Testing the relevance of binary, mosaic and continuous landscape conceptualisations to reptiles in regenerating dryland landscapes

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Abstract:

Context: Fauna distributions are assessed using discrete (binary and mosaic) or continuous conceptualisations of the landscape. The value of the information derived from these analyses depends on the relevance of the landscape representation (or model) used to the landscape and fauna of interest. Discrete representations dominate analyses of landscape context in disturbed and regenerating landscapes; however within-patch variation suggests that continuous representations may help explain the distribution of fauna in such landscapes.

Objectives: We tested the relevance of binary, mosaic, and continuous conceptualisations of landscape context to reptiles in regenerating dryland landscapes.

Methods: For each of thirteen reptile groups, we compared the fit of models consisting of one landscape composition and one landscape heterogeneity variable for each of six landscape representations (2 x binary, 2 x mosaic, and 2 x continuous), at three buffer distances. We used Akaike weights to assess the relative support for each model. Maps were created from Landsat satellite images.

Results: Reptiles varied in their response to landscape context; however, the binary landscape representation with classes 'intact/disturbed' was best supported overall. Species richness was best described by a binary landscape representation with classes 'wooded/clear', whereas reptile abundance was best described by a mosaic landscape representation with classes defined by vegetation type. Five out of ten reptile species responded strongly to a single landscape representation, with the most relevant representation and conceptualisation varying among species.

Conclusions: Our findings support the use of multiple landscape conceptualisations and representations during analyses of landscape context for fauna in regenerating landscapes.

Keywords: *Australia, biodiversity conservation, landscape context, land management, Landsat, Landscape gradient model, Queensland, remote sensing, scale*

1. Introduction:

Landscape models and representations allow researchers to understand and communicate how and why the distributions of fauna vary across landscapes (Fischer et al. 2004b; Hansson et al. 1995). Landscapes can be represented using discrete (binary or categorical), or continuous conceptualisations of vegetation and land cover (Fischer et al. 2004b; Franklin and Lindenmayer 2009; McIntyre and Barrett 1992). Discrete landscape representations, where the quality and context of habitat is defined using distinct patch boundaries (Fischer and Lindenmayer 2006; McIntyre and Hobbs 1999), are commonly applied to landscapes that have been historically subject to intensive native vegetation loss (Fischer and Lindenmayer 2006). However, these discrete landscape conceptualisations may not always be the best reflection of how fauna perceive and use these regenerating landscapes (Fischer and Lindenmayer 2006; Franklin and Lindenmayer 2009; Manning et al. 2004).

Discrete landscape conceptualisations are intuitively applied to disturbed and regenerating landscapes, whereas continuous landscape conceptualisations are used to analyse fauna distributions in landscapes where vegetation cover is heterogeneous and patch boundaries are not easily defined (McIntyre and Barrett 1992). However, the use of landscape conceptualisations that represent the landscape from an anthropocentric perspective can poorly describe the landscape as perceived by fauna (Fischer et al. 2004a; Lindenmayer et al. 2007; Manning et al. 2004). For example, in savanna landscapes, which are generally represented using continuous landscape models of tree and grass cover, models from discrete landscape representations outperformed models from continuous landscape representations in explaining the distribution of several bird species (Price et al. 2009). To date, a synonymous study that compares the applicability of discrete and continuous landscape conceptualisations to fauna inhabiting landscapes where distinct patch boundaries do occur, such as regenerating landscapes, is yet to be undertaken.

Regenerating landscapes contain vegetation patches that were cleared and are now on a successional trajectory, through either passive or active regeneration (e.g. Andruskiw et al. 2008; Parkes et al. 2012). Regenerating landscapes consist of clearly-defined vegetation mosaics that vary in disturbance history, and vegetation successional status or age (Bowen et al. 2007; Bruton et al. 2013). The information derived from the analysis of fauna distributions in regenerating landscapes can be used to guide future land management and conservation actions. However, the conceptualisations and representation used to define the landscape during these analyses affects the quality and accuracy of restoration information available (Amici et al. 2010; Cooke et al. 2012; McGarigal et al. 2009; Rittenhouse et al. 2011). Currently it is not clear if multiple landscape representations and conceptualisations are needed to assess the importance of landscape context for fauna in regenerating landscapes (Lindenmayer et al. 2007), or if a single landscape conceptualisation, based on successional status, is sufficient to inform land management decisions. It is imperative, therefore, that we compare the effectiveness of different landscape conceptualisations and representations to describe landscape context for fauna in these landscapes.

Reptile habitats are often described in relation to structural features (e.g. Wilson and Knowles 1988). However, to analyse the relationship between reptile distributions and the structure of the surrounding landscapes, landscapes are typically conceptualised using discrete patches of land cover that vary in habitat 'quality' (e.g. Cunningham et al. 2007; Loehle et al. 2005; Schutz and Driscoll 2008). This is because habitat elements that affect reptile distributions, such as cover of fallen timber and ground burrows, are at a resolution that is too fine to be detected by satellite and aerial imagery (McElhinny et al. 2006; Recio et al. 2013; Simbotwe 1984). These technological restrictions mean that only a few landscape elements that are relevant to reptiles can be measured and derived from remotely sensed data (Fischer et al. 2005). In seasonally dry landscapes, a time-series of Landsat satellite images can be processed to derive within-pixel proportions of woody vegetation, grass, and bare earth land cover values (Guerschman et al. 2009; Levin and Heimowitz 2012; Levin et al. 2009), and these values can be used to create continuous landscape representations that are ecologically relevant to reptiles (Pianka and Pianka 1976; Pike et al. 2011b; Price et al. 2010).

In this study, we compared the relevance of alternative landscape models, derived from discrete (binary and mosaic) and continuous landscape conceptualisations, to reptiles in a regenerating semi-arid woodland landscape in Queensland, Australia. We asked the question: which landscape representation(s) and conceptualisation(s) best reflect how reptile communities and species perceive landscape context in regenerating landscapes? This study builds on previous research by Bruton et al. (2013), which demonstrated that, at the site-level, regrowth and intact woodlands differ little in their value as habitat for reptile communities.

2. Methods:

### 2.1 Conceptualising regenerating landscapes

Regenerating landscapes can be depicted discretely using both binary (habitat & non-habitat, or island biogeography) and mosaic (multiple class types, or patch-mosaic) conceptualisations (Bennett et al. 2006; Hansson et al. 1995). For the purposes of this paper, we have considered the binary model concept as being distinct from the mosaic model concept, because we wished to highlight the conceptual difference between these landscape definitions in terms of land management approach and implications. A binary landscape conceptualisation can be applied in two ways to landscapes with cleared, regrowth and intact vegetation (see Table 1 for definitions). In the first binary representation, regrowth patches are combined with cleared patches to create non-habitat ('disturbed': cleared & regrowth) and habitat ('intact') areas. In the second binary representation, regrowth patches are combined with intact patches to create habitat ('wooded': intact & regrowth) and non-habitat ('clear'). These binary classifications reflect the traditional fragmentation landscape conceptualisation (Edwards et al. 2002), and we use both binary representations in our analyses (Figure 1).
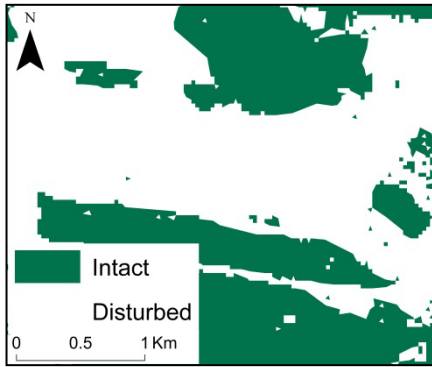
Binary Landscape Conceptualisation
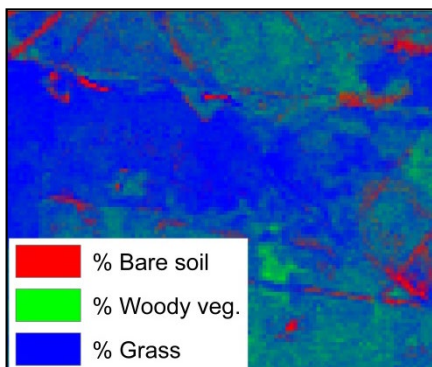
Displayed: Intact (or disturbed: regrowth & cleared)

Alternative: Wooded (intact & regrowth; or cleared)
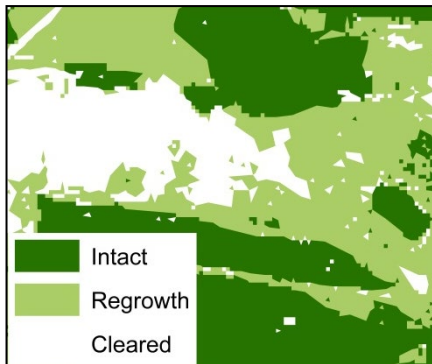
Mosaic Landscape Conceptualisation

Displayed: Vegetation status

Alternative: Vegetation type (e.g. grassland, *Acacia*-dominated woodland, or *Eucalyptus*-dominated woodland)

Continuous Landscape Conceptualisation

Displayed: Proportional cover of bare earth, perennial (woody) vegetation, and seasonal (grassy) vegetation

**Figure 1:** Binary, mosaic, and continuous representations of a regenerating landscape, derived from Landsat-5 satellite imagery. In the continuous landscape conceptualisation, the colour of each pixel is determined by the combined percentage of bare soil (red), woody vegetation (green), and grass (blue) i.e. reddish-blue pixels have a high percentage of bare soil and grass, with little woody vegetation.

Mosaic landscape conceptualisations classify discrete patches using three or more land cover classes (Bennett et al. 2006; Hansson et al. 1995). Regenerating landscapes can be represented using land cover classes based on vegetation successional status e.g. cleared, regrowth and intact (Figure 1). However, some reptile species have strong associations with vegetation types (Beck 1995; Lindenmayer et al. 2008; Wilson and Knowles 1988). Therefore, when studying reptiles, a mosaic landscape representation that defines patches based on vegetation type can be applied to landscapes where distinct boundaries occur between vegetation types. In this study, we applied a mosaic landscape representation based on successional status, as well as a mosaic landscape representation based on vegetation type (Figure 1).

For continuous landscape representations, landscapes are depicted as continuously varying in ecologically relevant variables such as the proportional cover of trees and bare earth, and distance to water (Fischer and Lindenmayer 2006). Here, land cover elements (e.g. tree and shrub cover) are mapped without reference to patches (McGarigal et al. 2009). At the site scale, reptiles are known to be influenced by the amount of canopy cover, grass cover, and bare earth (Pianka and Pianka 1976; Pike et al. 2011b; Price et al. 2010), and these are land cover variables that can be mapped across landscapes using current remote sensing technology (Levin and Heimowitz 2012). Therefore, for this study, we mapped our regenerating landscape as continuously varying in the proportional cover of woody vegetation (trees and shrubs), grass, and bare soil (Figure 1). We used these variables to create two continuous landscape representations to derive landscape context predictor variables: one displaying tree & grass cover, and the other displaying grass & bare earth cover.

2.2 Study area & survey sites

Our study site was located in a semi-arid woodland reserve of approximately 25 000 hectares, in southern Queensland, Australia (Figure 2, approximately 27.5ºS, 148.5ºE). Sections of this privately-owned reserve were historically cleared to promote pasture for stock grazing prior to the land being allocated to conservation. Vegetation on the reserve consists of a mosaic of *Eucalyptus*- and *Acacia*-dominated woodlands, in three distinct vegetation stages: cleared (induced grasslands), woody regrowth (10-23 years old), and intact woodlands (see Table 1 and below for definitions and details). Reptile community surveys were completed at fifty-five cleared, regrowth and intact survey sites, located > 1 km apart (Figure 2). Sampling effort was equal for all sites. Survey sites were selected using a stratified-random sampling design to ensure that all of the major vegetation types and vegetation status classes were surveyed (see Appendix A for survey site breakdown) and the composition of the landscape surrounding the survey sites varied (Table 1, Appendix A).
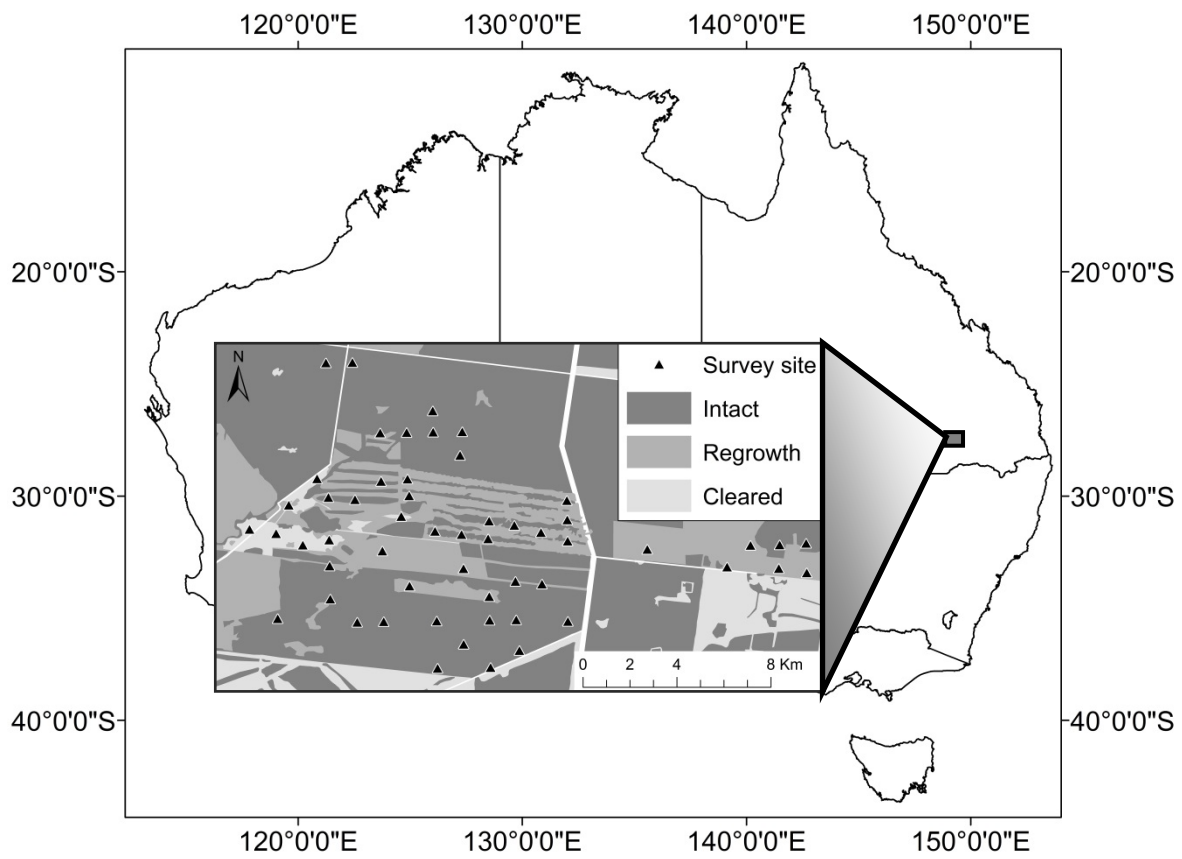
Figure 2: Study site location in southern Queensland, Australia; with the layout of the survey sites. Here, the landscape is depicted using a coarse mosaic landscape representation based on woodland clearing status, with large polygons derived from Queensland Government Regional Ecosystem mapping and aerial photography.

Table 1: Land cover classifications and their proportional cover within a 500 m radius of the survey sites.

Land cover category	Conceptualisation	Details	Mapping method[1]	Min.	Mean	Max.
Intact	Binary, mosaic	Pixels with no record of historical clearing[2]	Supervised classification	1	61	100
Regrowth	Binary, mosaic	Pixels historically cleared, with naturally regenerating woodlands of age 10-23yrs[2], and approximately half the canopy height of intact woodlands	Supervised classification	0	31	99
Clear/grassland	Binary, mosaic	Pixels historically cleared to create and maintain stock pastures, with no woodland regrowth present[2]	Supervised classification	0	5	61
Bare	Mosaic	Pixels dominated by bare soil	Supervised classification	0	2	24
Acacia	Mosaic	*Acacia*-dominated pixels	Supervised classification	1	52	95
Eucalyptus	Mosaic	*Eucalyptus*-dominated pixels	Supervised classification	5	40	95
Woody vegetation cover	Continuous	% cover of woody vegetation in each pixel	Multi-season NDVI	7	47	75
Grass cover	Continuous	% cover of grassy vegetation in each pixel	Multi-season NDVI	25	50	91
Bare earth	Continuous	% cover of bare earth in each pixel	Multi-season NDVI	0	3	18

[1]See sections 2.4 and 2.5 for mapping details

[2]Historically cleared areas were identified using a series of five photo mosaics of the study area from 1953-2006.

The reptile community at each of the fifty-five sites was surveyed using pit and funnel traps, as described in Bruton et al. (2013). Three rounds of four-day surveys were completed at each site between October 2010 and April 2012 (total = 2640 pit trap nights, 2640 funnel trap nights). To minimise weather biases (Spence-Bailey et al. 2010), sites within different land cover categories (Appendix A) were surveyed simultaneously in groups of seven or eight, and the group compositions were changed for each of the three separate survey rounds. Further detail on the reptile survey protocol is available in Bruton et al. (2013).

2.3 Mapping the study site

We used five sources of remotely sensed information to derive land cover maps for our study area: i) a Regional Ecosystem (RE) map layer (Queensland Government 2006a) to identify intact (remnant) and disturbed (non-remnant) patches; ii) a series of five orthorectified and mosaicked aerial photographs of the study area from 1953-2006 (Department of Natural Resources and Mines, Queensland Government) to identify regrowth patches; iii) a pre-clearing regional ecosystem (RE) map layer (Queensland Government 2006b) to identify the vegetation type in regrowth patches; iv) a series of four Landsat-5 satellite images from the U.S. Geological Survey (www.usgs.gov) to derive within-pixel proportional cover of woody vegetation, grass, and bare earth (Levin and Heimowitz 2012), and to create a land cover class raster map for analyses; and v) a high spatial resolution SPOT-6 satellite image (10th April 2013; resolution = 1.5m) to calibrate Landsat-derived NDVI values with vegetation cover.

The Regional Ecosystem map layers provided by the Queensland Government define remnant (intact) areas as follows: i) cover more than 50% of the undisturbed canopy, ii) average more than 70% of the undisturbed height, and iii) contain species characteristic of the undisturbed canopy (Neldner et al. 2012). Old regrowth areas that meet these criteria are classified as remnant on these maps. At the study site, 'remnant' areas constitute large continuous tracts of vegetation rather than residual pockets of vegetation in an otherwise disturbed landscape. Therefore, to more accurately describe these areas in this study, we re-named areas classed as 'remnant' to 'intact'.

2.4 Deriving continuous land cover maps

We conceptualised the landscape as continuously varying in the proportional cover of woody vegetation, grass, and bare earth. Using the method of Levin and Heimowitz (2012), we quantified the proportional cover of these land cover classes in every 30 m x 30 m Landsat-5 pixel across the study area. Land cover values were derived using Landsat-5 imagery from 21 January 2011, 27 April 2011, 17 August 2011, and 18 September 2011. The January and April images represent periods of maximum green-ness of ground vegetation ('wet'), and the August and September images represent periods of minimum green-ness of ground vegetation ('dry'). The dates of the Landsat-5 images were selected by taking into account seasonal and annual rainfall patterns, cloud cover, and coincidence with the reptile surveys for this study.

The four Landsat-5 images were atmospherically corrected using the Quick Atmospheric Correction tool in ENVI version 5.0 (Exelis Visual Information Solutions, Boulder, Colorado) and the NDVI value, a measure of vegetation green-ness (Tucker 1979), was derived for each pixel in each image. To calibrate the NDVI values with vegetation cover for the two wet season images, 10 regions of interest (ROI) with 0 % vegetation cover, and 35 ROI with 100% woody vegetation cover (*Eucalyptus*-dominated, *Acacia*-dominated, and mixed woody vegetation) were visually identified using the Spot-6 satellite image and aerial photographs. Using these ROI, the NDVI values < 0.07 and > 0.41 defined 0% and 100% woody vegetation cover respectively for the January image, and NDVI values of < 0.11 and > 0.49 defined these values for the April image (Levin and Heimowitz 2012). A unique linear calibration was used to derive vegetation cover values between 0 and 100% for each image.

For the two dry season Landsat-5 images, the NDVI green-ness values were calibrated with vegetation cover using field surveys. Tree cover and shrub cover were measured at each of the 55 survey sites using the line-intersect method in January 2011. The resulting correlation between surveyed woody vegetation cover (tree + shrub cover) and NDVI was satisfactory for both dry season images ($R^2_{(August)} = 0.63$, $p < 0.001$; $R^2_{(September)} = 0.61$, $p < 0.001$). Using the derived zero-intercept linear equation for each dry season image, the NDVI values were converted to woody vegetation cover scores, with a minor correction where pixels with NDVI values >0.96 (August image) and >0.79 (September image) were considered to have 100% woody vegetation cover.

The calibrated vegetation cover scores from all four Landsat-5 images (2x wet, 2x dry) were used to calculate the proportional cover of woody vegetation (perennial), grass (seasonal), and bare earth for each 30 m x 30 m Landsat-5 pixel following the method of Levin and Heimowitz (2012). This method uses the maximum and minimum vegetation cover score for each pixel from all four images to allocate proportional land cover for each pixel. We used this Landsat-derived continuous land cover map to develop relevant continuous landscape representations for our analyses (Table 2).

2.5 Deriving discrete land cover classification maps

For our discrete landscape maps, we classified each 30 m x 30 m Landsat-pixel in the study area 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). To classify each pixel, we used the Support Vector Machine supervised classification method (Hsu et al. 2010; Moses and Holland 2010) in ENVI. We selected 50 land cover regions of interest (ROI) to train the classification using all bands from the January ('wet') and September ('dry') Landsat images, and our Landsat-derived vegetation cover map. We selected the ROI based on a composite land cover polygon map created using a Regional Ecosystem (Queensland Government 2006a) vegetation type map layer, a pre-clearing vegetation type (Queensland Government 2006b) map layer, and a regrowth polygon layer that we developed from a series of aerial photographs that were dated from 1953-2006.

For this composite map, we classified polygons from the Regional Ecosystem and pre-clearing vegetation type layers with dominant classes 11.7.2, 6.5.1, and 11.4.2 as *Acacia*-dominated woodlands, and polygons with dominant class 11.5.13 as *Eucalyptus*-dominated woodlands (Sattler and Williams 1999).

Table 2: Description of the landscape composition and landscape heterogeneity predictor variables for each of six landscape representations (2 x binary, 2 x mosaic, and 2 x continuous). Each predictor variable was quantified within 100m, 250m, and 500m of each survey site.

Conceptualisation	Variable code[1]	Description
Binary	Intact (c)	Proportion of intact vegetation
Binary	Intact (h)	Shannon's diversity of intact and disturbed vegetation patches
Binary	Wooded (c)	Proportion of wooded (intact & regrowth) vegetation
Binary	Wooded (h)	Shannon's diversity of wooded patches and patches that are clear of woody vegetation
Mosaic	Status (c)	Proportion of regrowth woodlands
Mosaic	Status (h)	Shannon's diversity of intact, regrowth and cleared patches
Mosaic	Type (c)	Proportion of *Eucalyptus*-dominated woodlands
Mosaic	Type (h)	Shannon's diversity of *Eucalyptus, Acacia*, & grassland patches
Continuous	Woody (c)	Mean proportion of woody vegetation cover
Continuous	Woody (h)	Coefficient of variation of woody and grassy vegetation cover
Continuous	Bare (c)	Mean proportion of bare land cover
Continuous	Bare (h)	Coefficient of variation of grassy and bare land cover

[1] c = landscape composition, h = landscape heterogeneity (non-configurational)

We assessed the accuracy of our Landsat-derived land cover classes map against a rasterised version of our Regional Ecosystem-derived composite land cover polygon map (Figure 3). We used confusion matrices (Boser et al. 1992) to calculate the overall agreement between the two maps (71%). In addition, we calculated the Kappa Index of agreement (Cohen 1960; Hoechstetter et al. 2011), which expresses the proportion of correct classification above the expected correct proportion due to chance ($\kappa = 0.57$). We used a polygon version of the Landsat-derived land cover classification map to create four discrete (2x binary and 2x mosaic) landscape representations (maps) for deriving landscape context variables for our models (Figure 1).
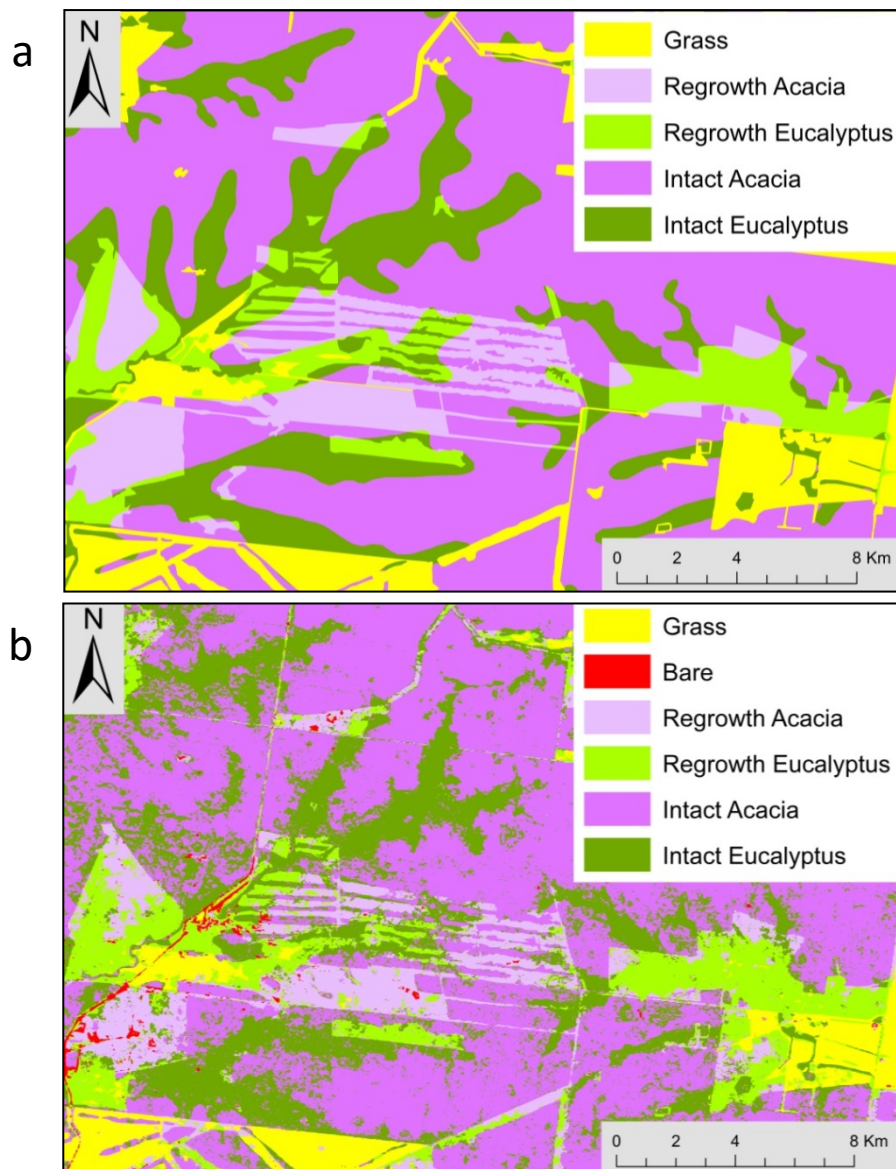
Figure 3: a) Composite land cover class polygon map of the study site, derived from Regional Ecosystem map layers and historical photos. b) Land cover class raster map of the study site, derived from Support Vector Machine classification of Landsat-5 images.

2.6 Deriving landscape context predictor variables

We used six landscape representations (2 x binary, 2 x mosaic, and 2 x continuous; Figure 1) to derive six landscape context variables for each reptile response variable (Table 2). For consistency in scale and resolution among the landscape conceptualisations, all of our landscape maps were prepared using Landsat-5 images with a resolution of 0.09 ha (30 m x 30 m). For each landscape representation, which corresponded to a landscape model, we quantified landscape structure surrounding each of the reptile survey sites (landscape context) at three buffer distances: 100 m, 250 m and 500 m.

When selecting variables and the scale for landscape context analyses, it is important to consider the ecology of the study species (With 1994). We used 100 m, 250 m, and 500 m buffers based on the limited reptile movement information available: a) recaptures at survey grids suggest that dryland geckoes and skinks have home ranges of less than 100 linear metres (Fitch 1955; Read 1998), b) iguanids, which are ecologically and morphologically similar to agamids, move approximately 150 m per day (Stark et al. 2005), and c) large reptiles such as varanids and snakes can move up to an average of 350 m per day (Guarino 2002). Thermal and moisture gradients can be important landscape variables for reptiles in wet and topographically variable environments (e.g. Fischer et al. 2004a). However, here we assessed reptile distributions in a flat, dryland landscape. Thermal and moisture gradients vary little in these landscapes, with the variation in these factors being correlated with variation in the amount of cover provided by vegetation and fallen timber.

We quantified the composition and heterogeneity of the surrounding landscape to derive two landscape context predictor variables for each of the six landscape models (Table 2). We measured landscape heterogeneity because reptile species vary in their habitat requirements, with more compositionally heterogeneous landscapes potentially providing greater access to suitable habitat for more species (Fischer et al. 2004a; Leyequien et al. 2007; Price et al. 2010). For simplicity and relevance to reptiles, in this study we focused on landscape composition, rather than landscape configuration, as this was considered to be more relevant to reptiles. Therefore we used the Shannon's diversity index to measure heterogeneity for the discrete landscape models (Fahrig et al. 2011), and the coefficient of variation to measure landscape heterogeneity for the continuous landscape models (Table 2).

The proportion of intact and regrowth vegetation surrounding the survey sites were highly correlated at all three buffer distances (R^2 = 0.86 to 0.87). Therefore, we selected the proportion of regrowth in the landscape to denote the mosaic landscape representation of vegetation 'Status' (Table 2). Similarly, the proportion of *Eucalyptus*-dominated and *Acacia*-dominated woodlands (a mosaic landscape conceptualisation), and the proportion of woody and grassy vegetation (a continuous landscape conceptualisation) surrounding the survey sites were highly correlated (R^2 = 0.86 to 0.87, and R^2 = 0.76 to 0.96 respectively). Therefore, we selected the proportion of *Eucalyptus* 'Type', and the mean proportion of woody vegetation in the surrounding landscape 'Woody' for these landscape representations (Table 2). For direct comparison of the effect sizes in the statistical analyses, all the landscape variables were standardised to mean = 0 and standard deviation = 1.

2.7 Analyses

We assessed two reptile community-level response variables (abundance and species richness), and the distribution of 11 lower-level taxa. Due to data constraints, we restricted the latter to the 10 reptile species that were present at more than 1/3 of the survey sites, and one morphological-group. The reptile species assessed were three terrestrial geckos *Heteronotia binoei, Diplodactylus vittatus,* and *Lucasium steindachneri*; five terrestrial

skinks *Morethia boulengeri, Eremiascincus richardsonii, Lygisaurus foliorum, Ctenotus ingrami,* and *C. robustus*; one arboreal skink *Egernia striolata*; and one semi-arboreal agamid (dragon) *Amphibolurus burnsi*. No varanid (goanna), pygopodid (legless lizard), or snake species were surveyed at a sufficient number of sites for species-level analyses; however, due to similarities in morphology, we pooled all the snake records to create a group called 'snakes' (Lindenmayer and Likens 2009).

We assessed the distribution of the ten reptile species, and the group 'snakes', using binomial generalised linear models. To determine if a Poisson distribution was appropriate for community-level species richness and abundance analyses, or if a dispersion parameter was required (Ismail and Jemain 2007), we used the maximum log-likelihood odTest from the "pscl" package (Jackman 2013) in the statistical program R (R Core Team 2014). A Poisson distribution was appropriate for species richness; however, an additional dispersion parameter (negative binomial model structure) was required in models of reptile abundance. Binomial and Poisson models were developed using the base instalment of R, and the negative binomial models were developed using the "pscl" package.

For each of the reptile response variables, we used a comparative information-theoretic approach (Anderson 2008; Burnham and Anderson 2002) to compare the relative fit of eighteen generalised linear models: one model for each of the six landscape representations (2 x binary, 2 x mosaic, 2 x continuous, Table 2) at each of the three buffer distances (100 m, 250 m and 500 m). Each model contained a landscape composition predictor variable and a landscape heterogeneity predictor variable from the same landscape representation (Table 2). The models were fitted using log-likelihood estimation and the relative support for each of the 18 models in the candidate model set was assessed using Akaike weights (ω) derived from the log-likelihood score (Burnham and Anderson 2002; Burnham et al. 2011).

For each reptile response variable, we used multi-model inference, based on the sum of the model Akaike weights (Σ_ω), to derive the relative (proportional) support for each landscape representation (e.g. intact/disturbed, veg type, tree/grass cover) and conceptualisation (binary, mosaic or continuous) across buffer distances (Burnham and Anderson 2002). To assess the effect of landscape scale on each reptile response variable, we calculated the sum of the model Akaike weights (Σ_ω) for each buffer distance. To assess the effect of the index used to quantify the landscape (composition or heterogeneity) on each reptile response variable, we used a model averaging approach (Burnham and Anderson 2002) to compare the mean absolute values of the landscape composition and heterogeneity coefficients ($\mu[abs(\beta)]$) for all the models in the candidate set.

3. Results

Reptiles varied in the way they responded to landscape context in regenerating landscapes, with no single landscape conceptualisation dominating (mean Σ_ω (binary) = 0.42, mean Σ_ω (mosaic) = 0.29, Σ_ω (continuous) = 0.29; see Table 3). We found there was little support for the mosaic landscape representation with patches classed by vegetation succession status (Σ_ω (status): mean = 0.09, max = 0.19, Table 3). In contrast, the alternative mosaic landscape representation, where patches were classed by vegetation type, had higher overall support (mean $\Sigma_{\omega(type)}$ = 0.20) and was the best supported landscape representation for the abundance of reptiles (Σ_ω (type) = 0.42), and for the distribution of the terrestrial skink *Lygisaurus foliorum* (Σ_ω (type) = 0.77, Table 3). Although the binary landscape representation 'Intact' had the highest level of overall support (mean Σ_ω (intact) = 0.26), this level of support was not considerably higher than for the other five landscape representations (mean Σ_ω = 0.20, 0.17, 0.16, 0.12 & 0.09, Table 3).

At the community level, reptile species richness and abundance were best described by different landscape representations and conceptualisations, with species richness best described by the binary landscape representation 'Wooded' (wooded vs. clear), and reptile abundance best described by the mosaic landscape representation 'Type', where patches were classed by dominant vegetation type (Table 3). At the species level, the distributions of the semi-arboreal agamid *Amphibolurus burnsi,* the terrestrial skinks *Lygisaurus foliorum, Ctenotus robustus,* and *Morethia boulengeri* and the terrestrial gecko *Diplodactylus vittatus,* were best explained by landscape context variables derived from a single landscape conceptualisation, with the best representation varying among species (see Table 3). In contrast, the weight of evidence was spread evenly across the three landscape conceptualisations (binary, mosaic and continuous) for the terrestrial geckos *Heteronotia binoei* and *Lucasium steindachneri*, the terrestrial skink *Ctenotus ingrami*, the arboreal skink *Egernia striolata*, and the group 'snakes' (Table 3). There was little indication that reptile species life history (terrestrial, semi-arboreal, arboreal) or phylogeny (skink, gecko, agamid) correlated with the best-fit landscape conceptualisations or representations (Table 3).

Overall, the scale of landscape measurement had minimal impact on our findings (Table 4, Figure 4). However, three reptile species responded strongly to landscape models from a single buffer distance ($\Sigma_\omega > 0.5$): *Amphibolurus burnsi* ($\Sigma_{\omega(100m)}$ = 0.65), *Ctenotus robustus* (Σ_ω (250m) = 0.55), and *Morethia boulengeri* (Σ_ω (500m) = 0.55; Table 4).

Table 3: The relative support (sum of model Akaike weights: Σ_ω) for each landscape conceptualisation (binary, mosaic & continuous) and each landscape representation (intact, wooded etc.), across scales. Bold text highlights the strongest weight of evidence (highest Σ_ω) for each reptile group.

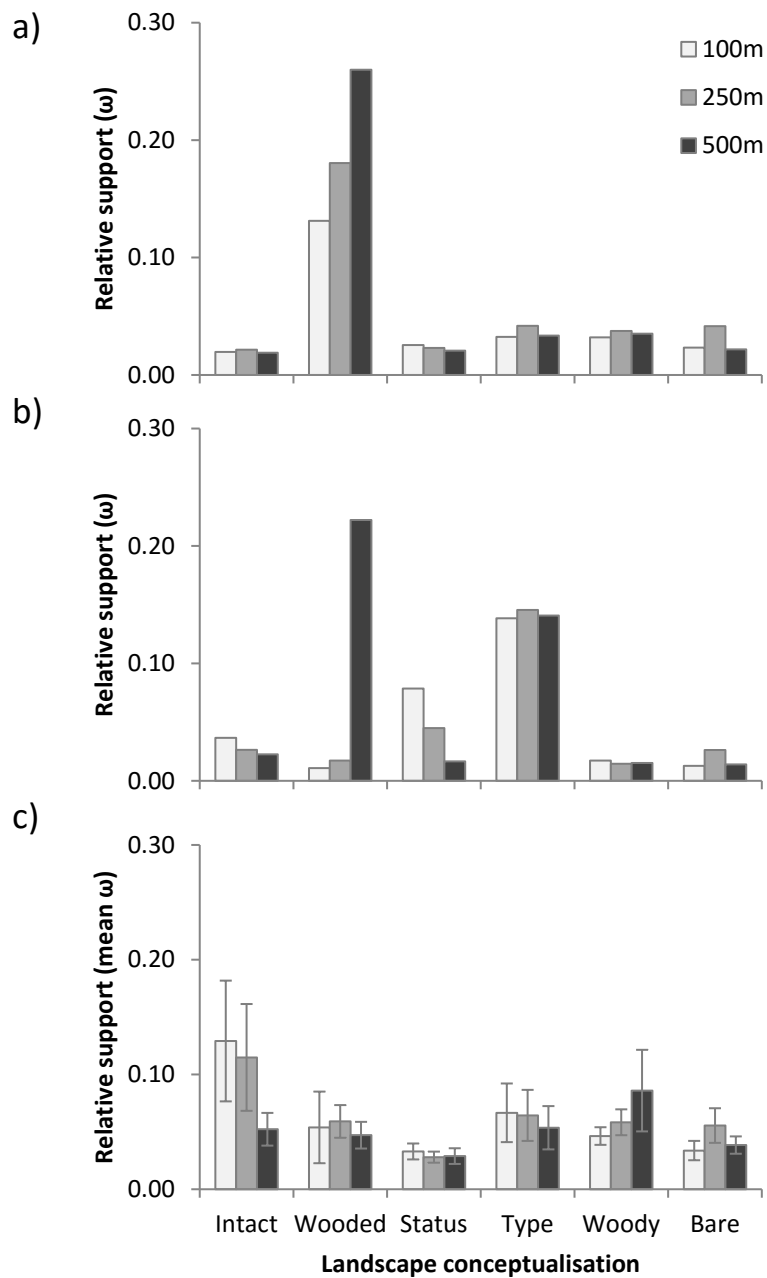|	Landscape conceptualisation			Landscape representation					
				Binary		*Mosaic*		*Continuous*	
Response[1]	*Binary*	*Mosaic*	*Continuous*	Intact	Wooded	Status	Type	Woody	Bare
Richness	**0.63**	0.18	0.19	0.06	**0.57**	0.07	0.11	0.10	0.09
Abundance	0.34	**0.56**	0.10	0.09	0.25	0.14	**0.42**	0.05	0.05
Amphibolurus burnsi (ag)	**0.96**	0.03	0.02	**0.95**	0.01	0.02	0.00	0.02	0.00
Lygisaurus foliorum (sk)	0.06	**0.82**	0.12	0.04	0.03	0.04	**0.77**	0.08	0.04
Ctenotus robustus (sk)	**0.84**	0.03	0.13	**0.76**	0.09	0.03	0.00	0.13	0.00
Morethia boulengeri (sk)	0.08	0.09	**0.83**	0.04	0.04	0.05	0.04	**0.66**	0.17
Diplodactylus vittatus (g)	**0.62**	0.15	0.23	**0.62**	0.00	0.10	0.05	0.18	0.05
Heteronotia binoei (g)	**0.44**	0.21	0.36	0.10	**0.33**	0.07	0.13	0.17	0.19
Ctenotus ingrami (sk)	0.23	**0.40**	0.37	0.09	0.14	0.11	**0.29**	0.18	0.20
Eremiascincus richardsonii (sk)	0.14	**0.45**	0.41	0.14	0.00	0.19	0.26	0.14	**0.27**
Egernia striolata (as)	**0.39**	0.30	0.30	**0.27**	0.12	0.09	0.21	0.17	0.13
Snakes	**0.37**	0.26	**0.37**	0.12	**0.25**	0.14	0.12	**0.25**	0.12
Lucasium steindachneri (g)	0.34	0.29	**0.36**	0.12	0.22	0.15	0.14	0.13	**0.23**
Mean (Σ_ω) :	*0.42*	*0.29*	*0.29*	*0.26*	*0.16*	*0.09*	*0.20*	*0.17*	*0.12*

[1] g = gecko (all terrestrial), ag = agamid (semi-arboreal), sk = terrestrial skink, as = arboreal skink

The composition of the landscape was a more useful measure of landscape context than landscape heterogeneity for reptiles in regenerating landscapes ($\mu[abs(\beta)]_{(composition)}$ = 0.71, $\mu[abs(\beta)]_{(heterogeneity)}$ = 0.40; Table 4); however, landscape heterogeneity was more relevant for one reptile species: the terrestrial skink *Lygisaurus foliorum* ($\mu[abs(\beta)]_{(het.)}$ = 0.41, $\mu[abs(\beta)]_{(comp.)}$ = 0.36). Landscape composition and landscape heterogeneity were equally relevant to the terrestrial skink *Morethia boulengeri* ($\mu[abs(\beta)]_{(het.)}$ = 0.65, $\mu[abs(\beta)]_{(comp.)}$ = 0.66; Table 4).

Table 4: The importance of scale and the landscape measure used to assess the perception of landscape context by reptiles. Scale was assessed using relative support for each of three buffer distances, based on the sum of model Akaike weights (Σ_ω). The effects of landscape composition and landscape heterogeneity (non-configurational) were compared using the mean absolute value of β ($\mu[abs(\beta)]$)). Bold text highlights the strongest influence (highest value) for each reptile group.

Response	Scale (Σ_ω)			Landscape measure ($\mu[abs(\beta)]$)	
	100m	250m	500m	Composition	Heterogeneity
Abundance	0.29	0.27	**0.43**	**0.11**	0.06
Richness	0.26	0.35	**0.39**	**0.09**	0.05
Amphibolurus burnsi	**0.61**	0.37	0.03	**1.82**	0.81
Ctenotus robustus	0.21	**0.55**	0.23	**1.36**	0.48
Morethia boulengeri	0.17	0.28	**0.55**	**0.66**	**0.65**
Heteronotia binoei	**0.46**	0.26	0.28	**0.71**	0.33
Ctenotus ingrami	0.26	**0.45**	0.29	**0.93**	0.60
Diplodactylus vittatus	**0.40**	0.29	0.31	**1.07**	0.47
Lucasium steindachneri	0.25	**0.39**	0.36	**0.68**	0.54
Eremiascincus richardsonii	0.34	**0.39**	0.27	**0.26**	0.19
Egernia striolata	**0.36**	0.32	0.32	**0.73**	0.33
Lygisaurus foliorum	**0.36**	0.34	0.30	0.36	**0.41**
Snakes	0.31	**0.35**	0.34	**0.50**	0.23
Mean:	*0.33*	*0.36*	*0.32*	*0.71*	*0.40*

Figure 4: The relative support (ω) for each landscape conceptualisation at three buffer distances: a) reptile species richness, b) reptile abundance, and c) the mean Akaike weight (μ ω) for the ten individual reptile species and the group 'snakes'. Error bars are standard error.

4. Discussion

Lindenmayer et al. (2007) asked the question: 'In which situations is a patch model appropriate, and in which situations does a continuum model or some other kind of conceptual landscape model work better?' Our study is the first to empirically answer this question in regenerating landscapes, by testing the relative support for discrete (patch) and continuous conceptualisations of landscape context for reptiles. We found that no single landscape conceptualisation (binary, mosaic, or continuous) or representation (e.g. intact/disturbed, veg type, tree/grass cover) consistently outperformed the others, with the landscape conceptualisation and representation that was best supported varying among reptile groups (Table 3). These findings support the use of pluralistic models that use variables derived from multiple landscape conceptualisations and representations to analyse the distribution of fauna across regenerating landscapes.

We hypothesised that continuous landscape conceptualisation would have some power (mean $\Sigma\omega_{(continuous)} > 0.2$) in explaining the distribution of fauna in regenerating landscapes, due to within-patch variation in vegetation cover (Bowen et al. 2007). This hypothesis was supported for 6 of the 9 reptile species assessed, but there was limited support for continuous landscape representations at the community level (Table 3). In this study, each of the continuous landscape models compared the distribution of reptiles with the cover of just two habitat features in the surrounding landscape: trees and grass, and grass and bare earth. The richness and overall abundance of fauna communities are driven by resource heterogeneity (Tews et al. 2004); however, individual habitat features such as grass clumps and trees are limited in their capacity to provide a heterogeneous mix of habitat resources. In contrast, resource heterogeneity varies markedly with vegetation clearing status (Newsome et al. 2013; Pike et al. 2011a) and vegetation type (Kitchener et al. 1988; van Jaarsveld et al. 1998). This may explain the minimal community-level response to continuous landscape representations observed in our study, and a stronger response to discrete landscape context representations.

In regenerating landscapes, the assessment of fauna distributions is dominated by community-level analyses (Bowen et al. 2007). However, our study clearly demonstrated that reptile communities and reptile species differed markedly in their response to conceptualisations of landscape context. For example, we found that there was little support at the community-level for the binary landscape context representation 'intact/disturbed', which best explained the distribution of three of our study species (Table 3). The alternative binary landscape context representation 'wooded/clear' best explained species richness (a community-level measure) with little support for this representation at the species level (Table 3). Similarly, the models derived from continuous landscape representations were unimportant for reptiles at the community-level, but this was the most important landscape conceptualisation for the terrestrial skink *Morethia boulengeri* (Table 3). These findings highlight the variation among responses by fauna at different taxonomic levels (Sarre 1998),

and the need to consider multiple taxonomic groupings during conservation planning (Wall and Shine 2013) and the evaluation of alternative land management options.

Fischer et al. (2004a) and Price et al. (2010) both demonstrated that the conceptualisation that best reflects how reptiles respond to the surrounding landscape varies among species and the landscape of interest. This finding was supported by our study, with three species strongly supported by a binary landscape representation, one species by a mosaic landscape representation, and one species by the continuous landscape representations (Table 3). However, several of our study species showed little bias towards any of the six landscape representations, which suggests that site-level attributes may be more important to the distribution of these species (Price et al. 2009). In addition, neither life history attributes nor phylogenetic lineage appear to be linked to landscape conceptualisation (Table 3); a finding also observed in a fire-affected landscape (Lindenmayer et al. 2008) and a savanna landscape (Price et al. 2010). These results make predictions and generalisations about the perception of landscape context problematic for reptile species, and encourage further exploration of potential criteria for grouping reptiles into relevant functional groups or guilds for landscape change studies (Lindenmayer and Likens 2009). Until such research is undertaken, we support the use of pluralistic linear models that incorporate variables derived from multiple landscape conceptualisations and representations, at multiple scales, when analysing the distribution of reptiles across landscapes (sensu Lindenmayer et al. 2007; Price et al. 2009).

4.1 Quantifying the landscape for reptiles

The capacity of remote sensing to map and monitor landscapes has revolutionised landscape ecology (Nagendra et al. 2013; Yang et al. 2013). New image processing techniques allow the definition and quantification of landscape features as small as 5 m^2 (Recio et al. 2013). However, the resources that are regularly used by reptiles, such as fallen timber and underground burrows, are smaller than this, and unable to be mapped using existing remote sensing techniques. With the launch of the WorldView 3 satellite in August 2014 (www.digitalglobe.com /about-us/content-collection), which has a panchromatic resolution of 0.31 m and 8 short-wave infrared bands at a spatial resolution of 3.7 m, there is now a better potential to map the distribution and percentage cover of shelter resources, such as fallen timber and hollow logs, across landscapes. The amount and distribution of these structural features in the landscape are likely to be more relevant to reptile distributions than vegetation measures. As such, we advocate this high-resolution landscape mapping as a growth area for understanding the distribution of reptiles at the landscape scale.

The landscape context measure (composition or heterogeneity) used during the assessment of species distributions can affect the quality of information that is fed into land management decision analyses (Fischer and Lindenmayer 2007). We found that landscape composition is generally a more useful measure of landscape context for reptiles than non-configurational landscape heterogeneity. In savanna landscapes, Price et al. (2010) also found

that landscape composition is a more useful measure of landscape context for reptiles than landscape heterogeneity. We found only one other study that assessed the effect of heterogeneity in the surrounding landscape on reptiles. That study concluded that forest age heterogeneity within 250 m of regenerating moist oak and pine forest landscapes had a positive influence on species richness (Loehle et al. 2005). However, that study did not compare the relative influences of landscape heterogeneity and landscape composition on reptiles. Therefore, it appears that landscape composition is likely to be more important to reptiles than non-configurational landscape heterogeneity. However, there was a clear exception to this generalisation in our study (*Lygisaurus foliorum*, Table 4), and more comparative research is needed in other biomes before generalisations can be made.

4.2 Conclusion

Our study supports the use of variables from multiple discrete and continuous landscape conceptualisations when assessing the impact of the surrounding landscape on the distribution of fauna (Price et al. 2009). We demonstrated that continuous landscape conceptualisations can better reflect the way fauna perceive landscapes with distinct patch boundaries, than the more 'intuitive' discrete landscape conceptualisations. Therefore, we advocate for testing landscape context variables derived from continuous landscape conceptualisations during the assessment of fauna distributions in regenerating landscapes.

5. Acknowledgements

6. References

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Appendix A

Reptile survey site selection criteria and breakdown of the 55 sites selected for surveys. Cleared and regrowth *Acacia*-dominated sites were always structurally simple, whilst the regrowth and intact *Eucalyptus*-dominated sites were always structurally complex. Simple and complex sites were available in both continuous and fragmented intact *Acacia*-dominated woodlands.

Vegetation Type:	Cleared	*Acacia*–dominated (RE = 11.7.2, 11.7.2/6.5.1 & 6.5.1/11.7.2)		*Eucalyptus*-dominated (RE = 11.5.13 & 11.5.13/11.3.25)	
Vegetation status:	Cleared	Regrowth	Intact	Regrowth	Intact
Site complexity:	Simple (n=7)	Simple (n=7)	Simple / Complex	Complex (n=8)	Complex (n=8)
Site configuration:			Fragmented (n=5) / Continuous (n=6) / Continuous (n=7) / Fragmented (n=7)		