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MS. HEATHER NEILLY (Orcid ID : 0000-0002-2006-2271)

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Arboreality increases reptile community resistance to disturbance from livestock grazing

H. Neilly*, E. Nordberg, J. VanDerWal, and L. Schwarzkopf

College of Science and Engineering, James Cook University, Townsville, Australia

***Corresponding author: heather.neilly@my.jcu.edu.au**

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ABSTRACT

1. Domestic livestock grazing directly alters ground-level habitat but its effects on arboreal habitat are poorly known. Similarly, the response to grazing of ground-dwelling fauna has been examined, but there are few studies of arboreal fauna. Globally, grazing has been implicated in the decline of vertebrate fauna species, but some species appear resistant to the effects of grazing, either benefiting from the structural changes at ground level or avoiding them, as may be the case with arboreal species. Here we examine arboreal and terrestrial habitat

responses and reptile community responses to grazing, to determine whether arboreal reptile species are more resistant than terrestrial reptile species.

2. We conducted arboreal and terrestrial reptile surveys on four different grazing treatments, at a 19-year experimental grazing trial in northern Australia. To compare the grazing response of arboreal and terrestrial reptile assemblages, we used community, functional group and individual species-level analyses. Species responses were modelled in relation to landscape-scale and microhabitat variables.

3. Arboreal reptile species were resistant to the impact of grazing, whereas terrestrial reptiles were negatively affected by heavy grazing. Terrestrial reptiles were positively associated with complex ground structures, which were greatly reduced in heavily grazed areas. Arboreal lizards responded positively to microhabitat features such as tree hollows.

4. *Synthesis and applications*. Arboreal and terrestrial reptiles have different responses to the impact of livestock grazing. This has implications for rangeland management, particularly if management objectives include goals relating to conserving certain species or functional groups. Arboreal reptiles showed resistance in a landscape that is grazed, but where trees have not been cleared. We highlight the importance of retaining trees in rangelands for both terrestrial and arboreal microhabitats.

Keywords: cattle grazing, habitat fragmentation, herpetofauna, off-reserve conservation, rangelands, reptiles, response mechanisms, agriculture, arboreal

Introduction

Grazing by domestic livestock occurs across 25% of the Earth's land surface (Asner *et al.* 2004) and is implicated as a contributing factor in the decline of vertebrate species' richness and abundance (Donald, Green & Heath 2001). The extent of grazing impact will depend on how much that species relies on the niches that are affected by grazing (Milchunas, Sala & Lauenroth 1988). Grazing alters ground-level habitat structures such as vegetation, woody debris and leaf litter (Eldridge, Val & James 2011; Brown, Dorrough & Ramsey 2011). It is, however, unclear exactly how grazing effects arboreal habitat. Alterations in habitat structure affect the vertebrate fauna that live in grazed environments, potentially impacting on their ability to access food, avoid predation, and thermoregulate (Neilly, Vanderwal & Schwarzkopf 2016). Grazing impacts can have a positive effect on species, causing them to increase in abundance ('increasers'), have a negative effect ('decreasers'), or have no effect.

Within a fauna community, the presence of increaser species, or a lack of decreaser species, suggests a degree of resistance to grazing. Here, 'resistance' means the ability to tolerate (i.e. not be negatively impacted by) livestock grazing (Carpenter et al. 2001). Resistance may be represented by an increase in abundance, or no detectable response to grazing. In arid Australia and North America, some reptiles show no response to grazing, due to their preference for the open habitats and higher ground temperatures promoted by heavy grazing (Read 2002; Read & Cunningham 2010; Germano, Rathbun & Saslaw 2012).

Likewise, bird communities can remain unaffected by grazing or even show an increase in diversity, provided trees are not cleared (Martin & McIntyre 2007; Lusk & Koper 2013). At a functional group or species level, heavy grazing may facilitate predation (Curry & Hacker 1990; Kutt et al. 2013; Piana & Marsden 2014) or affect predator avoidance strategies (Pettigrew & Bull 2014; Bylo, Koper & Molloy 2014). Overall, those species resistant to grazing either benefit directly or indirectly from the structural changes at ground level, or avoid these areas by using other habitat strata, for example arboreal niches.

The degree to which 'arboreality' influences a species' response to grazing impacts, has been explored for birds, where bird foraging height has been used to predict species response to grazing (Martin & Possingham 2005; Kutt & Martin 2010), but has yet to be explicitly addressed in reptiles. Arboreal reptiles are abundant in disturbed areas, including areas grazed by domestic livestock (Woinarski & Ash 2002; Knox, Cree & Seddon 2012) and generally use upper-strata microhabitats such as tree hollows, cracks and fissures in dead branches, and loose bark (Gibbons & Lindenmayer 2002). Therefore, they may be unaffected by ground-level disturbances because they spend little time in the altered habitat layer. They may also benefit where other species have declined due to reduced competition for food and other resources.

The effect of grazing on arboreal habitat has received less attention compared to the obvious, ground-based impacts. However, livestock may indirectly affect trees through soil compaction (Fleischner 1994), consuming or trampling saplings (Pitt et al. 1998), breaking low branches or consuming palatable shrubs (Jones 1981). Furthermore, soil compaction leads to excess run-off, erosion, and ultimately a decrease in water infiltration to root systems (Castellano & Valone 2007). Bare ground, created by a lack of herbaceous foliage, grasses, or even leaf litter, can lead to increased soil temperatures, resulting in high evaporative water loss (Yates, Norton & Hobbs 2000). A decrease in water and nutrient absorption begins to change the vegetation community and structure, including trees, leading to desertification (Fleischner 1994; Blesky & Blumenthal 1997). Arboreal species may also respond to grazing-related land management techniques, such as tree clearing. Tree clearing is used in conjunction with livestock grazing to promote grass growth, directly impacting arboreal fauna by removing habitat (Gibbons & Lindenmayer 2000; Martin & McIntyre 2007).

Here we investigate the response of arboreal and terrestrial reptile communities to four different cattle grazing strategies at a long-running, experimental grazing trial in a northern Australian, tropical savanna woodland. The reptile community at this location is diverse and abundant and, importantly, operates at scales appropriate to the size of this grazing trial, as opposed to more vagile avian and mammalian fauna. We measured the effect of different grazing treatments on ground and arboreal habitat, hypothesising that ground-level habitat would be more impacted than arboreal habitat. We aimed to identify how arboreal and terrestrial reptiles responded to the grazing treatments as a community, as functional groups and individual species. We predicted that those species that relied on ground-level heterogeneity (e.g., ground-dwelling litter skinks) would likely respond negatively to higher levels of grazing. Conversely, we predicted that arboreal reptile species may be more likely to exhibit resistance to the effects of grazing.

Materials and methods

Wambiana grazing trial

This study was conducted at the Wambiana Grazing Trial (WGT), located on a commercial cattle station near Charters Towers, Queensland, Australia. The trial is 1040ha and surrounded by extensive cattle grazing. Average annual rainfall at the study site is 643mm, with a summer wet season and winter dry season. The WGT was established in 1997 by the Queensland Department of Agriculture and Fisheries to determine the effect of several grazing strategies on cattle production, profitability, and land condition (O'Reagain *et al.* 2009; O'Reagain, Bushell & Holmes 2011). The WGT consists of two dominant vegetation types: Reid River Box (*Eucalyptus brownii)* and Silver-leaf Ironbark (*Eucalyptus melanophloia*; see Kutt et al. 2012 for vegetation community descriptions). Each vegetation community has an understorey of grass species and patchily distributed Currant Bush (*Carissa ovata*). Eight paddocks were randomly assigned one of four grazing treatments, therefore each treatment paddock was replicated twice (Table 1).

Reptile surveys

Twenty-four 1-ha sites were established, with six sites located in each of the four grazing treatments. Additionally, sites were located in different vegetation types; 16 in Reid River Box and eight in Silver-leaf Ironbark. The different number of sites in the vegetation communities reflects their relative area within each paddock. The sites were located at least 100m from vegetation boundaries and 200m from cattle watering points. Within a treatment and vegetation type, adjacent sites were at least 400m apart. Species detectability was assumed to be equal as standardised survey methods were used at each site and our primary aim was to compare among treatments.

Terrestrial reptile survey

Four surveys were conducted to assess the terrestrial reptile community. These occurred in 2014 and 2015, in April (end of the wet season) and October (end of the dry season). At each site, a trap array was set-up and comprised: 4 x 30cm diameter pitfall buckets at 10m intervals in a 'T' configuration, intersected by drift fence (one 20m length and one 10m length); and 6 x funnel traps (18cm x 18cm x 79cm), two placed either side of the drift fence at each of the 3 ends of the fence. Pitfall and funnel traps were opened for 10 nights and checked twice daily. Captured animals were removed from traps, identified, weighed, measured and then released at the site of capture.

Arboreal reptile survey

Timed nocturnal spotlighting was conducted at each site, twice per trapping session, where observers searched the ground, bushes and trees for arboreal reptiles. We conducted 16 spotlight surveys (5.3 man-hours) per site between 2014 and 2015. In addition, 24 arboreal cover boards (ACBs; Nordberg & Schwarzkopf 2015) were used to monitor populations of both diurnal and nocturnal arboreal lizards in April and October of 2015 only (total of 2304 trap nights). ACBs were set up a day prior to the surveys, allowing animals time to utilize the shelters and then checked each morning (0700 - 1100 h). Due to variation in trapping methods and survey dates, capture data of *Cryptoblepharus australis,* was excluded from community analysis, but was used for individual species analyses.

Micro-habitat surveys

Structural complexity of microhabitat features was measured during each of the four reptile surveys. At each site*,* 3 x 100 m parallel transects, 50m apart, were established. Terrestrial features such as ground cover (e.g., bare ground, leaf litter, grass cover, etc.) were categorized along each transect (Table 2). All trees within one metre on either side of the transects were identified and their height and diameter at breast height (DBH) was measured. Arboreal habitat characteristics were measured in overstory trees throughout the site, including canopy cover, number of dead trees and hollows (Table 2).

Data Analysis

We used a range of complementary univariate and multivariate analyses in R (R Core Team, 2016). Where relevant, optimal models were determined by comparing models based on the Akaike Information Criterion (AICc) using the *dredge* function in *MuMIn* (Bartoń 2015), pairwise comparisons were made of the terms in the optimal model using the Tukey test in *lsmeans* (Lenth 2016) and the final models were validated by examining the deviance residuals.

Habitat characteristics

Structural habitat features were analyzed using two-way analysis of variance to investigate the effects of vegetation type and grazing treatment on the mean cover of structural variables in the lower strata (ground level) as well as mean values for arboreal habitat characteristics. Pairwise comparisons were made using Tukey's tests.

Reptile abundance and richness

Abundance and species richness were collated for a trapping session (n=96) for arboreal and terrestrial species. Generalised linear mixed models (GLMM) with a negative binomial distribution (accounting for overdispersion) were used to examine abundance and species richness in relation to grazing treatments and vegetation type (fixed effects), with year and season as random effects (*lme4*; Bates *et al*. 2015). Variables were explored for collinearity before including them in the model.

Reptile community composition

Arboreal and terrestrial community compositional differences were explored using a multivariate extension of a generalised linear model (GLM), using the function *manyglm* in *mvabund* (Wang et al. 2012). This analysis is an alternative to distance-based multivariate analyses. Multiple GLMs are fitted to many variables simultaneously and an *anova.manyglm* function can be used for hypothesis testing. Univariate test statistics and p-values were calculated for each species in the model to indicate their relative contribution to the overall variance among the communities. We constructed a site-by-species table populated by the abundance of species that were present in at least five sites. This function does not allow for mixed effects models and so each year was analysed separately. Multivariate GLMs with a negative binomial distribution were applied, with grazing treatment, vegetation type, season and year (and their interactions) as the explanatory variables. Arboreal and terrestrial reptile communities were modelled separately. To visualise the overall community response to grazing we plotted the standardised model co-efficients from a GLM with LASOO penalties to create a ‘heat-map’ (Brown et al. 2014). Reptile species taxonomy followed Wilson (2015).

Individual species and functional group responses

GLMs, with a negative binomial distribution, were used to analyse the responses of the most abundant arboreal and terrestrial species, and functional groups, to the relevant arboreal and terrestrial microhabitat variables (Table 2). We analysed two terrestrial functional groups: diurnal litter skinks and terrestrial geckos, and one arboreal functional group: arboreal geckos (see Appendix S4 in Supporting Information). Their responses to grazing treatment and vegetation type (landscape-scale variables) were analysed with GLMMs using year and season as random effects (*lme4*; Bates et al. 2015). A poisson or negative binomial distribution was applied where appropriate.

Results

Micro-habitat Characteristics

Grazing treatment had a major effect on the structural complexity available to terrestrial reptiles. Six of eight terrestrial habitat features were significantly affected by grazing treatment (Fig. 1). Grass cover, grass height, leaf litter, and coarse woody debris were all greatly reduced in areas with high stocking rates. In H, the consumption of grasses and leaf litter by cattle lead to large areas with bare ground and low structural complexity. Conversely, only two of 10 arboreal habitat characteristics (% Canopy connectivity and #

Trees > 30 cm DBH) were significantly different among the grazing treatments (Fig. 2, Appendix S1, Table 1).

Reptile abundance and species richness

Over 3840 pitfall and 5760 funnel trap nights, 684 terrestrial reptiles of 18 species were observed. Over 57.6 hours of spotlighting and 288 ACB trap nights, 624 arboreal reptiles of 8 species were observed. The optimal GLMM for terrestrial reptile abundance included grazing treatment and vegetation type (Table 3, Fig. 3a). M, R and V all had significantly higher terrestrial reptile abundance than in H, but were not different from each other. Overall, the H sites in Ironbark had significantly lower terrestrial reptile abundance than all the other grazing treatment and vegetation type combinations. The Box vegetation type had higher terrestrial reptile abundance than the Ironbark.

Arboreal reptile abundance was also significantly affected by grazing treatment and vegetation type, however, in this case, H and V supported higher abundances (Table 3, Fig. 3b). Furthermore, reptile abundance was higher in Ironbark than in Box. The interaction of these two variables, although included in the second best model, was not statistically significant. The optimal model for terrestrial reptile richness included vegetation, although it was not statistically distinguishable from the null model (ΔAICc=0.12). The best arboreal reptile richness model was the null model. Model coefficients for the optimal abundance models are included in Appendix S2 (Table 1, 2).

Reptile Community

Eight species were included in the terrestrial community analysis: three small, litter-dwelling, diurnal skinks (*Carlia munda, Menetia greyii* and *Morethia taeniopleura*), a larger, surface active, diurnal striped skink (*Ctenotus robustus*), a diurnal dragon (*Diporiphora nobbi*), and a group of nocturnal, ground-dwelling geckos, including the fat-tailed gecko (*Diplodactylus conspiculatus*), Bynoe's gecko (*Heternotia binoei*), and the box-patterned gecko (*Lucasium steindachneri*). Overall, the response of the terrestrial reptile community to grazing was more negative than the response of the arboreal reptile community (Figure 4). In 2014 and 2015, terrestrial reptile community composition was explained by season and an interaction between grazing and vegetation (Table 4). The seasonal responses were driven by the same individual species (*C. munda, M. greyii, C. robustus, M. taeniopleura*), however the individual species driving the interaction of grazing and vegetation changed from 2014 to 2015. Only *H. binoei* consistently influenced this interaction term. The H Ironbark community was most different from the other communities, with a lower abundance of all species, except at the end of the dry season in 2015. During this trapping session, abundance of all species was much lower than at any other time in any other year, so detecting differences among treatments was difficult (Appendix S3, Figure 1).

Four arboreal species were included in the community analysis: house geckos (*Gehyra dubia*), pale-headed snakes (*Hoplocephalus bitorquatus*), northern velvet geckos (*Oedura castlenaui*), and eastern spiny-tailed geckos (*Strophurus williamsi*). *Gehyra dubia* was the most abundant species in this community subset. In the arboreal reptile community there was a significant effect of season in 2014 and of vegetation type in 2015, strongly driven by

G. dubia (Table 4). Fitted value plots for *H. bitorquatus, O. castlenaui and S. williamsi* could not be drawn due to their relatively low abundance. Due to the overwhelming influence of *G. dubia*, individual species analysis may be more appropriate than community analysis. *Cryptoblepharus australis* was not included in the arboreal community analysis due to a difference in trapping method and effort (ACBs), as well as the limitation that surveys were only conducted in 2015, however this species is examined individually.

Individual species and functional group responses

The five most abundant terrestrial species and the terrestrial functional groups (see Appendix S4) were analysed separately (Table 5). There was a significant effect of grazing on four of the five species, and in the litter skink and terrestrial gecko functional groups (Table 5, Fig. 5a-g). *Carlia munda* (Fig. 5a) and *M. taeniopleura* (Fig. 5c) both had highest abundance in M and were lowest in H. The interaction between grazing and vegetation is evident for *H. binoei* (Fig 5b), where abundance was higher in Box in H, M and R but not in V. Overall, litter skinks were less abundant in H, whereas terrestrial geckos typically showed different responses to grazing in different vegetation types. Individual species responded to various microhabitat features (Table 5). Litter skinks were negatively associated with bare ground and positively associated with grass cover, whereas terrestrial gecko abundance was influenced by fine-woody debris and *C. ovata* cover.

Only two arboreal species could be analysed separately (Table 5, Fig. 6a-c). *Gehyra dubia* responded to grazing and vegetation (Fig. 6a), and were least abundant in M and R and most abundant in H and V. There was no significant effect of grazing on *C. australis*. Both species were more abundant in Ironbark. *Gehyra dubia* was negatively associated with small trees (trees 5 – 10 cm DBH) whereas *C. australis* was negatively associated with trees 10 – 20 cm DBH and positively associated with the Bark Index (they were more common on trees with more complex bark). Arboreal geckos responded negatively to small trees (5 – 10 cm DBH) and positively to the number of trees with hollows and cavities.

Discussion

While habitat features at ground level were significantly modified by grazing treatment, the arboreal habitat was not affected. In H, ground-level microhabitat was significantly altered, and vegetation structural complexity was reduced. Diverse structural habitat is of great importance to ground-dwelling reptile communities as they create a mosaic of thermal and other conditions (Dorrough et al. 2012). The simplified ground habitat found in H had major implications for the ground-dwelling herpetofauna in this study.

Conversely, the only differences we found in arboreal habitat features among the grazing treatments were in terms of canopy connectivity and number of Trees > 30 cm DBH. R had significantly lower canopy connectivity than H, and V had more large, overstory trees. In both cases, if grazing were the driving mechanism, then we would have expected to see the largest differences among the highest contrast treatments (i.e., H vs. M). Further, younger size classes of trees were not different among the grazing treatments, suggesting no difference in recruitment. It is possible that changes to arboreal habitat will be identified in the future, as a result of long-term soil compaction, decreased water infiltration, and increased soil temperature (Yates, Norton & Hobbs 2000; Castellano & Valone 2007). Trees may take a long time to respond to grazing disturbance, but after 19 years of the WGT, the impact on overstory trees and arboreal habitat features is minimal.

Arboreal reptile response to grazing

Arboreal reptiles were not only resistant to the impacts of heavy livestock grazing, but had an apparent preference for H and V. However, while there was a diverse assemblage of arboreal reptiles at our sites, overall abundance patterns were driven by *G. dubia*. Most arboreal reptile species were much less abundant than *G. dubia*, so our community analysis was limited to four species. While community composition was not strongly affected by grazing treatment, the abundance of individual species (namely *G. dubia*) was affected (positively) by grazing.

The most abundant arboreal reptiles, *G. dubia* and *C. australis*, flourished in all of the grazing treatments, including the heavily stocked paddocks, where many ground-dwelling reptiles suffered. *Cryptoblepharus australis* did not respond to grazing, and was, therefore resistant to the effects of heavy grazing, whereas *G. dubia* showed an increaser pattern, increasing in abundance with increasing stocking rate. Both species were apparently buffered from the direct negative impacts of grazing, such as microhabitat loss. This supports a similar study, where several arboreal lizard species were more abundant in communal rangelands (high disturbance area) compared to adjacent protected rangeland (low disturbance) (Smart, Whiting & Twine 2003).

Here, the arboreal community was not negatively impacted by heavy grazing, but this may not be the case elsewhere, depending on the extent of tree clearing, fire, and other indirect impacts on arboreal habitats. Tree clearing, often associated with grazing, is a major threat to arboreal fauna (Gibbons & Lindenmayer 2002; Parsons et al. 2017). Indirectly, long-term soil compaction, may suppress new tree growth (Fischer, Lindenmayer & Cowling 2004) and grazing can interact with browsing by large native herbivores, resulting in changes to arboreal structure (Ogada et al. 2008; Pringle 2008). Fischer et al (2009) suggest that current grazing management styles are leading to major tree declines. As keystone structures, loss of trees will have major impacts on the distribution and biodiversity across vast regions of the world (Manning, Cunningham & Lindenmayer 2006). Both dead and living trees, and the accumulation of course woody debris, are prime habitat for diverse animal communities (Whiles & Grubaugh 1996). Even damaged trees increase structural complexity, and can increase occupancy of arboreal lizards (Pringle 2008). Unlike other areas used for livestock grazing, the WGT has not been cleared within the last 100 years and therefore has many old, overstory trees. Additionally, fire is not regularly used to suppress woody growth at this location. While open-canopy woodlands such as the WGT have naturally sparse tree cover, the trees that are present support a wide variety of wildlife, especially old trees with hollows and flaking bark (Gibbons & Lindenmayer 2002; Bryant, Dundas & Fleming 2012).

We could only model *G. dubia* and *C. australis* individually, but made observations of other arboreal reptiles on the WGT. For example, *O. castelnaui* and *H. bitorquatus* were found in every grazing treatment and were not linked to vegetation type. Both *O. castelnaui* and *H. bitorquatus* use loose bark and hollows as diurnal refugia and forage on branches and the trunks of trees at night (Gibbons & Lindenmayer 2002; Fitzgerald et al. 2010). Both species appear resistant to the effects of grazing. *Strophurus williamsi* were generally found in the lower strata (on small trees and shrubs) and were not present in either H or V. By using the lower strata, *S. williamsi* may be less tolerant to the impacts of grazing than other arboreal reptiles. In our analyses, we have applied a binary notion of arboreality (either arboreal or terrestrial), but in reality, arboreal species use vertical habitat strata to different extents. In a more diverse arboreal community, it may be beneficial to classify species along an 'arboreality gradient' and use this as a predictor of resistance to disturbance. This has been used effectively to predict bird response to livestock grazing (Martin & Possingham 2005) and the resilience of frogs and lizards to extreme climatic events (Scheffers et al. 2014).

Terrestrial reptile response to grazing

Unlike arboreal reptiles, terrestrial reptiles generally had a negative association with increasing grazing pressure. This relationship was clearly seen in overall abundance, most individual species responses, and at a functional group level. The community compositional differences were complex and subtle, making interpretation of these results difficult on their own. The community analysis is greatly complemented by the assessment of individual species using GLMMs, where we had the benefit of treating year and season as random effects.

As a group, litter skinks performed as typical decreaser species, supporting the results from other Australian grazing studies with similar terrestrial reptile assemblages (Woinarski & Ash 2002; James 2003; Kutt & Woinarski 2007). The litter skinks that were analysed separately mostly showed the same negative response to increased grazing. *Carlia munda* and *M. taeniopleura* were both least abundant in the heavily stocked sites. *Ctenotus robustus* also responded negatively to heavy grazing, in accordance with the response of *Ctenotus sp.* in other grazed locations, and likely due to a reduction of thermal refuges at ground level in heavily grazed areas (Hacking, Abom & Schwarzkopf 2014; Abom & Schwarzkopf 2016).

The response of terrestrial geckos is clearly influenced by the most abundant terrestrial gecko *H. binoei.* While seemingly unaffected by grazing in the Box vegetation type, *H. binoei* was significantly less abundant in H Ironbark. In other vegetation types, *H. binoei* is more abundant in areas of heavy grazing (Woinarski & Ash 2002), further suggesting this species' response to grazing is greatly influenced by the surrounding vegetation community. Ground-dwelling reptiles often respond to habitat characteristics such as woody debris, leaf litter and fallen logs, which are actually a function of arboreal habitat structure (Fischer, Lindenmayer & Cowling 2004). The importance of tree-provided structure to ground features further supports the importance of retaining trees in grazed environments, for both the arboreal and terrestrial fauna.

The terrestrial reptile assemblage at this location was dominated by abundant diurnal skinks susceptible to grazing. At other locations, particularly more arid areas, the terrestrial reptile assemblage often has a higher proportion of increaser species, that prefer more open, less complex ground environments (Read 2002; Read & Cunningham 2010; Germano, Rathbun & Saslaw 2012). One agamid species found during the study, *D. nobbi*, would likely prefer open habitats and higher ground temperatures, however, due to low capture numbers we could not detect differences in its abundance among grazing treatments.

Our interpretation of reptile responses to grazing is limited by our knowledge of species' habitat requirements, for thermoregulation, predator avoidance and food. Here, we suggest the negative response of many species to grazing is driven by a loss of microhabitat complexity, but we have not determined the mechanism allowing arboreal groups or species to be resistant. It is likely there are complex indirect mechanisms driving arboreal reptile abundance and it would be beneficial to test these. Reptiles can be affected by changed predator-prey dynamics in grazed environments (e.g. Curry & Hacker 1990; Knox, Cree & Seddon 2012; Pafilis et al. 2013; Pettigrew & Bull 2014). Most grazing response mechanisms are suggested or assumed, and very few have been experimentally tested or examined in detail (but see Rosi et al. 2009; Villar et al. 2013). A better understanding of the mechanisms behind individual species' responses may make it possible to predict species responses to grazing.

Our results illustrate the importance of examining arboreal and terrestrial community composition separately, and individual species in more detail, rather than focusing on just overall biodiversity measures such as abundance and richness. Species and functional groups often respond to disturbances in different (even opposite) ways (Neilly, Vanderwal &

Schwarzkopf 2016), thus we highlight the importance of analysing community response data appropriately.

Management implications

Measures of plant and animal resistance and resilience have been successfully used to build risk-based frameworks to guide rangeland management (Chambers et al. 2017). An understanding of the attributes that influence resistance, such as arboreality, can help when devising grazing management strategies. In this case, the recommended grazing strategy for conserving arboreal geckos would be different compared to a grazing strategy aimed at conserving diurnal litter skinks. The varied response of vertebrates to different grazing strategies calls for a nuanced approach to management recommendations (Neilly, Vanderwal & Schwarzkopf 2016).

Across the globe, a diversity of biomes support livestock grazing systems and these systems vary in their extent of vertical strata (Asner et al. 2004). Therefore, our findings will be more relevant to rangelands from similar biomes. Diverse arboreal reptile communities may be unique to Australian rangelands, however arboreal reptiles, mammals and birds, are found in rangelands globally (Neilly, Vanderwal & Schwarzkopf 2016). Furthermore, trees not only harbor extensive microhabitats for arboreal species, but indirectly provide habitat for terrestrial species (Fischer, Lindenmayer & Cowling 2004). It is widely accepted that the retention of trees increases biodiversity and landscape scale species richness (Benton, Vickery & Wilson 2003; Manning, Fischer & Lindenmayer 2006). Therefore, one universal management practice to increase or retain arboreal and terrestrial fauna may be to retain standing trees and woody debris. Unlike more intense agricultural land-uses (e.g. cropping), rangelands where trees are retained and stocking rates are moderate, are potentially areas where animal production and biodiversity conservation can co-exist.

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Authors’ Contributions

HN, EN, JV and LS conceived the ideas and designed methodology; HN and EN collected and analysed data, HN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Accessibility

Data available from the Dryad Digital Repository. DOI: http://dx.doi.org/10.5061/dryad.fn02v (Neilly et al., 2017)

Data files: Wambiana Reptile Community

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Table 1: The grazing treatments of the Wambiana Grazing Trial.

Table 2: Measured micro-habitat characteristics with a description of methodology.

Table 3: The relationship between reptile abundance and species richness and grazing treatment and vegetation type (fixed effects) and season and year (random effects) as described by a generalized linear mixed model (GLMM) with negative binomial distribution. Post hoc Tukey tests were used to examine the effect of each factor level and significant differences (p<0.05) are reported.

Table 4: The ManyGLM analysis showing the relationship between reptile assemblages (arboreal and terrestrial) and grazing treatment, vegetation type and season (and their interactions) for 2014 and 2015. The p values of the variables in the optimal model are given, first for the multivariate community analysis, and then broken down by individual species contribution.

Table 5: The response of reptile species and functional groups to habitat variables using generalised linear mixed models (GLMM) and generalised linear models (GLM). '+' indicates a positive association and '-', a negative association. GLMM distributions are indicated (P = poisson, NB = negative binomial). All GLM models use a negative binomial distribution. Post hoc Tukey tests were used to examine the effect of each factor level and significant differences (p<0.05) are reported.

Figure 1: Mean ± SE measures of terrestrial habitat characteristics. Only terms with a significant difference are presented, indicated by different letters (2-way ANOVA; Tukey posthoc test; α = 0.05).

Figure 2: Mean ± SE measures of arboreal habitat characteristics. Only terms with a significant difference are presented, indicated by different letters (2-way ANOVA; Tukey posthoc test; α = 0.05).

Figure 3: The mean fitted values with 95% confidence intervals of the negative binomial GLMMs for: a) Terrestrial Reptile Abundance ~ Grazing + Vegetation, and b) Arboreal Reptile Abundance ~ Grazing + Vegetation.

Figure 4: The response of arboreal and terrestrial reptile communities to grazing, as visualised using the standardised model co-efficients from a generalised linear model-LASOO model. Terms which do not explain any variation in species response are set to zero. The stronger the association, the brighter the square, positive associations are in green and negative associations are in red.

Figure 5: Fitted values with 95% confidence intervals for the optimal terrestrial reptile species and functional group models.

Figure 6: Fitted values with 95% confidence intervals for the optimal arboreal reptile species and functional group models

Table 1

Grazing treatment	**Description**	**Reasoning**
Moderate (M)	Stocking rate at the Long Term Carrying Capacity (LTCC); 8-10 ha per animal equivalent (AE)	Minimize the risk of over-grazing, maintains land condition
Rotational wet-season spelling (R)	Stocking at 50% above the LTCC and ⅓ of the paddock spelled (no grazing) on a rotation basis during the wet season; 7-10 ha per AE	Spelling can buffer against rainfall variability
Variable (V)	Stocking rate adjusted annually at the end of the wet season in accordance with remaining feed availability; 3-12 ha per AE	Stocking rate to match feed availability, which minimize the risk of over-grazing during dry years, but allows heavier stocking rates during wet years
Heavy (H)	Stocking at twice the LTCC; 4-6 ha per AE	Potentially high profitability, especially during wet years

Table 2

Habitat characteristics	**Description**
Terrestrial	
Ground cover	A tape measure was laid on the ground along the 100m transect. The amount of bare ground (BG), rock, leaf litter (LL) and leaf litter depth (mm), fine woody debris (<10cm diameter) (FWD), coarse woody debris (>10cm diameter) (CWD) was recorded and converted into a percentage.
Vegetative cover	Along the 100m transect, the amount of grass (and grass height), shrub and other vegetative cover was recorded and converted into a percentage.
Other features	Other ground features were noted along the 100m transect including termite mounds, and burrows.
Arboreal	
Trees	Any tree that fell 1-m either side of the 100m transect was identified and measured for diameter at breast height (DBH) (cm) and height category (m)
Canopy Cover (%)	Estimated canopy cover *via* spherical densitometer.
Distance to nearest tree (m)	Distance (m) between adjacent trees >2 m tall.
Bark Index (1-3)	An index of bark roughness/flakiness ranging from 1-3; 1 representing little or no flaking bark, and often little no known refuge options for sheltering lizards; 3 represents very flaky and loose bark with ample refuge microhabitats available for sheltering lizards.
Canopy connectivity (%)	The percentage of overstory trees sampled that had overlapping canopy or branches.
Tree hollows (%)	The percentage of overstory trees sampled that had hollows or cavities visible from the ground.

Table 3

Response Variable	Model	df	Log Likelihood	AIC	ΔAICc	AICc weight	Post hoc test
Terrestrial Reptile Abundance	Grazing + Vegetation	8	-262.837	543.3	0	0.521	Grazing Moderate>Heavy Rotational>Heavy Variable>Heavy Vegetation Box>Ironbark
	Grazing*Vegetation	11	-259.424	544.0	0.66	0.374	Grazing * Vegetation Moderate Box> Heavy Box Moderate Box> Heavy Ironbark Rotational Box> Heavy Ironbark Variable Box> Heavy Ironbark Moderate Ironbark>Heavy Ironbark Rotational Ironbark>Heavy Ironbark
	Grazing	7	-265.634	546.5	3.21	0.105	As above
Terrestrial Reptile Richness	~Vegetation	5	-168.561	347.8	0	0.252	Not significant
	~1 (null model)	4	-169.737	347.9	0.12	0.237	
	Grazing	7	-166.359	348.0	0.20	0.228	
Arboreal Reptile Abundance	Grazing + Vegetation	8	-214.477	446.6	0	0.856	Grazing Heavy>Moderate Variable>Moderate Vegetation Ironbark>Box
	Vegetation	5	-220.585	451.8	5.23	0.063	As above
	Grazing * Vegetation	11	-213.398	451.9	5.33	0.060	Not significant
Arboreal Reptile Richness	~1 (null model)	4	-100.222	208.9	0	0.669	Not significant
	Vegetation	5	-100.042	210.8	1.87	0.263	
	Grazing	7	-99.406	214.1	5.2	0.050	

Table 4

Terrestrial Reptile Community

Optimal Model	**Community (P value)**	**Individual Species Contributions (P value)**							
		Carlia munda	*Diplodactylus conspiculatus*	*Menetia greyii*	*Ctenotus robustus*	*Diporiphora nobbi*	*Heteronotia binoei*	*Lucasium steindachnerri*	*Morethia taeniopleura*
2014									
Grazing*Vegetation	<0.01	0.38	0.52	0.05	0.01	0.05	0.07	0.79	0.54
Season	<0.01	0.06	0.31	0.06	<0.01	0.06	0.14	0.14	0.06
2015									
Grazing*Vegetation	0.02	0.31	0.91	0.65	0.24	0.27	<0.01	0.15	0.60
Season	<0.01	<0.01	0.58	0.01	0.04	0.34	0.19	0.25	<0.01

Arboreal Reptile Community

Optimal model	**Community (P value)**	**Individual Species contribution (P value)**			
		Gehyra dubia	*Hoplocephalus bitorquatus*	*Oedura castlenaui*	*Strophurus williamsi*
2014					
Season	<0.01	0.01	0.113	1.00	1.00
2015					
Vegetation	<0.01	<0.01	1.00	0.68	0.23

Table 5

<table>
<tr><td rowspan="2">Terrestrial Species</td><td colspan="4">Landscape Scale
Full Model: GLMM
Grazing*Vegetation+(1|Year)+(1|Season)</td><td colspan="2">Microhabitat Scale
Full Model: GLM
Grass + Grass height + FWD + CWD + Carissa ovata + LL<5mm+LL>5mm + TM + BG+ CanopyCover</td></tr>
<tr><td>Terms in optimal model</td><td>Dist</td><td>P value</td><td>Post Hoc</td><td>Terms in optimal model</td><td>P value</td></tr>
<tr><td rowspan="2"><i>Carlia munda</i></td><td rowspan="2">Grazing</td><td rowspan="2">NB</td><td rowspan="2">0.03</td><td rowspan="2">M>H
V>H</td><td>Carissa ovata (-)</td><td>0.02</td></tr>
<tr><td>BG (-)</td><td><0.01</td></tr>
<tr><td rowspan="2"><i>Heternotia binoei</i></td><td rowspan="2">Grazing* Vegetation</td><td rowspan="2">P</td><td rowspan="2"><0.01</td><td rowspan="2">MB>HI
MB>MI
RB>HI
VI>HI
VI>MI</td><td>FWD (+)</td><td><0.01</td></tr>
<tr><td>Carissa ovata (+)</td><td><0.01</td></tr>
<tr><td rowspan="3"><i>Morethia taeniopleura</i></td><td>Grazing</td><td rowspan="3">NB</td><td>0.02</td><td>M>H</td><td>Carissa ovata (+)</td><td><0.01</td></tr>
<tr><td rowspan="2">Vegetation</td><td rowspan="2"><0.01</td><td rowspan="2">B>I</td><td>BG (-)</td><td>0.02</td></tr>
<tr><td>Grass (+)</td><td><0.01</td></tr>
<tr><td><i>Ctenotus robustus</i></td><td>Grazing * Vegetation</td><td>P</td><td>0.01</td><td>VB>HB</td><td>Grass (+)</td><td><0.01</td></tr>
<tr><td><i>Menetia greyii</i></td><td>Vegetation</td><td>P</td><td>0.08</td><td>Not significant</td><td>TM (+)</td><td>0.11</td></tr>
<tr><td rowspan="2">Litter skinks</td><td rowspan="2">Grazing</td><td rowspan="2">NB</td><td rowspan="2"><0.01</td><td rowspan="2">M>H
V>H</td><td>BG (-)</td><td><0.01</td></tr>
<tr><td>Grass (+)</td><td><0.01</td></tr>
<tr><td rowspan="2">Terrestrial Geckos</td><td rowspan="2">Grazing*Vegetation</td><td rowspan="2">NB</td><td rowspan="2"><0.01</td><td rowspan="2">MB>HI
RB>HI
VI>HI</td><td>FWD (+)</td><td><0.01</td></tr>
<tr><td>Carissa ovata (+)</td><td><0.01</td></tr>
<tr><td>Arbroeal Species</td><td colspan="4">Landscape Scale
Full Model: GLMM
Grazing*Vegetation+(1|Year)+(1|Season)</td><td colspan="2">Microhabitat Scale
Full Model: GLM
MeanDist.NearTree+Mean Bark Index+Hollows +Canopy Connectivity + Trees dead+Trees <5cm DBH+ Trees 5-10 cm DBH+ Trees 10-20cm DBH+ Trees 20-30cm DBH+Trees >30cm DBH +Canopy Cover</td></tr>
<tr><td rowspan="2"><i>Gehyra dubia</i></td><td>Grazing</td><td rowspan="2">NB</td><td><0.01</td><td>H>M
V>M</td><td rowspan="2">Trees 5-10cm DBH (-)</td><td rowspan="2">0.01</td></tr>
<tr><td>Vegetation</td><td><0.01</td><td>I>B</td></tr>
<tr><td rowspan="2"><i>Cryptoblepharus australis</i></td><td rowspan="2">Vegetation</td><td rowspan="2">NB</td><td rowspan="2"><0.01</td><td rowspan="2">I>B</td><td>Trees 10-20cm DBH (-)</td><td><0.01</td></tr>
<tr><td>Mean bark index (+)</td><td>0.05</td></tr>
<tr><td rowspan="2">Arboreal geckos</td><td>Grazing</td><td rowspan="2">NB</td><td><0.01</td><td>H>M
V>M</td><td>Trees 5-10cm DBH (-)</td><td>0.02</td></tr>
<tr><td>Vegetation</td><td><0.01</td><td>I>B</td><td>Hollows (+)</td><td>0.06</td></tr>
</table>

Figure 1

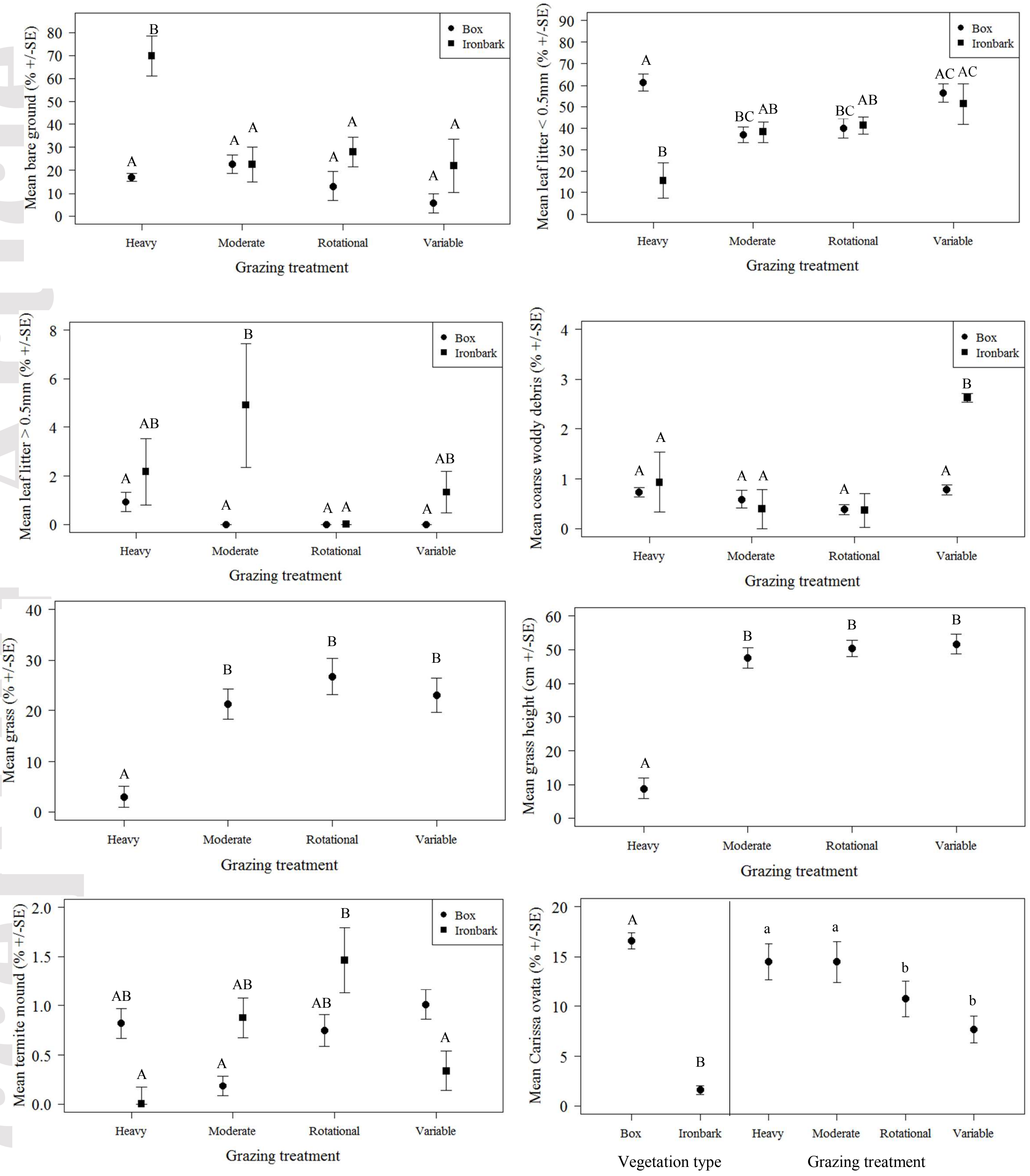

Mean bare ground (% +/-SE)
0
10
20
30
40
50
60
70
80
Box
Ironbark
B
A
A
A
A
A
A
A
Heavy
Moderate
Rotational
Variable
Grazing treatment
Mean leaf litter < 0.5mm (% +/-SE)
0
10
20
30
40
50
60
70
80
90
Box
Ironbark
A
B
BC
AB
BC
AB
AC
AC
Heavy
Moderate
Rotational
Variable
Grazing treatment
Mean leaf litter > 0.5mm (% +/-SE)
0
2
4
6
8
Box
Ironbark
A
AB
A
B
A
A
A
AB
Heavy
Moderate
Rotational
Variable
Grazing treatment
Mean coarse woddy debris (% +/-SE)
0
1
2
3
4
Box
Ironbark
A
A
A
A
A
A
A
B
Heavy
Moderate
Rotational
Variable
Grazing treatment
Mean grass (% +/-SE)
0
10
20
30
40
A
B
B
B
Heavy
Moderate
Rotational
Variable
Grazing treatment
Mean grass height (cm +/-SE)
0
10
20
30
40
50
60
A
B
B
B
Heavy
Moderate
Rotational
Variable
Grazing treatment
Mean termite mound (% +/-SE)
0.0
0.5
1.0
1.5
2.0
Box
Ironbark
AB
A
A
AB
AB
B
A
Heavy
Moderate
Rotational
Variable
Grazing treatment
Mean Carissa ovata (% +/-SE)
0
5
10
15
20
A
B
a
a
b
b
Box
Ironbark
Heavy
Moderate
Rotational
Variable
Vegetation type
Grazing treatment

Figure 2

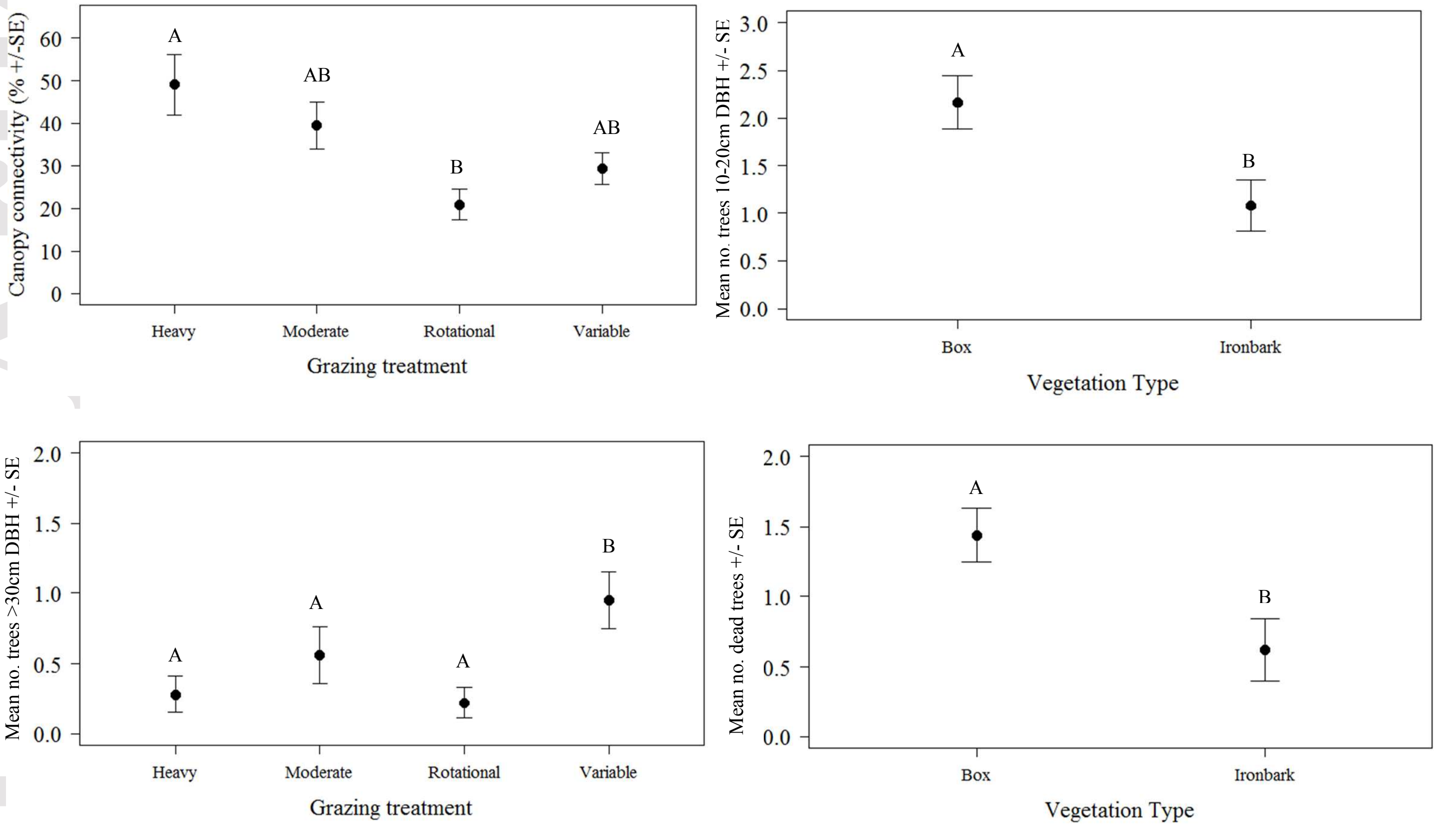
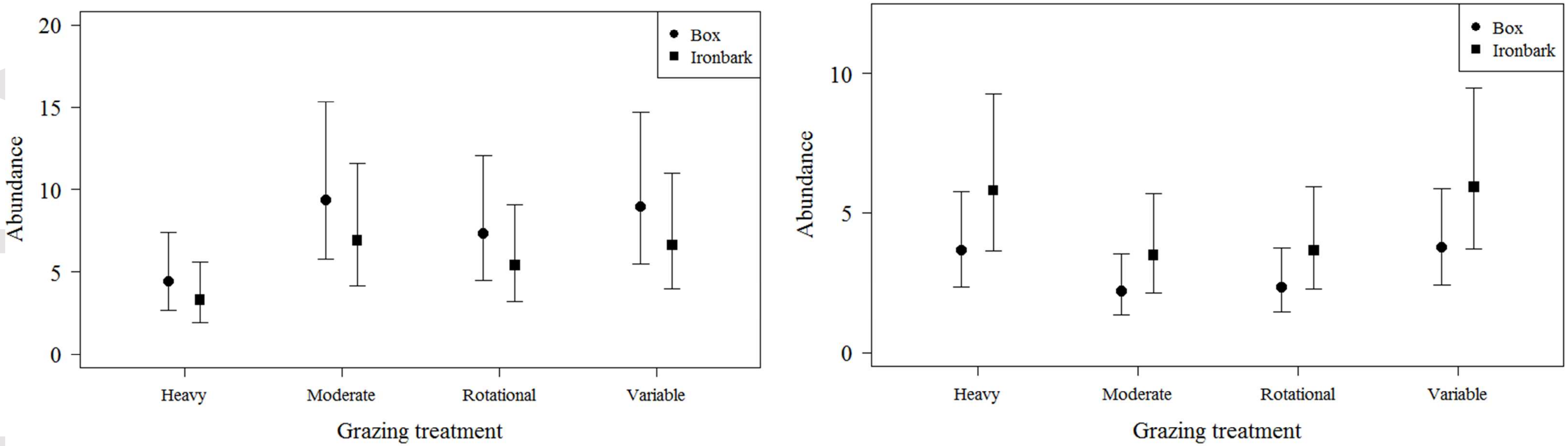

Canopy connectivity (% +/-SE)
60
50
40
30
20
10
0
A
AB
B
AB
Heavy
Moderate
Rotational
Variable
Grazing treatment
Mean no. trees 10-20cm DBH +/- SE
3.0
2.5
2.0
1.5
1.0
0.5
0.0
A
B
Box
Ironbark
Vegetation Type
Mean no. trees >30cm DBH +/- SE
2.0
1.5
1.0
0.5
0.0
A
A
A
B
Heavy
Moderate
Rotational
Variable
Grazing treatment
Mean no. dead trees +/- SE
2.0
1.5
1.0
0.5
0.0
A
B
Box
Ironbark
Vegetation Type

Figure 3



a) Terrestrial Reptile Abundance

b) Arboreal Reptile Abundance

Figure 4

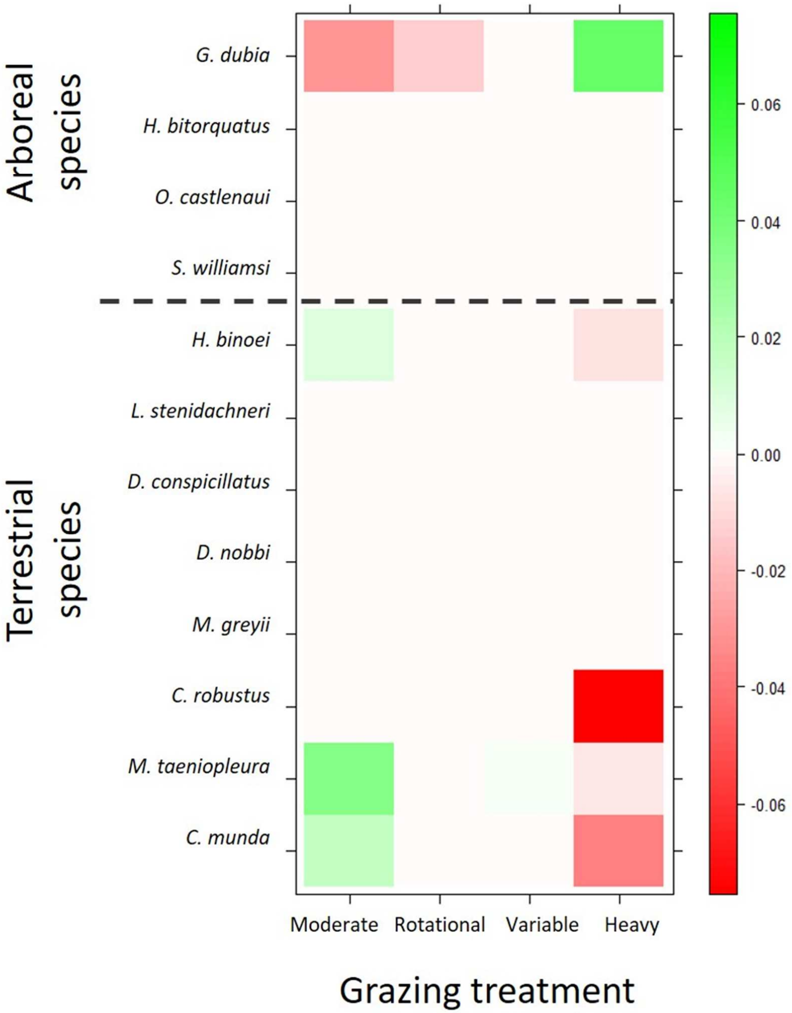
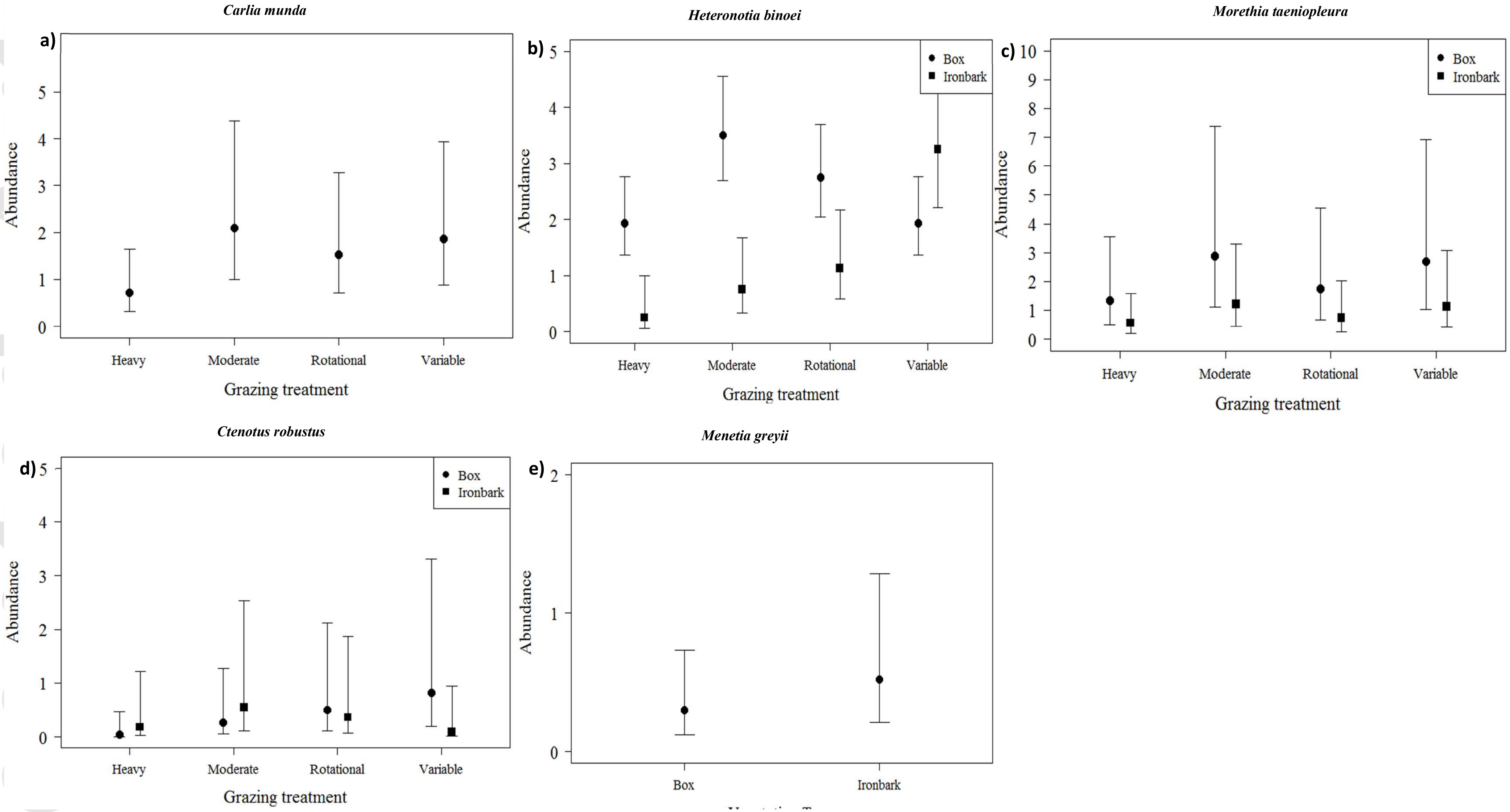
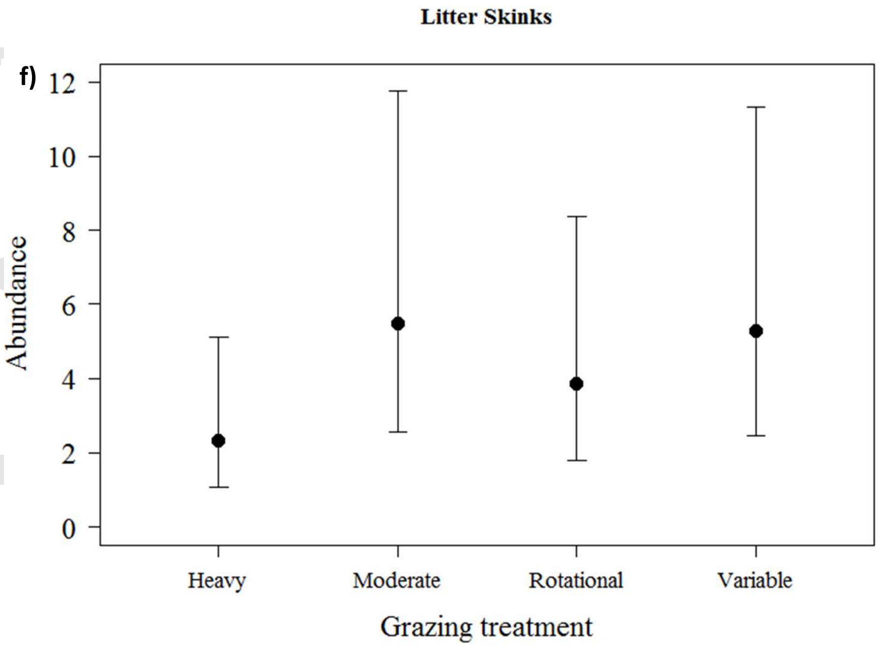

Arboreal species
G. dubia
H. bitorquatus
O. castlenaui
S. williamsi
Terrestrial species
H. binoei
L. stenidachneri
D. conspicillatus
D. nobbi
M. greyii
C. robustus
M. taeniopleura
C. munda
Moderate
Rotational
Variable
Heavy
Grazing treatment
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06

Figure 5


Carlia munda
a)
Abundance
0
1
2
3
4
5
Heavy
Moderate
Rotational
Variable
Grazing treatment
Heteronotia binoei
b)
Box
Ironbark
Abundance
0
1
2
3
4
5
Heavy
Moderate
Rotational
Variable
Grazing treatment
Morethia taeniopleura
c)
Box
Ironbark
Abundance
0
1
2
3
4
5
6
7
8
9
10
Heavy
Moderate
Rotational
Variable
Grazing treatment
Ctenotus robustus
d)
Box
Ironbark
Abundance
0
1
2
3
4
5
Heavy
Moderate
Rotational
Variable
Grazing treatment
Menetia greyii
e)
Abundance
0
1
2
Box
Ironbark


Litter Skinks
f)
Abundance
0
2
4
6
8
10
12
Heavy
Moderate
Rotational
Variable
Grazing treatment

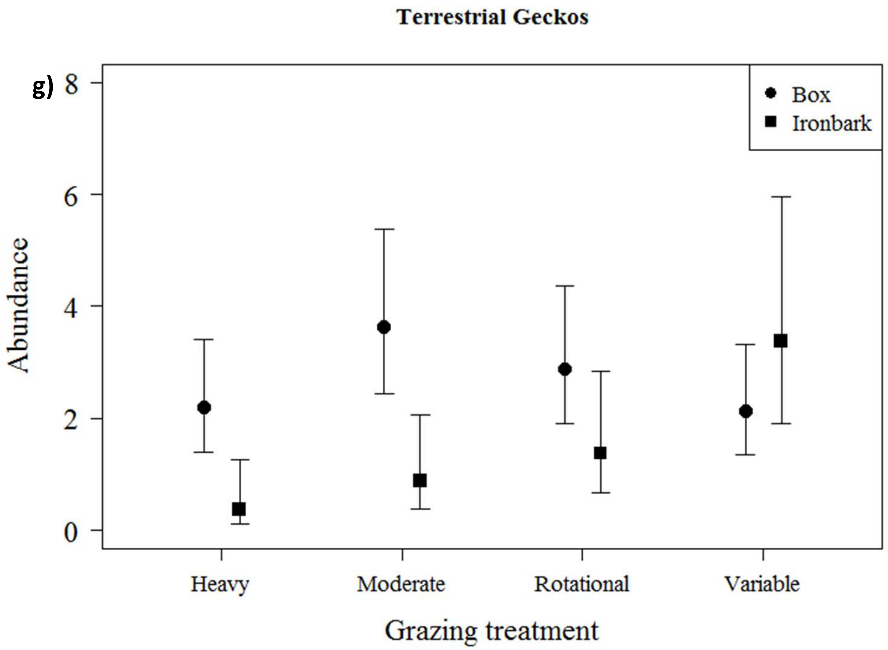
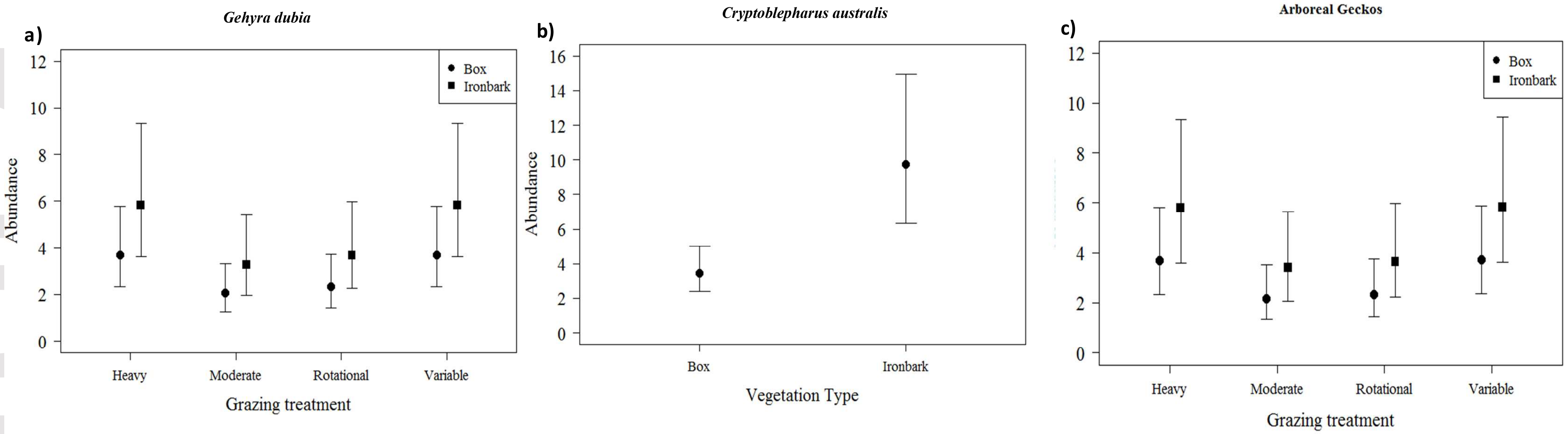

Terrestrial Geckos
g)
Abundance
0
2
4
6
8
● Box
■ Ironbark
Heavy
Moderate
Rotational
Variable
Grazing treatment

Figure 6


a)
Gehyra dubia
Box
Ironbark
Abundance
12
10
8
6
4
2
0
Heavy
Moderate
Rotational
Variable
Grazing treatment
b)
Cryptoblepharus australis
Abundance
16
14
12
10
8
6
4
2
0
Box
Ironbark
Vegetation Type
c)
Arboreal Geckos
Box
Ironbark
12
10
8
6
4
2
0
Heavy
Moderate
Rotational
Variable
Grazing treatment