

Incorporating regional-scale ecological knowledge to improve the effectiveness of large-scale conservation programmes

G. M. Kay¹, P. S. Barton¹, D. A. Driscoll², S. A. Cunningham³, W. Blanchard¹, S. McIntyre^{1,3} & D. B. Lindenmayer¹

¹ Fenner School of Environment and Society, The Australian National University, Canberra, ACT, Australia

² School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University Geelong, Melbourne Burwood Campus, Burwood, VIC, Australia

³ CSIRO Sustainable Ecosystems, Black Mountain Laboratories, Canberra, ACT, Australia

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Correspondence

Geoffrey M. Kay, Fenner School of Environment and Society, The Australian National University, Canberra, ACT, Australia.
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Abstract

Land-stewardship programmes are a major focus of investment by governments for conserving biodiversity in agricultural landscapes. These programmes are generally large-scale (e.g. >1000 km) spanning multiple biogeographic regions but developed using spatially limited (e.g. landscape-scale; <100 km) ecological data interpolated across broad areas for one, or a few, well-studied taxonomic groups. Information about how less-studied taxa respond to regional differences in management and environmental effects has potential to further inform land-stewardship conservation programmes, but suitable data sets are rarely available. In this study, we sought to enhance planning of large-scale conservation programmes by quantifying relationships between reptile assemblages and key environmental attributes at regional scales within a large-scale (>172 000 km²) Australian land-stewardship programme. Using 234 remnant woodland monitoring sites spanning four distinct biogeographic regions, we asked: Do reptile assemblages show different environmental associations across biogeographically distinct regions? We found that environmental features important to reptile diversity differed over each region. Abundance and rare species richness of reptiles responded at regional-scales to elevation, native ground-cover and aspect. We identified four implications from our study: (1) large-scale conservation schemes can achieve better outcomes for reptiles using regional-scale knowledge of environmental associations; (2) regional-scale knowledge is particularly valuable for conservation of rare reptile taxa; (3) consideration of abiotic environmental features which cannot be directly managed (e.g. aspect, elevation) is important; (4) programmes can be tailored to better support reptile groups at higher conservation risk. Our study shows that reptile-environment associations differ among biogeographic regions, and this presents opportunity for tailoring stronger policy and management strategies for conserving large-scale agricultural landscapes globally.

Introduction

Agricultural expansion and intensification are major causes of biodiversity loss (Barnosky *et al.*, 2011). To address this, billions of dollars are committed by governments to large-scale land-stewardship conservation programmes targeting private-tenure agricultural landscapes (European Commission, 2014; USDA, 2014). While increasing the scope of these programmes is a global priority (e.g. UN Millennium Development Goals; IUCN, 2010), they remain founded on spatially limited ecological data interpolated across broad areas (Whittingham *et al.*, 2007; Gonthier *et al.*, 2014) and largely

focus on one, or a few, well-studied taxonomic groups (Lüscher *et al.*, 2014). An emerging challenge for conservation practitioners is to find ways to refine large-scale land-stewardship programmes, by incorporating high-resolution ecological information for an increasing range of taxa.

Species respond to environmental drivers and ecological processes at multiple spatial scales (Cushman & McGarigal, 2002), so an understanding of these issues is likely to improve effectiveness of large-scale conservation programmes. However, it can be difficult to implement large-scale programmes (i.e. across >1000 km) while accommodating complexity in fine-scale (i.e. 1–10 km) biological pat-

terns. Subsequently, land-stewardship programmes have generally focused only on a few management objectives across coarse scales. Exploring regional-scale (i.e. 10–100 km) habitat relationships, using regions defined by shared environmental condition (e.g. biogeographic regions) is likely to capture important patterns of response to habitats and management (Batáry *et al.*, 2011; Concepción *et al.*, 2012; Báldi, Batáry & Kleijn, 2013) and provides a possible balance between generality and finer resolution. The benefits of incorporating regional-scale criteria into conservation planning have recently been acknowledged for some beetles (Liu *et al.*, 2014) and birds (Whittingham *et al.*, 2007), but there are only a few studies, limited to European landscapes. Broadening our understanding of biodiversity responses in larger multi-regional contexts, and in other parts of the world, is therefore important.

Another challenge facing conservation managers is to develop conservation programmes based on a wide variety of taxa. Data for large-scale land-stewardship programmes are generally limited to a few well-studied groups like plants, birds and some invertebrates (for review see Whittingham, 2011; Batáry *et al.*, 2015). Ground-dependent reptiles have received considerably less attention (but see Michael *et al.*, 2014) despite representing one of the most diverse and rapidly declining vertebrate groups in agricultural landscapes globally (Böhm *et al.*, 2013). Further, reptiles have ecological requirements that are distinct from other vertebrate taxa, such as limited dispersal capacity and temperature-dependent activity (Guisan & Hofer, 2003; Schutz & Driscoll, 2008). Consequently, building on known ecological requirements of reptiles by incorporating regional-scale knowledge of environmental associations can enhance effectiveness of large-scale conservation programmes.

In this study, we examined habitat requirements for reptiles by studying their associations with a set of biotic and abiotic environmental variables, across multiple biogeographic regions, within the Australian Environmental Stewardship Programme (Commonwealth of Australia, 2009, 2013; Lindenmayer *et al.*, 2012). This topic is of particular conservation interest, given its relevance to the widely adopted and costly agri-environment schemes (*sensu* Kleijn & Sutherland, 2003). These schemes aim to promote biodiversity in farming landscapes, but despite billions of dollars of investment annually, their benefit remains undemonstrated for declining ground-dwelling vertebrates including reptiles (see Michael *et al.*, 2014). Our study is the first to examine spatial variation in habitat requirements for reptiles across a conservation programme of this scale, covering >172 000 km² (approximately the size of Uruguay). Using 234 remnant woodland monitoring sites across four distinct biogeographic regions (*sensu* Thackway & Cresswell, 1995; Commonwealth of Australia, 2014), we asked: Do reptile assemblages show different environmental associations across biogeographically distinct region? To answer this question, we examined different aspects of the reptile assemblages, including total abundance and species richness, as well as richness of rare species and relative abundance (evenness) of the assemblage. Because reptiles exhibit strong associations

with climate and geography (McCain, 2010; Kay *et al.*, 2013), we predicted that the relationships between environmental variables and measures of reptile diversity would vary across the regions observed, providing opportunity for improving design of land-stewardship programmes. Our results identify four key conservation implications for decision makers, underscoring opportunities to advance conservation programmes in the future.

Materials and methods

Study area

Our study is set within the critically endangered Box Gum Grassy Woodland ecological community targeted under the Environmental Stewardship Programme in south-eastern Australia (Lindenmayer *et al.*, 2012). This woodland community is characterized by an understorey of native tussock grasses, herbs and scattered shrubs, and an open tree strata that was originally dominated by white box *Eucalyptus albens*, yellow box *E. melliodora* and Blakely's red gum *E. blakelyi* (Commonwealth of Australia, 2013). Spanning > 1000 km north-to-south, this community has been reduced to <4% of its original extent due to clearing over the past 150 years (Lindenmayer, Bennett & Hobbs, 2010). The southern extent is particularly threatened by intensive agriculture (Hoekstra *et al.*, 2005) and now occurs as small and isolated remnants of varying condition (Commonwealth of Australia, 2013). The community also supports a rich woodland-dependent reptile fauna (Kay *et al.*, 2013), with over 120 species of reptiles recorded across the extent of the study area (Wilson & Swan, 2013).

Experimental design

We established 234 monitoring sites in remnant woodland on 152 farms (\leq two sites per farm) involved in the Programme (Fig. 1). These sites represent the highest quality woodland remnants remaining (see Fig. S1 for typical site). An implicit assumption from the outset of the Programme was that its effectiveness for biodiversity would be homogeneous across its spatial extent despite spanning a range of biogeographic and climatic boundaries known to influence ecological communities (Commonwealth of Australia, 2009). To test this, we grouped sites of similar climate, geology and landform by well-defined biogeographic regions (*sensu* Thackway & Cresswell, 1995) which have been used to define agro-climatic systems throughout our study area (Hutchinson *et al.*, 2005).

We first separated sites on the basis of broad agro-climatic system from Hutchinson *et al.* (2005): a winter-rainfall improved-pasture system and a low-rainfall native-pasture system. Within each agro-climatic system, we then grouped sites by clearly defined biogeographic regions (Commonwealth of Australia, 2014). Sites within the winter-rainfall system were thus separated into the elevated Southern Highlands region (61 sites) and the fertile Southern Slopes region (82 sites). Sites within the low-rainfall system were similarly

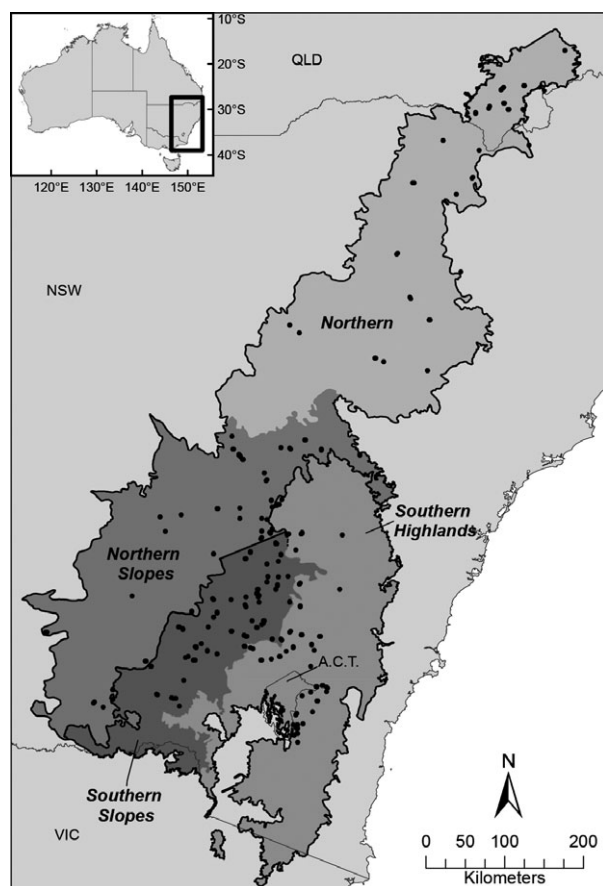


Figure 1 Location of the study area spanning New South Wales (NSW) and southern Queensland (QLD) of south-eastern Australia showing the location of monitoring sites ($n = 234$) surveyed across the four study regions (greyed fill) and two agro-climatic systems (black boundary).

separated into a Northern Slopes (53 sites) region and two smaller northern biogeographic regions that, due to limited sampling across both biogeographic regions, were combined to create a single Northern region (38 sites). Additional descriptions for the final set of four regions are provided as supporting information (Table S1).

Reptile surveys

We surveyed each site for reptiles three times (September 2010, February 2012 and September 2012) along a 200×40 m transect. We used a time- and area-constrained ($20 \text{ min} \times 0.8 \text{ ha}$) survey protocol (following Michael *et al.*, 2012), involving active searches of natural habitat and inspections of two artificial refuge arrays. Both arrays were placed 100 m apart and consisted of four concrete roof tiles ($32 \times 42 \text{ cm}$), one double-layered stack of corrugated galvanized steel and four wooden railway sleepers (1.2 m long).

We conducted surveys on clear days between 0900 and 1600 h with the same group of experienced field ecologists.

We identified species using Wilson & Swan (2013). Our analyses focussed on whole assemblages at site level, so we pooled observations within sites and across survey times to define a reptile assemblage at every site.

Measurement of environmental features

We measured a suite of environmental features relevant to conservation managers. We included variables commonly considered for management (e.g. vegetation characteristics) plus those likely to be important for reptiles but not influenced by management (e.g. topographic position, climate).

We surveyed vegetation at each site during February 2010 and 2012 and averaged data at the site level. We measured native plant species richness in a 20×20 m plot midway along the transect and recorded length of logs in two 50×20 m plots at the extreme ends of a transect. We estimated percentage cover of bare ground, organic litter, rock, overstorey and midstorey by recording these attributes every metre along two 50 m transects (for details see Michael *et al.*, 2014).

We obtained elevation and aspect for each site using nine-second resolution spatial data (Hutchinson, Stein & Stein, 2011). Large-scale geographic effects on species richness are known to occur for reptiles (Rodríguez, Belmontes & Hawkins, 2005; Brown, Dorrough & Ramsey, 2011) driven by latitudinal influences on ambient energy (temperature and solar radiation) and moisture-driven habitat gradients. Because our study area encompasses confounding latitudinal and rainfall gradients, we used a 'growth index' derived from ANUCLIM (Xu & Hutchinson, 2013) to combine the effect of temperature, moisture and daylight into one energy related variable (see Appendix S1 for details).

Statistical analysis

We used an information-theoretic approach (Burnham & Anderson, 2002) to test whether large-scale conservation programmes could be made more effective by incorporating regional-scale ecological knowledge of reptiles. We fitted generalized linear mixed models to examine the relationship between environmental variables and reptile diversity. Conservation programmes generally measure biodiversity success through change in overall richness or abundance over time (Batáry *et al.*, 2011) despite these being relatively crude measures (Morris *et al.*, 2014). Additionally, biodiversity success may be measured through a positive response in species of conservation concern (Cunningham *et al.*, 2014), as well as the relative abundance (evenness) of species, where greater evenness implies more robust populations (Magurran & McGill, 2011). Therefore, we used four measures of reptile diversity as our response variables, with higher values indicating improved outcome: (1) richness of all reptile species; (2) richness of rare reptile species (the number that occurred at $<5\%$ of all sites); (3) abundance of all reptile species, and (4) assemblage evenness (Shannon Evenness; Magurran & McGill, 2011). We used a Poisson distribution with a log link to model richness, rare species richness and overall abundance. For evenness, we used a Gaussian distri-

bution with an identity link. 'Farm' was fitted as a random effect in all models.

We reduced the number of potential explanatory variables for use in models by: (1) using features identified in previous studies of reptile ecological requirements (e.g. Brown *et al.*, 2011 and references within), as well as expert knowledge of experienced wildlife scientists, from within Australian temperate woodlands, and (2) eliminating highly correlated variables (examining pairwise scatterplots and correlation coefficients with $r > 0.5$ cutoff) (Zuur *et al.*, 2009). This gave a set of eight predictor variables useful for testing regional-scale habitat relationships for reptiles: growth index, aspect [scaled from +1 (northerly) to -1 (southerly)], elevation, richness of native groundcover, log cover (length), rock cover, bare ground cover, and native overstorey cover.

To test whether regional-scale information could enhance conservation programmes, we fitted region and the interaction of region with each of the eight predictor variables. To explore the correlative influence of region with the environment, we repeated our analysis with the environmental variables standardized within the region (i.e. the within-region mean subtracted from the values within that region). If the region was important in models only with standardized environmental variables, we inferred that regional differences are otherwise accounted for by environmental gradients across the whole study area. Conversely, if environmental variables are important only in models without standardization, it would imply that broad-scale regional differences drive changes in reptile diversity and within-region variation in these parameters is not important.

We used Akaike information criterion (Burnham & Anderson, 2002) to select top-ranked models and included all models within 2 units in our inference (Arnold, 2010). We checked for over-dispersion by dividing the Pearson goodness-of-fit statistic by the residual degrees of freedom and found no values greater than one suggesting that our data were not over-dispersed (McCullagh & Nelder, 1989). We inspected the residual vs. fitted plots of each model to confirm that residuals were approximately randomly distributed with respect to fitted values. We assumed sites on different farms were independent, and tested for spatial dependence in the residuals, using a Moran's I test (Cliff & Ord, 1981), finding no evidence of spatial autocorrelation. We undertook all analyses using the *MuMIn* package in R (Barton, 2009).

Results

We recorded 57 species of reptiles from ten families (Table S2). Species richness ranged from one to 10 species per site, with a decline in richness with increasing latitude (slope = -0.061 ± 0.018 , $P < 0.001$) corresponding to approximately one less species for every five degrees of latitude (Fig. S2). Species accumulation curves for each study region and the whole study area approached an asymptote (Fig. S3), ranging between 72.4 and 92.9% of the estimated true richness (Table S3).

The top-ranked model for species richness across the study area included a positive effect of growth index, log

cover, native groundcover richness and rock cover with lesser negative effects of elevation, native overstorey cover, and the northerly (sunlit) aspect (Table 1; Fig. 2). The region was included in the model although its effects were weak with no apparent interaction effect.

Rare species richness was explained across the study area by a positive effect of rock cover and, to a lesser extent, a negative effect of native overstorey cover (Table 1; Fig. 2). Rare species richness was negatively associated with elevation in the Southern Highlands and Northern Slopes regions, and positively in the remaining regions. An interactive effect of region also occurred with native groundcover richness, which was positively associated in all but the Northern region.

Reptile abundance was explained across the study area by a positive effect of rock cover and interactions of region with elevation, the northerly (sunlit) aspect and native groundcover richness (Table 1; Fig. 2). Reptile species evenness was explained across the study area by positive effects of growth index and, to a lesser extent, positive effects of rock cover and native groundcover richness and negative effects of elevation (Table 1; Fig. 2). There was no interaction effect of the region.

Standardizing predictor variables for all diversity measures revealed the same result, with evenness revealing an additional effect of region (Table S4), indicating environmental terms had similar effects at the within-region and between-region scales.

Discussion

We used an information-theoretic approach to assess how incorporating spatial variation in habitat requirements can assist large-scale conservation planning. Our study revealed that environmental features important in driving reptile diversity differed for each region. Critically, two of the four measures of reptile diversity responded at the regional-scale, in some cases reversing the direction of effect. Our work provides empirical support for incorporating regional-scale criteria into conservation planning, addressing an emerging need in conservation science (Lüscher *et al.*, 2015).

Biological interpretation of the models

To understand the appropriate regional-level conservation planning and management outcomes of this study, it is important to consider the mechanisms behind region-specific responses to environment by reptiles. We found two abiotic variables (elevation, aspect) and one biotic variable (native groundcover richness) were important drivers of abundance and rare species richness that varied in effect at the regional level (Fig. 2b). In two of the southern (colder) regions, lower elevation corresponded to lower numbers of reptiles and rare species, while in the warmer Northern and Northern Slopes regions the pattern was reversed. This is consistent with known thermoregulatory limits which reptiles experience at higher elevations (Fischer & Lindenmayer, 2005; McCain, 2010). In contradiction to this idea was the positive

Table 1 Summary of the best model for reptile diversity response (species richness, rare species richness, abundance, evenness) as predicted by eight environmental variables

Response	Model terms	Direction	Estimate	SE	F	P
Species richness	Reg + Rock + NGR + Gr_id + Asp_N + Elev + LogLth + NOS_cvr					
	(Intercept)		0.294	0.517	0.567	0.5705
	Reg(NS)	+	0.006	0.218	0.025	0.9798
	Reg(SH)	+	0.347	0.264	1.318	0.1876
	Reg(SS)	+	0.192	0.230	0.836	0.4029
	Rock	+	0.021	0.007	3.072	0.0021
	NGR	+	0.021	0.008	2.722	0.0065
	Gr_id	+	6.815	3.184	2.14	0.0323
	Asp_N	—	−0.106	0.058	−1.82	0.0686
	Elev	—	−0.001	3.17×10^{-04}	−2.01	0.0443
Rare species richness	Reg + Elev + Reg*Elev + Rock + NOS_cvr + Reg*NGR + NGR					
	(Intercept)		−0.161	0.840	−0.191	0.8482
	Reg(NS)	+	0.340	0.991	0.343	0.7315
	Reg(SH)	+	2.169	1.107	1.960	0.0500
	Reg(SS)	—	−0.811	0.936	−0.866	0.3862
	Rock	+	0.025	0.011	2.326	0.0200
	NOS_cvr	—	−0.005	0.003	−1.742	0.0815
	Elev	+	0.002	0.001	1.296	0.1951
	Reg(NS)*Elev	—	−0.003	0.002	−2.019	0.0435
	Reg(SH)*Elev	—	−0.004	0.002	−2.497	0.0125
	Reg(SS)*Elev	+	4.19×10^{-04}	0.001	0.280	0.7791
	NGR	—	−0.049	0.055	−0.889	0.3741
	Reg(NS)*NGR	+	0.119	0.061	1.949	0.0513
	Reg(SH)*NGR	+	0.068	0.057	1.190	0.2339
	Reg(SS)*NGR	+	0.085	0.059	1.452	0.1465
Abundance	Reg + Reg*NGR + NGR + Rock + Elev + Reg*Elev + Asp_N + Reg*Asp_N					
	(Intercept)		1.282	0.518	2.475	0.0133
	Reg(NS)	+	1.469	0.685	2.144	0.0320
	Reg(SH)	+	1.734	0.870	1.993	0.0462
	Reg(SS)	+	0.628	0.596	1.054	0.2918
	Rock	+	0.023	0.007	3.149	0.0016
	NGR	—	−0.025	0.027	−0.920	0.3575
	Reg(NS)*NGR	+	0.035	0.034	1.037	0.2998
	Reg(SH)*NGR	+	0.044	0.030	1.445	0.1484
	Reg(SS)*NGR	+	0.101	0.029	3.435	0.0006
	Elev	+	0.002	0.001	1.978	0.0480
	Reg(NS)*Elev	—	−0.005	0.001	−4.029	0.0001
	Reg(SH)*Elev	—	−0.004	0.001	−3.042	0.0023
	Reg(SS)*Elev	—	−0.004	0.001	−3.612	0.0003
	Asp_N	—	−0.347	0.150	−2.312	0.0208
	Reg(NS)*Asp_N	+	0.322	0.211	1.530	0.1260
	Reg(SH)*Asp_N	+	0.096	0.205	0.467	0.6402
	Reg(SS)*Asp_N	+	0.533	0.170	3.138	0.0017
Evenness	Rock + NGR + Elev + Gr_id					
	(Intercept)		0.477	0.116	4.124	0.0000
	Rock	+	0.009	0.005	1.890	0.0588
	NGR	+	0.007	0.004	1.587	0.1141
	Elev	—	$−2.25 \times 10^{-04}$	1.39×10^{-04}	−1.624	0.1044
	Gr_id	+	2.620	0.875	2.996	0.0027

The Northern Region is incorporated in the intercept as the reference category against which all regions, and their interactions, are measured. Unstandardized models are provided (these match the standardized models). Direction of response is given (sign).

Gr_id, growth index; Asp_N, northerly aspect; Elev, elevation; NGR, native groundcover richness; LogLth, length of log cover; Rock, rock cover; BG, bare ground cover; NOS_cvr, native overstorey cover; Reg, plus interaction with region.

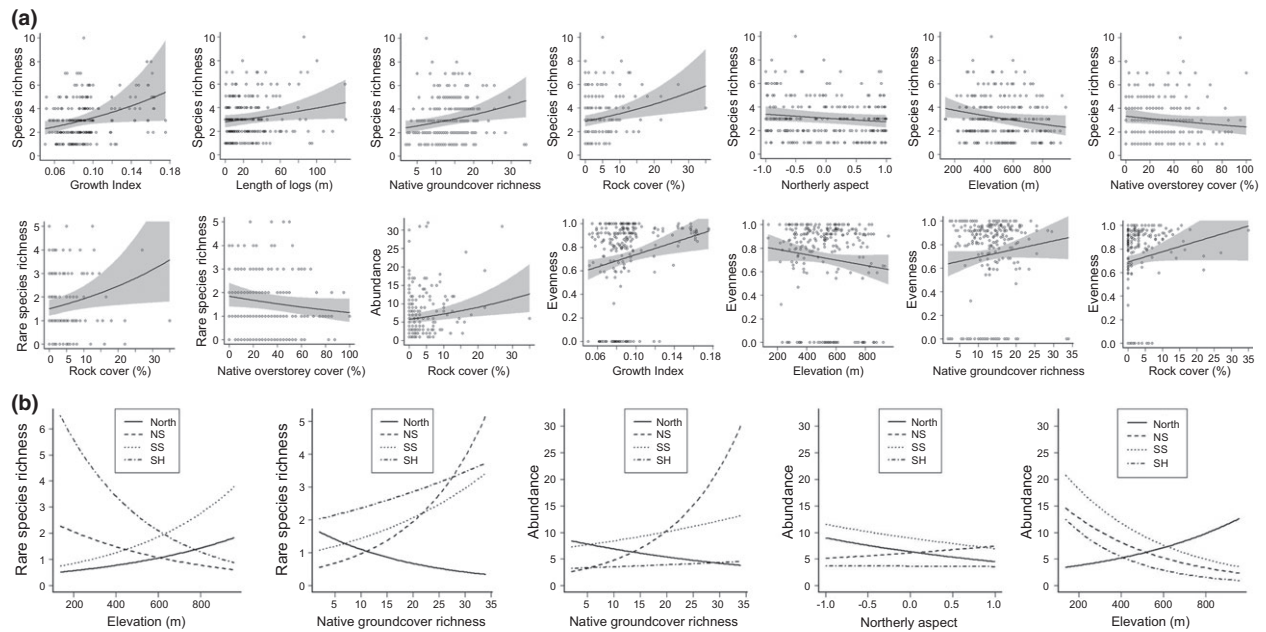


Figure 2 Relationships of all linear predictors (plus confidence intervals) in the top-ranked models for (a) the different reptile assemblage measures within the whole study area, and (b) important interactions with the four study regions: Northern (North), Northern Slopes (NS), Southern Slopes (SS) and Southern Highlands (SH) regions.

effect of elevation on rare species richness in the Southern Slopes (Fig. 2b). However, this might reflect extensive native vegetation loss in the fertile lower slopes of this region compared with hilltops where native vegetation is often retained (Fischer *et al.*, 2010).

Northerly (sunlit) aspects generally supported higher reptile abundance, although this also differed by region. At cooler (higher) latitudes, higher reptile abundance on northerly (sunlit) aspects within the Northern Slopes and Southern Highlands regions is consistent with reptile thermal requirements (Brown *et al.*, 2011). This effect also could be expected for the cooler Southern Slopes, although similar preference by livestock for these north-facing warmer and more productive pastures may contribute to lower reptile abundance observed here based on the demonstrated impact of grazing on reptiles (Dorrough *et al.*, 2012; Howland *et al.*, 2014). Higher abundance on southerly (shaded) aspects in the warmer Northern region may reflect a preference for species to occupy mesic refugia when thermoregulatory processes are not limiting, a recognized pattern in reptiles (Duckett & Stow, 2013).

Native groundcover richness influenced rare reptile species richness and abundance at the regional-level, with positive effects in all, but the Northern region. This regional effect probably reflects differences in climate (Hutchinson *et al.*, 2005) and cultivation histories (Hoekstra *et al.*, 2005) between the regions, with a greater reliance on native groundcover richness by reptiles in the more intensively cultivated southern regions. This is consistent with the well-established negative impact of agricultural land-use recognized for reptiles globally (Fabricius, Burger & Hockey, 2003; Ribeiro *et al.*, 2009).

Five of the seven environmental features identified in top models for reptile diversity were linked to reptile thermoregulatory behaviour. Ground-layer structural attributes related to reptile basking, including cover of rocks (Seebacher & Franklin, 2005) and overstorey (Pike, Webb & Shine, 2011), as well as broad thermally relevant climatic variables of growth index, elevation and aspect were important in driving reptile diversity. This suggests inclusion of features that influence thermoregulatory environments enhances regional effectiveness of conservation programmes for reptiles.

Implications for conservation

To facilitate adaptive learning (*sensu* Perkins *et al.*, 2010) from the Environmental Stewardship Programme that was the focus of this investigation, we present a summary of suggested management actions to inform future programmes. We summarize features important for conserving overall reptile diversity, and identify features important at the regional-level for conserving rare species within this Programme (Table 2). To help guide conservation planning more generally, we identify four key management recommendations that emerge from our study.

Incorporating regional-level responses of species diversity to environmental features allows greater sophistication in conservation programme design

The results of our study suggest conservation programmes will be more effective if they incorporate regional variation in important environmental features. The identification of

Table 2 Recommendations for scheme development, particularly targeting site prioritization aiming to enhance overall reptile richness and rare species richness for sites included in the four study regions within the study area

Region	To conserve overall richness	To conserve rare reptiles
Whole study	<ul style="list-style-type: none"> • Target high (>3%) rock cover • Target high (>300 m·ha⁻¹) log cover • Target open (<20%) overstorey • Target sites at low (<500 m) elevation • Target high (1.0) growth index • Target high (>0.033 species·m⁻²) native groundcover richness 	<ul style="list-style-type: none"> • Target high (>3%) rock cover • Target open (<20%) overstorey
Northern	<ul style="list-style-type: none"> • As for whole study 	<ul style="list-style-type: none"> • Target sites at high (<540 m) elevation • Target southerly (shaded) aspect • Target low (<0.037 species·m⁻²) native groundcover richness
Northern slopes	<ul style="list-style-type: none"> • As for whole study 	<ul style="list-style-type: none"> • Target sites at low (<430 m) elevation • Target high (>0.037 species·m⁻²) native groundcover richness
Southern slopes	<ul style="list-style-type: none"> • As for whole study 	<ul style="list-style-type: none"> • Target sites at high (>430 m) elevation • Target southerly (shaded) aspect • Target high (>0.033 species·m⁻²) native groundcover richness
Southern highlands	<ul style="list-style-type: none"> • As for whole study 	<ul style="list-style-type: none"> • Target sites at low (<730 m) elevation • Target northerly (sunlit) aspect • Target high (>0.038 species·m⁻²) native groundcover richness

regional patterns for reptile abundance and rare species is of specific value for conservation managers. This is because bolstering existing populations and increasing species of conservation concern is fundamental to arresting biodiversity erosion in fragmented agricultural landscapes (Gonthier *et al.*, 2014). Our work addresses the need to shift beyond the 'one-size-fits-all' approach commonly applied to large-scale programmes (Whittingham *et al.*, 2007; Batáry *et al.*, 2011), underscoring the value of considering the disproportionate benefit some environmental features provide in certain contexts. Managers can apply regional-level biodiversity information either by selecting sites containing certain attributes, or for targeted restoration activities. For example, restoration of native groundcover (e.g. Lindenmayer *et al.*, 2010) would be most effectively applied for restoring rare reptile diversity in southern regions of this study (Fig. 2b). Although similar studies across a suite of taxonomic groups are needed, the habitat recommendations identified in this study are largely consistent with, and unlikely to be detrimental for, many other ground-dependent fauna including mammals and amphibians (McElhinny *et al.*, 2006).

Rare species need special consideration

Despite the overarching objectives of many conservation programmes to conserve targeted ecological communities, it is evident that rare and threatened taxa may continue to decline (Kleijn *et al.*, 2006), or show time-lags in response to conservation programmes (Michael *et al.*, 2014). Procedures for ensuring robust protection of rare and threatened species in land-stewardship conservation programmes are limited (Batáry *et al.*, 2011; Whittingham, 2011) and have not previously involved recommendations for management at the regional-level (Table 2). An explicit recommendation from our study is to incorporate regional environmental features

important for conserving rare species at the site selection stage and focus management actions at this level. Applying this approach for rare species in other taxonomic groups may help identify important features for preventing multi-taxon species decline in agricultural landscapes. Where recommendations for different taxonomic groups clash (e.g. positive for reptiles while negative for birds), other approaches such as multi-criteria decision analyses (Huang, Keisler & Linkov, 2011) could be used to consider a range of contrasting management options.

There is a need to prioritize variables that cannot be managed

Some of the most important drivers of diversity at the site level are environmental attributes that cannot be influenced by site management, such as aspect, elevation and growth index. Despite their importance for diversity, these abiotic attributes are rarely considered when designing conservation programmes (Kleijn *et al.*, 2006). Because these features cannot be managed, their integration at the initial site selection stages of conservation planning, particularly at the regional-level, would enhance species diversity and therefore effectiveness of conservation programmes. Although large programmes may inadvertently capture these features, a targeted approach would be more effective. This could be achieved by ensuring sufficient representation of these variables in the preliminary stages of programme development, but then tailoring site selection to include key features relevant to particular regions.

Programmes can be tailored to better support species groups at higher conservation risk

Many conservation programmes differ in effectiveness among species and fail to support species-groups at higher

conservation risk. For example, land-stewardship conservation programmes are more effective for plants and some invertebrate groups (Whittingham, 2011) with no demonstrable benefit for other rapidly declining groups such as reptiles (Michael *et al.*, 2014). However, we contend that refining programmes by incorporating environmental features can benefit these at-risk groups. Our study shows that reptiles, a group experiencing global decline (Böhm *et al.*, 2013), are positively associated with features important for thermoregulation (e.g. aspect, elevation, rock cover). Maintaining important thermoregulatory features, either through site-selection (by considering elevation and aspect) or proposed management actions (such as maintaining rock cover as a non-renewable resource), would help reptiles and possibly other thermoregulating species groups (e.g. amphibians, invertebrates; Cossins & Bowler, 1987).

The management recommendations we have identified were developed with the goal of enhancing effectiveness of the large-scale land-stewardship conservation programmes. Such programmes have become one of the most used tools globally for conserving biodiversity in agricultural landscapes (European Commission, 2014; USDA, 2014). By examining the differences between regions, for an important yet poorly studied taxonomic group, we have identified new opportunities for better conservation management in agricultural landscapes that can improve effectiveness of large-scale conservation programmes globally.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Calculation of Growth Index.

Fig. S1. Example of a typical woodland site from our study.

Fig. S2. Relationship between reptile species richness and latitude.

Fig. S3. Accumulation curves of observed species richness for the study area and four study regions.

Table S1. Additional description of each study region.

Table S2. List of all reptile individuals surveyed.

Table S3. Observed and estimated species richness for the whole study area and each of the four study regions.

Table S4. GLMMs for the four measures of reptile community assembly in relation to eight environmental and habitat predictors.