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The relative importance of habitat quality and landscape context for reptiles in regenerating landscapes

Melissa J. Bruton [a,*], Martine Maron [a], Craig E. Franklin [b], Clive A. McAlpine [a]

[a] The University of Queensland, Landscape Ecology and Conservation Group, School of Geography, Planning and Environmental Management, St Lucia, Brisbane 4072, Australia
[b] The University of Queensland, School of Biological Sciences, St Lucia, Brisbane 4072, Australia

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ABSTRACT

Restoration activities are limited by funding and logistics. To optimise restoration efforts, we need to evaluate the effects of management actions on wildlife populations. In general, site-scale habitat quality has a stronger influence on habitat use by fauna than the landscape context. However, this is yet to be empirically tested for reptiles. In this study, we used model averaging and hierarchical partitioning to compare the relative importance of site-scale habitat quality and landscape context for reptile communities and species in a regenerating woodland landscape in semi-arid Queensland, Australia. Reptiles were surveyed at 55 sites. Habitat quality was assessed using relevant variables based on published habitat-associations for each species or group. Landscape context was assessed using binary, mosaic and continuous descriptions of vegetation cover within 250 m of the survey sites. We found that, in comparison to site-scale habitat quality, the composition of the surrounding landscape had little influence on reptiles, despite testing three alternative approaches for describing landscape context. Nine out of eleven reptile species and groups responded to variation in habitat quality, whereas just one species responded to variation in landscape context. Species richness, diversity, and abundance were unaffected by landscape context, but were influenced by site-scale structural complexity and vegetation type. Our findings suggest that reptiles, in general, benefit from conservation and restoration activities that focus on improving site-scale habitat quality, with increasing the amount and connectivity of surrounding vegetation of lesser value. This study also highlights the importance of better understanding the drivers of reptile distributions and abundances in dryland landscapes.

1. Introduction

Restoration activities are limited by their logistic capacity and funding availability (Sutherland et al., 2004). Therefore, to ensure that efforts are appropriately prioritised, the benefits of restoration and conservation options at the site (<1 ha) and landscape (10–1000s ha) scale need to be critically evaluated. Across taxa, site-scale habitat quality has a consistently greater influence on fauna than landscape context (Abensperg-Traun et al., 1996; Bergman et al., 2008; Bowen et al., 2009; Bowman et al., 2001; Weyrauch and Grubb, 2004). However, such comparisons are not currently available for reptiles. Atauri and de Lucio (2001); Fischer et al. (2004a) and Cunningham et al. (2007) indicate that site-scale habitat quality, in terms of the availability of resources, may also be more important for reptiles than the structure of the surrounding landscape. If so, then conservation and restoration activities will achieve greater benefits for reptiles by focusing on improving site-scale habitat quality, with increasing the amount and connectivity of habitat being a secondary priority.

Landscapes are spatially-defined mosaics of habitat elements that differ in quality and configuration (Wiens, 1999). Landscape context is the amount and spatial configuration of habitat elements in relation to a site. To study the effect of landscape context on reptiles, intact (or remnant) vegetation is generally used as a surrogate for suitable habitat, with species richness positively influenced by the amount of intact vegetation in the landscape (Cunningham et al., 2007; Lindenmayer et al., 2005; Mac Nally and Brown, 2001). However, the connectivity of intact vegetation and the spatial heterogeneity of vegetation cover generally have little influence on reptiles (Driscoll, 2004; Fischer et al., 2004a; Jellinek et al., 2004; Mac Nally and Brown, 2001). These findings, which are based on discrete landscape conceptualisations, suggest that the matrix may not be impermeable or hostile for many reptile species (Franklin and Lindenmayer, 2009; Kupfer et al., 2006; Ricketts, 2001), and/or discrete landscape models may poorly reflect how reptiles perceive and use the landscape (Franklin and Lindenmayer, 2009; Manning et al., 2004). To better understand the influence of landscape context on reptiles, it is imperative that, as suggested by Lindenmayer et al. (2007), multiple landscape conceptualisations (discrete and continuous) are considered during analyses, and that landscape patterns are mapped using land cover variables that are relevant to the ecology of reptiles (Bruton et al., 2015; Manning et al., 2004).

* Corresponding author.
E-mail address: melissa.bruton@uqconnect.edu.au (M.J. Bruton).

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For effective conservation and restoration planning, habitat quality should be defined from the point of view of the taxon of interest (Dennis et al., 2003; Manning et al., 2004; Mortelliti et al., 2010). Reptiles are typically hypo-metabolic (low-energy) specialists that require minimal amounts of food and water for survival (Pough, 1983). However, due to their inability to sustain or rapidly recover from aerobic activity, reptiles require reliable access to shelter resources to avoid predation (Pough, 1980, 1983); with shelters, such as burrows, and bushy shrubs, identified as key habitat resources (e.g. Beck and Jennings, 2003; Grillet et al., 2010; Lagarde et al., 2012). Reptile diversity and abundance are positively correlated with site-scale structural heterogeneity (Brown, 2001; Fischer et al., 2004a; Kanowski et al., 2006), and reptile species generally respond positively to the increased availability of shelter resources (Bonnet et al., 2012; Grillet et al., 2010; Souter et al., 2004). These findings suggest that the availability of suitable shelter resources may be an effective, but little used, proxy for reptile habitat quality.

Regenerating landscapes are landscapes containing vegetation patches that have been cleared and are now on a successional trajectory, through either passive or active regeneration (Parkes et al., 2012). Regenerating landscapes are usually created when agricultural lands are abandoned (Bowen et al., 2007; Hobbs and Cramer, 2007). Such landscapes offer an opportunity to assess the potential for alternative revegetation strategies to benefit fauna during regeneration, and once vegetation has reached maturity (Polyakov et al., 2011). Cunningham et al. (2007) found that the cover of planted trees had a negative relationship with reptiles in regenerating landscapes due to a lack of ground structure, whereas Bruton et al. (2013) found that the habitat value of passive regrowth vegetation in regenerating landscapes is high where ground-level habitat structures are retained. This suggests that the structure of vegetated areas, rather than vegetation status per se, may be the key determinant of habitat suitability for reptiles in regenerating landscapes.

In this study, we addressed the question: what are the relative importance of site-scale habitat quality and landscape context for reptile communities and species in regenerating landscapes? To address this question, we applied an information-theoretic model averaging approach, with variables derived from multiple alternative landscape conceptualisations (Bruton et al., 2015; Lindenmayer et al., 2007; Price et al., 2009). Our findings suggest that reptiles in regenerating landscapes will benefit from conservation and restoration activities that focus on improving site-scale habitat quality.

2. Methods

2.1. Study area

We assessed the relative importance of habitat quality and landscape context for reptiles in a regenerating semi-arid woodland landscape in subtropical Queensland, Australia (Fig. 1). The study area is a 34 000 ha conservation reserve. As a former cattle and sheep grazing property, it consists of a mosaic of cleared paddocks, areas of passive regrowth, and intact woodlands (Fig. 1). The woodlands can be broadly classified as *Acacia*- or *Eucalyptus*-dominated ecosystems (Bruton et al., 2015; Sattler and Williams, 1999). The *Acacia*-dominated ecosystems are relatively dense woodlands dominated by bendee *Acacia catenulata* and mulga *Acacia aneura*, with a sparse understory, limited ground cover, and abundant fallen timber. The *Eucalyptus*-dominated ecosystems are open woodlands dominated by poplar box *Eucalyptus populnea*, with a shrubby understory of false sandalwood *Eremophila mitchellii*, wilga *Geijera parviflora*, and/or cassia *Senna artemisioides*, abundant grass cover, and large hollow logs. For further details about the vegetation and the history of the study area see Bruton et al. (2013).

2.2. Reptile surveys

Reptiles were surveyed at fifty-five sites (Fig. 1) over twelve days (3 rounds of 4 days) during the warm seasons (Oct–Apr) of 2010/11 and 2011/12 as described in Bruton et al. (2013). We used a passive survey approach, with 4× unbaited pitfall and 4× unbaited funnel traps and 14 m of drift fences at each site (Fig. 2). Sites were randomly located with respect to natural and manmade features, and varied from 40 to

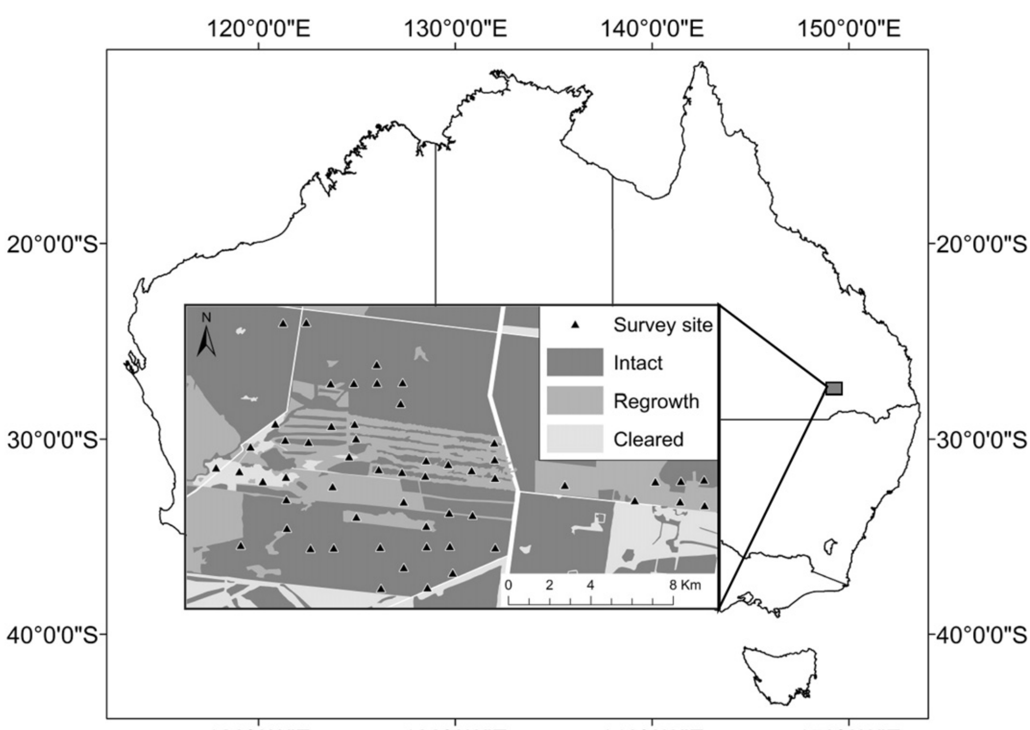

Fig. 1. Study site location in southern Queensland, Australia; with the survey sites. Here, the landscape is depicted using a landscape mosaic based on woodland clearing status, with polygons derived from Regional Ecosystem mapping (Queensland Government, 2010b) and aerial photography.

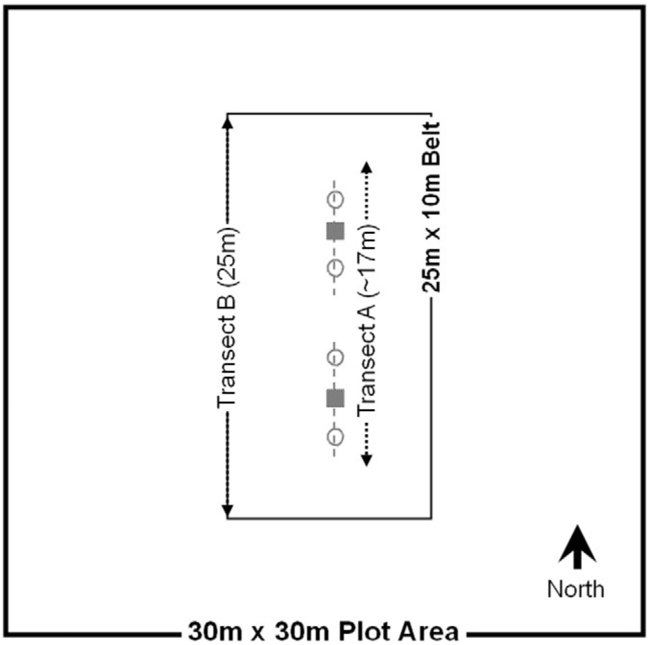

Fig. 2. Layout of transects and plots for the site-scale habitat quality surveys. Survey plots surrounded the trap line used for reptile surveys, which is depicted by circles (pit traps), squares (funnel traps), and dotted lines (drift fences).

660 m from the nearest access track. Sites from different habitat categories were surveyed at the same time to minimise seasonal and weather biases affecting reptile capture probabilities (Spence-Bailey et al., 2010). The sites were surveyed in groups of 7 or 8, with the group composition shuffled for each of three survey rounds.

2.3. Conceptualising and quantifying habitat quality

In this study, we used habitat structure and shelter availability as proxies for site-scale habitat quality (Mortelliti et al., 2010). Reptile species vary in their shelter requirements, due to morphology, sociality and physiological performance (Schulte et al., 2004). Therefore, using available literature, we a priori identified the shelter resources and habitats associated with each species likely to have sufficient captures for analysis (see Section 2.5). Whilst primary literature was prioritised, there is limited empirical information about reptile species-microhabitat associations available for reptiles (McDiarmid, 2012). Therefore, a substantial proportion of species-microhabitat information was derived from reptile identification guides with anecdotal shelter information (Cogger, 2000; Wilson and Knowles, 1988). We identified ten habitat structural variables that are associated with the presence or abundance of the focal reptile species in our study (see Appendix A, Table 1, and Section 2.5 below for details).

We measured relevant structural and vegetation variables at each survey site using the line-intersect method and plot counts as shown in Fig. 2. The proportional cover of shrubs, ground vegetation, and leaf litter cover were measured along two transects (Transects A and B). The density of fallen stems, fallen *Eucalyptus* hollows, standing hollows, ground burrows and termite mounds were calculated from counts within a 25 m × 10 m belt surrounding the reptile survey line. The densities of trees only, and trees and shrubs combined (woody stem density), were calculated from counts within a 30 m × 30 m plot area surrounding the reptile survey line.

2.4. Conceptualising and quantifying landscape context

In landscapes with distinct patch boundaries, discrete patch-matrix models are the standard landscape conceptualisation used, because they are intuitive, simple to apply, and easy to communicate to land managers (Fischer et al., 2004b). Supporting this, our earlier findings demonstrated that the mosaic landscape conceptualisation based on vegetation type is the most useful for predicting reptile distributions in regenerating landscapes (Bruton et al., 2015). However, reptile communities and the distribution of some reptile species also correlated well with continuous and binary conceptualisations of regenerating landscapes (Bruton et al., 2015). Therefore, to adequately assess the influence of landscape context on reptiles, we generated discrete (binary and mosaic) and continuous conceptualisations of features in the study landscape, to derive multiple landscape context predictor variables for each reptile response variable (Lindenmayer et al., 2007; Price et al., 2009, Table 1).

Table 1
Site-scale habitat quality and landscape context predictor variable descriptions and their variation across the 55 survey sites. Landscape context measurements are within a 250 m buffer surrounding the survey sites.

Level of scale	Variable	Details/categories	Min.	Mean	Max.
Site-scale (habitat quality)	Woodland status	Cleared, regrowth, intact			
	Vegetation type[a]	*Acacia*, *Eucalyptus*, grass			
	Woody vegetated	Woody vegetation present or absent			
	Intact	Intact or disturbed			
	Shrub cover	Vegetation cover 0.3–2 m high (%)	0	11	48
	Ground vegetation cover	Cover of grasses, forbs and sedges to 0.3 m high (%)	0	44	92
	Leaf litter cover	Presence (%)	0	47	94
	Fallen stems	Length of fallen stems >2 cm diameter (mm/m^2)	0	61	420
	Fallen hollows	Fallen *Eucalyptus* hollows >3 cm diameter (mm/m^2)	0	55	310
	Standing hollows	With entries >1 cm diameter (hollows/m^2)	0	0.014	0.06
	Ground burrows	With entries >3 cm diameter (hollows/m^2)	0	0.013	0.04
	Termite mounds	Mounds/m^2	0	0.005	0.02
	Tree density	Density of tree species (stems/m^2)	0	0.058	0.28
	Stem density	Density of trees and shrubs (stems/m^2)	0	0.097	0.96
Landscape context: discrete models	Intact	Intact vegetation (%)	0	55	100
	Cleared	Woodlands converted to grassy paddocks (%)	0	10	100
	Acacia	*Acacia*-dominated regrowth and intact woodlands[a] (%)	0	59	100
	Eucalyptus	Eucalyptus-dominated regrowth and intact woodlands[a] (%)	0	31	100
Landscape context: continuous models	Woody	Cover of perennial (woody) vegetation (%)	3	48	76
	Grassy	Cover of seasonal (grassy) vegetation (%)	24	49	95
	Bare	Cover of bare earth (%)	0	3	34

[a] Derived from Regional Ecosystem (RE) and pre-clearing map layers version 6.0 (Queensland Government, 2010a, 2010b). We classified "*Acacia*-dominated woodlands" as patch classes 11.7.2, 11.7.2/6.5.1, and 6.5.1/11.7.2/6.5.2; and "*Eucalyptus*-dominated woodlands" as patch classes 11.5.13 and 11.5.13/11.3.25.

The distribution and abundance of reptile species can vary with vegetation type and land use (Driscoll, 2004; Sass, 2006; Swan and Foster, 2005). Therefore, landscape context variables were derived from 4× discrete (binary and mosaic) landscape conceptualisations where patches were classed by either vegetation type or clearing status (Table 1). Patches were defined as: i) either disturbed (regrowth and cleared) or intact, ii) either woody-vegetated (regrowth and intact) or not woody-vegetated, iii) by clearing status, and iv) by woodland type (see Bruton et al., 2015 for details). In addition to the discrete landscape classifications, we also conceptualised the landscape as continuously varying in the proportional cover of three structural variables: i) woody vegetation, ii) grassy vegetation, and iii) bare earth. We selected these continuous landscape variables because they are known to influence reptile distributions (Pianka and Pianka, 1976; Pike et al., 2011; Price et al., 2010) and they can be quantified across landscapes using satellite imagery (Levin and Heimowitz, 2012).

To map the landscape as continuously varying in the proportion of woody vegetation, grassy vegetation, and bare earth, we processed four Landsat-5 images of the study area, using the method of Levin and Heimowitz (2012), to create a land cover map with the proportional cover of these three land cover classes within each 30 m × 30 m Landsat pixels. For the discrete landscape maps, we classified each Landsat-pixel into one of six land cover categories: bare earth, grass, regrowth *Acacia* woodland, regrowth *Eucalyptus* woodland, intact *Acacia* woodland, and intact *Eucalyptus* woodland (Table 1) using the Support Vector Machine supervised classification method (Cohen, 1960; Hsu et al., 2010; Moses and Holland, 2010) in ENVI. Further details regarding the mapping and classification of the study site are available in Bruton et al. (2015).

We used the proportional cover (spatial extent) of the land cover classes to derive relevant landscape context variables for the discrete landscape conceptualisations, and the mean proportional cover of each land cover class for the continuous landscape conceptualisations (Table 1). We quantified all the landscape context variables within a 250 m radius of each survey site. This distance was based our previous study, which found little difference in the influence on reptiles of landscape context predictor variables measured within 100 m, 250 m, and 500 m (Bruton et al., 2015).

2.5. Analyses

The response of terrestrial vertebrates to landscape change is usually assessed using community-level measures such as species richness (Bowen et al., 2007; Bruton et al., 2013). Whilst informative, the use of community-level assessments alone can simplify ecological complexity, resulting in misguided perceptions of the effects of landscape-scale processes on fauna (Fischer et al., 2004a; Manning et al., 2004). Therefore, to effectively assess the relative importance of site- and landscape-scale influences on reptiles, we assessed 3× complete reptile community indices, the abundance of snakes, and the abundance of ten reptile species (Table 2). The community response variables assessed were i) species richness, ii) abundance, and iii) diversity. Diversity was calculated using the Hill's diversity index (exp[H`]); the most ecologically informative measure of diversity (Jost, 2006; Tuomisto, 2012). The eight species of snakes that were grouped together for analyses were all active predators from the family Elapidae (*Pseudechis*, *Pseudonaja*, *Demansia*, *Parasuta*, *Furina*, *Brachyurophis*, and *Vermicella* spp.). Due to information constraints, we restricted the species-level analyses to the ten reptile species that were present at more than 1/3 of the survey sites.

Pluralistic models are an essential tool for evaluating the relative importance of environmental influences from multiple scales and multiple landscape conceptualisations, on fauna (Lindenmayer et al., 2007; Price et al., 2010; Wu and Loucks, 1995). We used model averaging to rank the importance of predictor variables based on Akaike weights, and to derive an estimated β coefficient value (effect magnitude and direction) with confidence intervals for each predictor variable (Barton, 2013; Burnham and Anderson, 2002). We also used hierarchical partitioning to identify the strength of independent and joint effects of predictor variables on reptiles (Burnham and Anderson, 2002; Mac Nally, 1996).

Reptile diversity was assessed using a Gaussian distribution family, reptile species richness with a Poisson distribution family, and reptile abundance with a negative binomial distribution family. Negative binomial models were developed using the 'glm.nb' function in the package 'pscl' (Jackman, 2013), with the 'odTest' function (log-likelihood) used to determine whether a dispersion parameter was required (negative binomial model distribution) or if a Poisson distribution was suitable (Molla and Muniswamy, 2012). The reptile species were modelled using negative binomial distribution families, except for the gecko species *Diplodactylus vittatus* and the group 'snakes', where a dispersion parameter was not required and Poisson distributions were used.

To ensure adequate simplicity and even representation for both site- and landscape-level factors in the global models, for each of the fourteen reptile response variables the three most relevant site-scale habitat quality, and three most relevant landscape context, predictor variables were selected for each pluralistic model (Table 2). For global models with highly correlated predictor variables ($R^2 > 0.6$, Spearman), the variable with the poorest univariate fit was removed from the analysis and an alternative site- or landscape-level variable was substituted.

We used the statistical programme R (R Core Team, 2014) for all analyses. We used the 'hier.part' and 'rand.hp' functions in the 'hier.part'

Table 2
Predictor variables selected for each reptile response group. Predictor variables were chosen based on the literature summary available in Appendix A.

Reptile response	Site-scale variables	Landscape-scale variables	
		Discrete	Continuous
Species richness	Complexity[a], vegetation type, intact	Cleared, Eucalyptus	Wooded
Abundance	Complexity[a], vegetation type, woody vegetated	Cleared, Eucalyptus	Wooded
Diversity	Complexity[a], vegetation type, woody vegetated	Cleared, Eucalyptus	Wooded
Snakes	Burrows, fallen hollows, termite mounds	Cleared, Eucalyptus	Wooded
Egernia striolata (skink)	Standing hollows, tree density, woody vegetated	Cleared, intact	Bare
Morethia boulengeri (skink)	Stem density, fallen hollows, vegetation type	Eucalyptus, cleared	Grassy
Lygisaurus foliorum (skink)	Ground vegetation, fallen stems, Vegetation type	Eucalyptus, cleared	Wooded
Eremiascincus richardsonii (skink)	Leaf litter, ground vegetation, vegetation status	Cleared	Grassy, bare
Ctenotus ingrami (skink)	Shrubs, vegetation type, intact	Acacia, cleared	Grassy
Ctenotus robustus (skink)	Burrows, ground vegetation, woody vegetated	Cleared, intact	Bare
Heteronotia binoei (gecko)	Fallen stems, termites, woody vegetated	Cleared	Grassy, bare
Lucasium steindachneri (gecko)	Fallen stems, ground vegetation, vegetation type	Cleared, Acacia	Wooded
Diplodactylus vittatus (gecko)	Fallen hollows, leaf litter, woody vegetated	Cleared, Acacia	Wooded
Amphibolurus burnsi (agamid)	Tree density, vegetation type, woody vegetated	Cleared, intact	Wooded

[a] An additive index based on the amount of fallen timber, shrub cover, ground vegetation cover, leaf litter cover, number of termite mounds, and number of vegetation layers present (see Bruton et al., 2013 for details).

package (Walsh and Mac Nally, 2013) to identify significant independent effects, and the 'model.avg' function with a 95% confidence set of models in the 'MuMIn' package (Barton, 2013) to identify the strength and direction of influence for each variable in the global model.

The fit of all 14 global models (i.e. models with all six parameters) was tested by plotting the standardised residuals against the half-normal scores. The residuals were homogenous and normally distributed, indicating that underlying model assumptions were met (Dobson, 2002; McCue et al., 2008). Spatial autocorrelation among model residuals in the global models was tested with a spline correlogram with 95% bootstrapped confidence intervals using the 'spline.correlog' function in the package 'ncf' (Bjørnstad, 2013). All global model splines were within the confidence interval bounds, indicating spatial independence of the model residuals (Bjørnstad and Falck, 2001).

3. Results

In total, 754 individual reptiles from 34 species were surveyed for this study (see Appendix B for details). Site-scale habitat quality had a greater influence on all fourteen reptile response variables than landscape context, as demonstrated by both hierarchical partitioning and model averaging (Fig. 3, Table 3). Landscape context has little influence on reptile communities and species (Table 3).

We found that site-scale habitat quality is important for reptile communities, with reptile diversity higher at wooded (intact and regrowth), and complex sites (Table 3). Total reptile abundance was influenced by vegetation type (Table 3), with more individuals in *Eucalyptus*-dominated woodlands (*Eucalyptus* = 18.1 +/− 2.0 SE; cleared = 13.3 +/− 2.2 SE; *Acacia* = 11.6 +/− 0.7 SE).

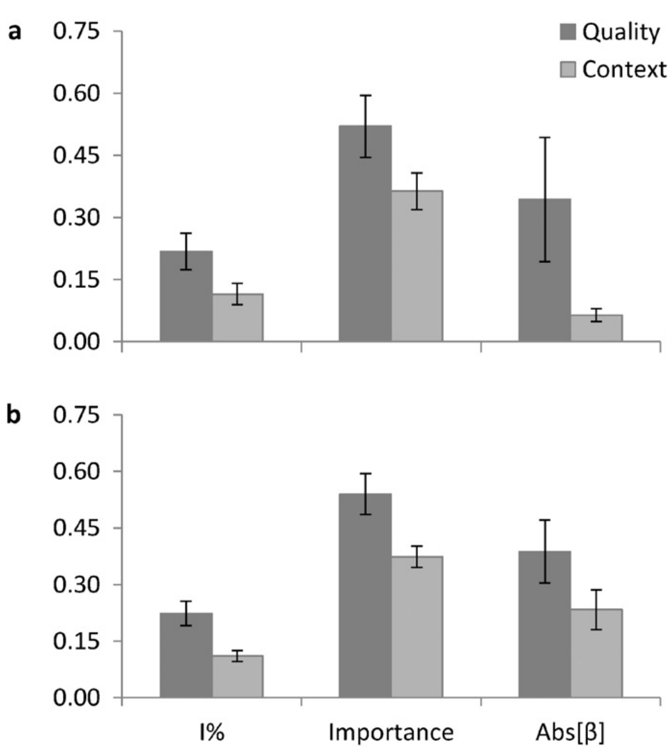

Fig. 3. Summary of the average relative effect of site-scale habitat quality and landscape context on: a) reptile communities, and b) reptile species and the group 'snakes'. I% = proportion of the independently-explained variance attributable to the predictor, derived from hierarchical partitioning; Importance = the sum of Akaike weights for all the models that include the explanatory variable, which is derived from model averaging; and Abs[β] = the absolute value of the estimated coefficient for continuous variables, also derived from model averaging. The unit of measure for 'I%' is mean proportional independent influence, ranging from 0 to 1. The unit of measure for 'Importance' is a unitless relative scale from 0 (no influence) to 1 (very large influence). Abs[β] is also unitless, with higher values representing larger effects (larger model coefficients).

Site-scale habitat quality influenced the abundance of eight out of the ten reptile species assessed, as well as the group 'snakes' (Table 3). In contrast, the gecko *Lucasium steindachneri* and the skink *Morethia boulengeri* did not respond to either site-scale habitat quality or landscape context variables, although there is some indication that the abundance of *M. boulengeri* may be affected by woodland type (Table 3). Landscape context influenced one of the fourteen reptile response variables: the terrestrial skink *Ctenotus robustus*, which responded negatively to the amount of intact woodland in the surrounding landscape (Table 3).

4. Discussion

4.1. Habitat quality vs landscape context

This is the first study to compare the relative importance of site-scale habitat quality and landscape context for reptiles. In regenerating woodland landscapes, the composition of the surrounding landscape had little influence on reptile communities and species, with just one species affected. In contrast, site-scale habitat quality affected all reptile community metrics, and the distribution of the majority of the reptile species and groups assessed in this study. These findings support focusing on improving site-scale habitat quality for reptiles, particularly by increasing structural complexity, rather than focusing on landscape context during landscape restoration planning (Collinge, 1996). The results from this study provide essential quantitative information for assessing the impact of conservation options and land management scenarios on reptiles (Brudvig, 2011; Lindenmayer et al., 2007; Mortelliti et al., 2012).

Across taxa, species and fauna communities often respond to landscape context; however, site-scale habitat factors have a consistently larger impact (Abensperg-Traun et al., 1996; Bergman et al., 2008; Bowen, 2009; Bowman et al., 2001; Collinge et al., 2003; Michel et al., 2007; Poyry et al., 2009; Weyrauch and Grubb, 2004), with two notable exceptions – the koala (McAlpine et al., 2006) and Dupont's lark *Chersophilus duponti* (Vogeli et al., 2010). Because of the existence of these exceptions, and to inform restoration activities, many more comparisons in a variety of terrestrial environments and scenarios are needed to identify trends where landscape-scale factors play a crucial role, and to identify species and groups that respond strongly to factors at this scale.

In this study, one out of eleven (9%) reptile species or groups responded to landscape context. To compare, 44% (4/9) of avian species (Bowen et al., 2009) and 6% (2/31) of arthropod groups (Abensperg-Traun et al., 1996) respond to variation in landscape context. These studies indicate a discrepancy between the proportion of bird species, and the proportion of reptile and arthropod species and groups, that respond to variation in landscape context, which could be related to body size (Haskell et al., 2002), energy requirements and rates of movement (Nagy, 2005), and/or microhabitat use (Chiari et al., 2013; Negro et al., 2008; Perry and Garland, 2002), which differ markedly between endotherms and ectotherms (Nagy, 2005; Nagy et al., 1999). Potential correlations between energy system, i.e. endothermy and ectothermy, and the influence of landscape context on taxa, require further investigation.

4.2. Species responses

The only species that responded to variation in landscape context in this study was the medium-sized terrestrial skink *Ctenotus robustus*. This common species prefers open and disturbed habitats, and is associated with areas with a high proportion of ground cover (Bragg et al., 2005; Michael et al., 2010; Price et al., 2010; Taylor and Fox, 2001). In this study, we confirmed that *C. robustus* has a strong and positive relationship with ground cover at the site level. We also found that, at the landscape level, more *C. robustus* were present at sites with less intact

Table 3
The relative importance of site-scale habitat quality, and landscape context, variables for reptile communities and species. Bold text is used to highlight significant independent effects (I%), summed Akaike weights of >0.7 (importance), and derived coefficients with a confidence interval that does not include zero (β). Coefficient values (β) are not supplied for the categorical predictor variables with more than one category.

Species/group	Method	Habitat quality			Landscape context		
Abundance		***Veg type***	*Woody*	*Complexity*	***Eucalyptus***	*Cleared*	*Wooded*
	I%	**0.43**	0.01	0.14	**0.24**	0.11	0.07
	Importance	**0.90**	0.46	0.28	0.44	0.50	0.29
	β		0.00	0.02	-0.05	-0.14	-0.02
Diversity		***Complexity***	***Woody***	***Veg type***	*Cleared*	*Wooded*	*Eucalyptus*
	I%	**0.24**	**0.23**	**0.25**	0.19	0.09	0.01
	Importance	**0.71**	0.66	0.41	0.31	0.28	0.27
	β	0.39	**1.21**		-0.12	-0.08	-0.05
Richness		***Complexity***	*Intact*	*Veg type*	*Cleared*	*Wooded*	*Eucalyptus*
	I%	**0.34**	0.06	0.26	0.21	0.06	0.06
	Importance	0.67	0.34	0.25	0.64	0.29	0.25
	β	0.08	-0.04		-0.10	-0.01	0.01
Ctenotus robustus		***Ground veg***	***Woody***	*Burrows*	***Intact***	***Cleared***	*Bare*
Eastern striped skink	I%	**0.24**	**0.36**	0.02	**0.15**	**0.21**	0.01
	Importance	**1.00**	0.38	0.55	**0.94**	0.30	0.22
	β	**1.22**	-0.35	-0.22	**-0.66**	-0.07	0.01
Lygisaurus foliorum		***Veg type***	*Ground veg*	*Fallen stems*	*Eucalyptus*	*Wooded*	*Cleared*
Iridescent skink	I%	**0.55**	0.03	0.02	0.35	0.02	0.04
	Importance	**1.00**	0.41	0.19	0.21	0.24	0.19
	β		0.12	0.00	-0.02	-0.05	-0.02
Snakes		***Term. mounds***	***Fallen hollows***	*Burrows*	*Wooded*	*Cleared*	*Eucalyptus*
	I%	**0.36**	**0.36**	0.09	0.06	0.07	0.07
	Importance	**1.00**	**0.95**	0.22	0.42	0.40	0.29
	β	**-0.70**	**0.53**	0.00	0.12	-0.14	-0.02
Amphibolurus burnsi		***Veg type***	*Woody*	*Tree density*	*Acacia*	*Wooded*	*Cleared*
Burns' dragon	I%	**0.46**	0.08	0.03	0.26	0.10	0.07
	Importance	**0.97**	0.50	0.21	0.63	0.24	0.23
	β		0.33	-0.01	-0.84	0.03	0.14
Eremiascincus richardsonii		***Ground veg***	***Leaf litter***	*Veg status*	*Cleared*	*Grassy*	*Bare*
Broad-banded sand swimmer	I%	**0.48**	0.25	0.12	0.09	0.02	0.04
	Importance	**0.92**	**0.87**	0.11	0.52	0.24	0.50
	β	**-0.65**	**-0.75**		-0.67	-0.05	-0.41
Diplodactylus vittatus		***Leaf litter***	*Woody*	*Fallen hollows*	*Wooded*	*Cleared*	*Acacia*
Eastern stone gecko	I%	**0.46**	0.07	0.07	0.23	0.07	0.11
	Importance	**0.88**	0.29	0.28	0.46	0.45	0.23
	β	**0.61**	1.23	-0.06	0.21	-15.56	0.02
Ctenotus ingrami		***Intact***	*Veg type*	*Shrubs*	*Cleared*	*Grassy*	*Acacia*
Unspotted yellow-sided ctenotus	I%	**0.40**	0.17	0.03	0.07	0.20	0.12
	Importance	**0.86**	0.40	0.22	0.52	0.51	0.37
	β	**-1.03**		0.01	-0.91	-0.30	0.14
Heteronotia binoei		***Fallen stems***	***Woody***	*Termite mound*	*Cleared*	*Grassy*	*Bare*
Bynoe's gecko	I%	**0.37**	0.25	0.09	0.14	0.07	0.08
	Importance	**0.76**	**0.99**	0.27	0.66	0.47	0.40
	β	**0.19**	6.24	0.03	1.12	0.13	-0.11
Egernia striolata		***Standing hollows***	*Woody*	*Tree density*	*Cleared*	*Bare*	*Intact*
Tree skink	I%	**0.65**	0.14	0.01	0.11	0.02	0.06
	Importance	0.68	0.53	0.20	0.45	0.22	0.22
	β	**0.31**	14.47	-0.01	-0.61	0.02	0.01
Lucasium steindachneri		*Fallen stems*	*Ground veg*	*Veg type*	*Bare*	*Eucalyptus*	*Intact*
Box-patterned gecko	I%	0.15	0.00	0.43	0.18	0.22	0.02
	Importance	0.61	0.21	0.19	0.30	0.26	0.22
	β	-0.42	0.00		0.05	-0.01	-0.03
Morethia boulengeri		***Veg type***	*Fallen hollows*	*Stem density*	*Cleared*	*Eucalyptus*	*Grassy*
South-eastern morethia skink	I%	**0.41**	0.19	0.02	0.12	0.22	0.05
	Importance	0.36	0.56	0.22	0.40	0.34	0.32
	β		0.24	0.02	-0.28	-0.07	-0.08

woodland in the surrounding landscape. In our study area, the intact woodlands are relatively dense, with mean canopy cover values of 60% (*Acacia*) and 40% (*Eucalyptus*), whereas regrowth woodlands are less dense (canopy cover: *Acacia* = 28%; *Eucalyptus* = 22%), and there were no trees in cleared areas. Price et al. (2010) also found that *C. robustus* responded positively to low tree cover in the surrounding landscape. These two studies confirm that *C. robustus* is affected by variation in both site- and landscape-scale factors, responding to positively to grass cover at the site level and negatively to tree cover at the landscape level.

Two species of reptiles did not respond to either site-scale habitat quality or landscape context: *Morethia boulengeri* and *Lucasium steindachneri*. The terrestrial skink *M. boulengeri* is a common species that is known to respond to the amount of fallen timber present and the density of overstorey vegetation (Fischer et al., 2004a; Michael et al., 2010; Michael et al., 2004). Although *M. boulengeri* was abundant at the study site, these site-scale habitat associations were not confirmed in this study, possibly due to variations in habitat use and suitability among different populations of this species across its distribution, a trend that has been demonstrated by Vitt et al. (1997) for geckoes in the Amazon. *L. steindachneri* shelters in spider burrows and soil cracks (Cogger, 2000; Wilson and Knowles, 1988). These fine-scale habitat features were unable to be quantified during this study because of their small size and prolific grass growth at the survey sites during surveys.

4.3. Management implications

Shelter is an important environmental resource for reptiles, with reptile populations increasing when suitable shelter resources are provided (Grillet et al., 2010; Manning et al., 2013). In this study, four reptile species demonstrated a strong and positive response to the availability of shelter resources (ground vegetation, leaf litter, fallen stems, and standing hollows). Shelters protect reptiles from predators, and they can also be excellent thermal buffers (Anderson and Richardson, 2005; Bulova, 2002; Whittington-Jones et al., 2011). Reptiles are susceptible to predation at cool temperatures because they are less able to detect and respond to predators (Ford and Burghardt, 1993; Peterson et al., 1993). Shelter sites can protect reptiles from predation when temperatures are low and they are more vulnerable. Shelter sites can also allow reptiles the capacity to cool and slow their metabolism with fewer risks, thereby preserving their energy stores (Nagy et al., 1999), which is a beneficial strategy in dry environments where food and water resources are scarce and pulsed in their availability (Ffolliott et al., 2003). Therefore, the re-colonisation potential of disturbed and recovering dryland landscapes by reptiles is improved when shelter resources are retained or added to the landscape.

This study has provided quantitative information that allows land managers and conservation planners to more accurately analyse the costs and benefits of conservation and land management scenarios in landscapes where reptiles play a critical functional role (Brudvig, 2011; Lindenmayer et al., 2007; Mortelliti et al., 2012). The findings of this study support management actions and restoration activities that improve site-scale habitat quality, rather than focussing on the position and context of intact and regenerating vegetation patches in areas where reptiles are key fauna, such as deserts, woodlands and savannas (Ayal, 2007; Blench, 2004; Pough, 1983).

In earlier work using this dataset, Bruton et al. (2013) found that the reptile communities in regrowth and remnant woodlands were similar. Supporting this, only one species in this study responded to vegetation succession status at the site or landscape level (Table 3: *Ctenotus ingrami*). However, vegetation type was an important factor at the site level for two species, *Lygisaurus foliorum* and *Amphibolurus burnsi*, and for overall reptile abundance (Table 3). These findings suggest that vegetation type may be an equally or more important factor in driving reptile abundances and distributions in regenerating woodland landscapes, as vegetation succession status. Therefore, the implementation of management and conservation plans that consider the availability of patches of different vegetation types, as well as focusing on the successional stage of vegetation, will benefit reptiles in regenerating woodland landscapes.

This study confirms the findings of Brown (2001); Fischer et al. (2004a) and Kanowski et al. (2006), that reptiles are more abundant and diverse in structurally heterogenous environments. It also supports the findings of Grillet et al. (2010) and Souter et al. (2004) that reptile species are more abundant where there is a high density of structures that create suitable shelter resources. However, one species in this study preferred areas with less ground vegetation and leaf litter cover (Table 3: *Eremiascincus richardsonii*). To increase reptile diversity and abundance in regenerating landscapes, management actions that increase the availability of shelter resources, and structural diversity across the landscape are needed. However, to achieve maximum benefits, the creation of heterogenous landscapes will ensure that the habitat requirements of the maximum number of reptile species are met. This requires landscape architectural planning to create mosaics of patches with high structural heterogeneity interspersed with open areas of limited ground-level structure (Collinge, 1996; Hansson et al., 1995).

Conservation and restoration activities will achieve greater benefits for reptiles by focusing on improving site-scale habitat quality, with increasing the amount and connectivity of intact vegetation a lesser priority. Although reptiles as a group respond positively to increased structural heterogeneity at the site level, there is a need for a greater understanding about the drivers of variation in habitat quality for many reptile species (McDiarmid, 2012). This study has highlighted the importance of identifying these site-scale drivers of habitat quality for local reptiles, and ensuring the provision of such habitat features is prioritised during restoration activities in landscapes where reptiles play an important functional role.

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Appendix A. Potential and confirmed shelter and habitat associations for assessed species.

Species[a]	Habitat associations	Microhabitat[1]	Microhabitat[2]	Other microhabitat sources
Amphibolurus burnsi (*Lophognathus*/*Gemmatophora gilberti centralis*/*gilberti*)	*G. g. gilberti* — woodland areas[1]	*G. g. centralis* — perched on timber, termitaria, among foliage. Hollows, dense veg. Sleeping exposed tree/shrub limbs warm weather	*L. gilberti* — trees, termitaria	*Amphibolurus* — *Acacia* foliage[3]. *G. g. gilberti* logged, cattle disturbed areas[3]

(*continued on next page*)

Appendix A (*continued*)

Species[a]	Habitat associations	Microhabitat[1]	Microhabitat[2]	Other microhabitat sources
Ctenotus ingrami	Variety of soil types supporting woodlands over sparse understorey of chenopod shrubs or tussock grasses[1]	Shallow burrows at the base of low shrubs or grass tussocks		
Ctenotus robustus	Open areas. None in shrubby veg areas[9]. Grazed only[4]	Tunnels under slabs of rock, or debris, at base of low vegetation or beneath fallen timber	Short, shallow burrows underground debris	<Bare earth[6]. Logs, burrows, high ground cover, high bare ground, >grass:tree ratio[7]
Diplodactylus vittatus	Reserves and grazed[4]. Mallee[8]. Wide variety, incl. woodlands[1]	Small stones, fallen bark, timber, surface debris, perches on small sticks at night	Under fallen timber, stones and litter	Burrows, under rocks, bark and stumps[3]. Under boards, in rotten logs, beneath bark on stump[3]
Egernia striolata	Treed and rocky areas[5]	Hollow trunks, limbs, beneath loose bark, rock slabs, crevices	Hollow limbs and cracks or under bark of standing trees. Fallen timber, exfoliating rock outcrops	Less bare earth[6]. stumps, ring-barked trees[3]
Eremiascincus richardsonii	Variety — particularly hard or stony substrates w woodlands, shrublands or hummock grasslands[1]	*Eremiascincus* — leaf litter, loose sand, abandoned burrows	Similar to *E. fasciolatus* — shallow burrows under logs, stones or litter	
Heteronotia binoei	Ubiquitous[10]. Ubiquitous[5]. Widespread[1]	Rocks, logs, loose bark, base of stumps, dead vegetation, soil cracks, beneath surface debris	Rock crevices, ground litter and debris	Under logs, in litter and termite mounds, in animal burrows. Bare ground[10]. Under bark[3]. Rocks, fallen timber, bark, high bare ground, >grass:tree ratio[7]
Lucasium (*Diplodactylus*) *steindachneri*	Closed woodland[7]. Red soil plains[5]. Hard soils with woodlands[1]	Spider burrows, soil cracks, surface debris, open spaces, sparse ground cover	Ground litter, ground crevices or holes esp. abandoned insect nests and spider burrows	Spider holes, fallen timber[7]
Lygisaurus (*Carlia*) *foliorum*		*Carlia* — leaf-litter, grass, fallen bark at bases of trees	*Carlia* — litter	*Carlia* — though heliothermic, active in heavily shaded areas and dappled sunlight[2]
Morethia boulengeri	More in reserves, also in grazed[4]. Woodland but not Mallee[4]. Ubiquitous[5]. Various veg. incl. woodlands, shrublands[1]	*Morethia* — leaf litter, low vegetation at bases of trees, shrubs, rock outcrops	Ground litter, fallen timber, under bark of fallen and standing dead, ring-barked trees	Fallen logs, fallen *eucalyptus* logs[11]. <overstorey stem density[6]

[a] There have been many changes to Australian reptile taxonomy in the last 50 years. Therefore the literature search included all known pseudonyms, which were extracted from Uetz (2011).

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Appendix B. List of species captured (surveyed), and their rarity at the study site

Species[a]	Family	Habit[b]	Thermal source[c]	Number surveyed	Rarity at study site[d]	Habitats[e]
Agamids (dragons)						
Amphibolurus burnsi	Agamidae	T, A	H	61	Very common	re, ME, ra, MA
Diporiphora nobbi	Agamidae	SA	H	19	Common	re, ME, ra, MA

Appendix B (*continued*)

Species[a]	Family	Habit[b]	Thermal source[c]	Number surveyed	Rarity at study site[d]	Habitats[e]
Pogona barbata	Agamidae	T, SA	H	3	Common	c, ra
Skinks						
Ctenotus allotropis	Scincidae	T	H	20	Common	c, re, ME, MA
Ctenotus ingrami	Scincidae	T	H	35	Very common	re, ME, ra, MA
Ctenotus robustus	Scincidae	T, F	H	97	Very common	All
Cryptoblepharus spp.[f]	Scincidae	SA	H	14	Uncommon	re, ME, ra
Egernia striolata	Scincidae	A	H/T	31	Common	re, ME, ra, MA
Eremiascincus richardsonii	Scincidae	T, F	T	56	Very common	All
Lerista punctatovittata	Scincidae	F	T	16	Uncommon	re, ME, ra, MA
Lerista timida	Scincidae	F	T	28	Common	c, re, ME, ra
Lygisaurus foliorum	Scincidae	T	H	72	Very common	All
Menetia greyii	Scincidae	T	H	3	Rare	c
Morethia boulengeri	Scincidae	T, SA	H	54	Very common	All
Gekkoes						
Diplodactylus vittatus	Gekkonidae	T	T	29	Very common	re, ME, ra, MA
Heteronotia binoei	Gekkonidae	T	T	84	Very common	All
Lucasium steindachneri	Gekkonidae	T	T	38	Very common	All
Oedura monilis	Gekkonidae	A	T	4	Common	ra
Rhynchoedura ormsbyi[g]	Gekkonidae	T	T	20	Very common	All
Strophurus williamsi	Gekkonidae	A	T	19	Very common	re, ME, ra, MA
Pygopodids						
Lialis burtonis	Pygopodidae	T	T/H	5	Uncommon	re, ME, MA
Paradelma orientalis	Pygopodidae	T, SA	T	1	Rare	ME
Pygopus schraderi	Pygopodidae	T	T	2	Uncommon	MA
Snakes						
Brachyurophis australis	Elapidae	F	T	3	Uncommon	re, ra
Demansia psammophis	Elapidae	T	H	1	Rare	re
Furina diadema	Elapidae	T	T	4	Uncommon	re, ra
Parasuta dwyeri	Elapidae	T, F	T	13	Common	c, re, ME, MA
Pseudechis australis	Elapidae	T, F	H/T	3	Common	ra, MA
Pseudonaja aspidorhyncha	Elapidae	T	H/T	3	Uncommon	ME, MA
Pseudonaja textilis	Elapidae	T	H/T	3	Uncommon	MA
Ramphotyphlops spp.[h]	Typhlopidae	F	T	3	Rare	re, MA
Vermicella annulata	Elapidae	F	T	4	Uncommon	re, ME, ra
Varanids (goannas)						
Varanus gouldii	Varanidae	T, F	H	3	Very common	ra, re
Varanus tristis	Varanidae	A	H	3	Uncommon	ME, MA

[a] Species classification follows Wilson and Swan (2010).
[b] Habit = terrestrial (T), fossorial (F), arboreal (A), or semi-arboreal (SA) from Wilson and Knowles (1988) and Cogger (2000).
[c] H = heliothermic, T = thigmothermic.
[d] Rarity was assessed using the quartile method of Gaston (1994) based on both road transect and trapping records at the study site from 2010 to 2012.
[e] Cleared (c), regrowth *Eucalyptus* (re), mature *Eucalyptus* (ME), regrowth *Acacia* (ra), mature *Acacia* (MA).
[f] Due to difficulties in field differentiation, the superficially similar skinks *Cryptoblepharus metallicus*, *C. pulcher* and *C. pannosus* were grouped as *Cryptoblepharus* spp.
[g] *Rhynchoedura ornata* has recently been split into five species. The species found at the study site is likely to be *Rhynochoedura ormsbyi* (Pepper et al., 2011).
[h] The superficially similar blindsnakes *Ramphotyphlops affinis* and *R. weidii* were recorded as *Ramphotyphlops* spp.

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Glossary

Community: a group of interacting species living in the same place.
Dryland: zones where precipitation is counterbalanced by evaporation and transpiration i.e. areas with aridity index of <0.65.
Habitat quality: the ability of the environment to provide conditions appropriate for individual and population persistence.
Intact: native vegetation with no historical record or indication of major structural disturbance by humans, such as logging, clearing, grazing etc.
Landscape conceptualisation: the way the landscape is defined for distribution analyses e.g. continuously varying in the density of a land cover variable, or using discrete patch classes.
Landscape context: the spatial context of a habitat/site i.e. what surrounds that location.
Matrix: the background of a landscape in which patches of suitable habitat are embedded — species specific.
Resource: the environmental materials necessary for habitat occupation i.e. food, water and shelter.
Restoration: the process of assisting the recovery of an indigenous ecosystem that has been degraded, damaged, or destroyed.
Woodland: low density, open forest with plenty of sunlight and limited shade. Woodlands are generally located in the drier areas that form transition zones between closed forest and arid or cool regions.