer conditions in the alpine regions are likely to suit both lower elevation species and their ectoparasites, which could lead to alpine zone reptiles being exposed to parasites they are less adapted to dealing with.

Ectoparasitic load increased throughout the active season. Hosts had higher parasite loads in January compared to November and December. This indicated that parasite population dynamics and infection cycles are influenced by temporal changes or differences in activity season of their hosts (Godfrey *et al.* 2008; Lumbad *et al.* 2011). Many skink species in the Australian montane to alpine regions undergo a period of dormancy during the cold winter months (Greer 1989). The seasonal infection cycle of the parasites is therefore likely to be closely tied to the activity period of the host species (Oliver 1989). Lower elevation species become active earlier in the season compared with alpine species due to the differences in prevailing weather across the elevational zones and the latent snow cover in the higher elevations (observed differences). This could also help to explain the higher prevalence of ectoparasites found in montane and subalpine communities. The active season of montane and subalpine zones is longer than that of the alpine region as they experience less snow cover. The present study found increased parasite prevalence through the months of summer. Similarly, mite loads of infected Tuatara (*Sphenodon punctatus*) were found in summer and early autumn but were undetected throughout the rest of the year (Godfrey *et al.* 2008). The increased activity season of hosts and the milder seasonal conditions may provide greater opportunities for ectoparasites to locate hosts and complete their lifecycles. There is significant evidence that some species of ectoparasites have the capacity to delay life stages in order to persist under harsh conditions (Wharton 1999). Their increased prevalence over the active season suggests that they are following a seasonal cycle, with host-dependent life stages taking place over the warmer active period of the year.

Ectoparasite presence was consistent amongst species, although only six species caught throughout the study had ectoparasites. *Acritoscinus platynotum*, *E. cunninghami* and *C. taeniolatus* were not infested with ectoparasites, despite co-existing at sites with species that were consistently infected. Ectoparasites have the potential to have negative influences on their host fitness. However, they can also indirectly benefit uninfested species or conspecifics within the community by helping to shape host population dynamics (Hudson *et al.* 1992). For instance, parasite intensity dramatically influenced survival and reproduction success in red grouse (*Trichostrongylus tenuis*), effectively acting as a density-dependant mechanism controlling population productivity (Hudson *et al.* 1992). Whilst parasites have also been found to display some sex-dependant effects on their hosts (Mugabo *et al.* 2015), no such relationship was found in this study. Mugabo *et al.* (2015) found sex-dependant relationships between tick density and populations of the common lizard (*Zootoca vivipara*), with tick prevalence declining with decreased female density, but not male lizard density. Sex differences in parasite load were not found in our study, although the lizards used are viviparous and do not make nests, males and females are therefore less likely to differ substantially in their behaviour or habitat use. The present study raises the intriguing hypothesis that ectoparasites could shape the lizard community by affecting only a subset of individuals and species. Testing of this hypothesis would reveal the importance of intra- and interspecific competition and resource allocation in infested individuals (Biaggini *et al.* 2009).

Ectoparasites type varied across elevation. Ticks were only found below 920 m. All parasitic tick life stages were detected on the same host animal, suggesting that this species is capable of completing its lifecycle with only one host species. That said, the same species of tick was found across multiple species of skink, indicating that it is not endemic to one host species. The distribution of ticks across the elevational zones may be influenced by host density. Lizard density and diversity were highest below 920 m (Site: Montane2), potentially enabling ticks to locate hosts. Infestation of a host by the immature free stage of ticks is strongly dependant on host behaviour as the tick has limited mobility and survival in the vegetation (De Garine-Wichatitsky *et al.* 1999). Ectoparasites also select habitat that will bring them into contact with potential hosts, and so it is likely that the optimal environmental conditions for free-living parasites are similar to optimal host conditions. Montane2 consisted of a particularly rich reptile community, and so it is very likely that conditions were optimal for host and parasite alike. Bull and Burzacott (1993) found that sleepy lizards (*T. rugosa*) living in good quality habitat also had higher tick loads from that habitat, suggesting that parasites may mediate the fitness benefit of high-quality habitat. The lack of ticks found at higher elevation sites may also have been due to the upper range limit of the parasite. The impacts of parasites in natural populations are not well understood but are likely to have significant ramifications for host population structure, particularly along elevational gradients where host species have the potential to encounter different assemblages of parasites.

## CONCLUSIONS

We demonstrate that elevation has a significant influence on skink community structure in Australian mountain systems. Overall, the diversity and abundance of skinks decreased with elevation. The niche occupation of certain species changed with variations in the structure of the community, potentially indicating competitive exclusion from preferred habitat. Whilst we did not actively test for competitive exclusion, our results suggest that the presence or abundance of *Liopholis* species within a site may influence habitat selection by smaller skinks. Further study into the potential role of ectoparasites in shaping host population dynamics is also warranted. In particular, further study is required to investigate the absence of ectoparasites at the higher elevation locations. Under warmer climate conditions, alpine skinks are predicted to experience increased rates of competition from lower elevation species. The potential for lower elevation species to bring ectoparasites into contact with alpine species is also a cause for concern. Future studies focused on the influence and potential elevational range of ectoparasites with projected climate change are highly recommended. In addition, it is likely that little is known about the ecology, population dynamics and conservation status of the ectoparasite species, and targeted research on these species is clearly warranted.

## ACKNOWLEDGEMENTS

We thank D. Barton, L. Bonafacio, K. Buchholz, M. Feeney, R.B. Halliday, R Hayes, C. Johnstone, C. MacKay, M. Michelangeli, I. Pham and B. Sykes for assistance during the study. This work was supported by an Australian Research Council Discovery Project grant (DP150102900, grant to DGC, MMG and GMW).

## AUTHOR CONTRIBUTIONS

**Katelyn Hamilton:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing-original draft (equal). **Celine Goulet:** Formal analysis (equal); methodology (equal); writing-original draft (equal). **Emily Drummond:** Conceptualization (supporting); investigation (supporting); methodology (supporting); writing-review & editing (supporting). **Anna Senior:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); supervision (supporting); writing-review & editing (equal). **Mellesa Schroder:** Methodology (supporting); project administration (supporting); resources (supporting); writing-review & editing (supporting). **Michael Gardner:** Funding acquisition (equal); project administration (supporting); resources (supporting); writing-review & editing (supporting). **Geoffrey M While:** Funding acquisition (equal); project administration (supporting); resources (supporting); writing-review & editing (equal). **David G. Chapple:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); supervision (equal); writing-review & editing (equal).

## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## AUTHOR CONTRIBUTIONS

KH, DGC, AFS, MGG and GMW conceived and designed the study. KH, EMD, AFS and MS

doi:10.1111/aec.12951

conducted the fieldwork. KH and CTG analysed the data. KH, DGC and CTG wrote the manuscript, with input from all other authors.

## ETHICAL APPROVAL

All applicable institutional and/or national guidelines for the care and use of animals were followed.

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## SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

**Appendix S1.** Latitude and longitude of each sampling location used in this study.

**Appendix S2.** Results of generalized linear models examining variation in the abundance of mites and ticks on captured lizard species.

**Appendix S3.** Location of the study sites in the Mt Kosciuszko region.

**Appendix S4.** Example locations where lizards were caught during the fieldwork, indicating that quadrat (1 × 1 m) placed around the capture location.

**Appendix S5.** Principal components analyses of microhabitat variables within 1-m$^2$ quadrats surrounding lizard locations.

**Appendix S6.** Principal components analyses of morphological traits of each captured lizard.

**Appendix S7.** The percentage of individuals of each species caught with ectoparasites across all elevational zones.

doi:10.1111/aec.12951