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Annegret Grimm-Seyfarth, Jean-Baptiste Mihoub, Klaus Henle. Functional traits determine the different effects of prey, predators, and climatic extremes on desert reptiles. *Ecosphere*, 2019, 10 (9), 10.1002/ecs2.2865 . hal-02344845

HAL Id: hal-02344845

<https://hal.sorbonne-universite.fr/hal-02344845v1>

Submitted on 4 Nov 2019

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Functional traits determine the different effects of prey, predators, and climatic extremes on desert reptiles

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Citation: Grimm-Seyfarth, A., J.-B. Mihoub, and K. Henle. 2019. Functional traits determine the different effects of prey, predators, and climatic extremes on desert reptiles. *Ecosphere* 10(9):e02865. 10.1002/ecs2.2865

Abstract. Terrestrial reptiles are particularly vulnerable to climate change. Their highest density and diversity can be found in hot drylands, ecosystems which demonstrate extreme climatic conditions. However, reptiles are not isolated systems but part of a large species assemblage with many trophic dependencies. While direct relations among climatic conditions, invertebrates, vegetation, or reptiles have already been explored, to our knowledge, species' responses to direct and indirect pathways of multiple climatic and biotic factors and their interactions have rarely been examined comprehensively. We investigated direct and indirect effects of climatic and biotic parameters on the individual (body condition) and population level (occupancy) of eight abundant lizard species with different functional traits in an arid Australian lizard community using a 30-yr multi-trophic monitoring study. We used structural equation modeling to disentangle single and interactive effects. We then assessed whether species could be grouped into functional groups according to their functional traits and their responses to different parameters. We found that lizard species differed strongly in how they responded to climatic and biotic factors. However, the factors to which they responded seemed to be determined by their functional traits. While responses on body condition were determined by habitat, activity time, and prey, responses on occupancy were determined by habitat specialization, body size, and longevity. Our findings highlight the importance of indirect pathways through climatic and biotic interactions, which should be included into predictive models to increase accuracy when predicting species' responses to climate change. Since one might never obtain all mechanistic pathways at the species level, we propose an approach of identifying relevant species traits that help grouping species into functional groups at different ecological levels, which could then be used for predictive modeling.

Key words: Australia; climate change; Gekkonidae; periodic flooding; Scincidae; species functional traits; species interactions; structural equation modeling.

Received 12 June 2019; **accepted** 14 June 2019; **final version received** 5 August 2019. Corresponding Editor: Robert R. Parmenter.

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INTRODUCTION

In a world driven by climate change (IPCC 2014), it is an urgent need to understand how species might respond. Ectotherms, and especially terrestrial reptiles, are assumed to be particularly vulnerable (Kearney et al. 2009, Gunderson and Stillman 2015). Among the

highest reptile density and diversity on earth can be found in hot drylands (Pianka and Schall 1981, Powney et al. 2010) making the conservation of dryland reptiles particularly important. Hot drylands are characterized by extremely high temperatures and low precipitation, and cover over 40% of the global terrestrial area (Millennium Ecosystem Assessment 2005).

Desert reptile communities will likely react asynchronously to fluctuations of local climatic conditions (Read 1995, Dickman et al. 1999, Read et al. 2012). Individual conditions and life-history parameters of single reptile species can be either enhanced or diminished in reaction to temperature (Chamaillé-Jammes et al. 2006, Monasterio et al. 2013), rainfall (Dickman et al. 1999, Ryan et al. 2016), or a combination thereof (Barrows 2011, Grimm-Seyfarth et al. 2018). However, no climatic factor will affect reptiles only directly but rather through multiple pathways (Ockendon 2014, Deguines et al. 2017). Exemplarily, effects of rainfall on lizards were frequently interpreted through resource availability (Barrows 2011, Read et al. 2012, Grimm-Seyfarth et al. 2018). Indeed, lizards are strongly dependent on food availability (Ballinger 1977, Pianka 1986) and vegetation cover (Kearney et al. 2009, Grimm-Seyfarth et al. 2017). In turn, desert invertebrates, which are both the most common food of arid-zone lizards (Pianka 1986) and potential predators (Henle 1990a), depend on water, temperature, and vegetation abundance and composition (Read 1995, Kwok et al. 2016), with the latter being also related to rainfall (Shmida et al. 1986, Robertson 1988) or to standing water in flooded anabranches (Shmida et al. 1986).

While direct relations among climatic conditions, invertebrates, vegetation, or reptiles have been frequently explored, to our knowledge, the multiple pathways along which climatic and biotic relations interact have rarely been examined. Results of studies simultaneously considering the effects from multiple pathways may differ fundamentally from those analyzing isolated climatic or biotic factors since single factors could be enhanced by synergistic or diminished by antagonistic pathways (Deguines et al. 2017). Therefore, Ockendon (2014) recently advocated monitoring of multiple trophic levels to understand the overall effects of drivers of global change on single species.

A limitation for such integrative investigations is that they are only possible through long-term multi-species monitoring. Taking advantage of a unique multi-trophic monitoring study of 20 lizard species in arid Australia across 30 yr, we investigated direct and indirect effects of climatic and biotic parameters on body condition and occupancy of the eight most abundant lizard

species using structural equation modeling. We expected that biotic factors are at least as important as climatic factors (Ockendon 2014), but that the effects differ between the individual level and the population level (Grimm-Seyfarth et al. 2018). The eight lizard species differed in their functional traits (Table 1), which could potentially explain different reactions among species (Read et al. 2012). Therefore, we tested whether individual and population responses were related to species' functional traits.

MATERIALS AND METHODS

Study site and study species

The study was conducted in Kinchega National Park, New South Wales, Australia (32°28' S, 142°20' E). Kinchega is situated at the eastern margin of Australia's arid zone and characterized by high and increasing summer temperatures and low but highly variable rainfall without seasonal patterns. Additionally, Kinchega contains floodplains with flooding being related to rainfall in inland Queensland due to La Niña events (Grimm-Seyfarth et al. 2018). We monitored three study plots (Appendix S1: Figs. S1–S5): two different riverine woodlands and the Kinchega field station as described in Henle (1989a, 1990a). The first riverine woodland (RWI, ~100 × 150 m) was characterized by cracking clay, 60 widely dispersed black box eucalypts (*Eucalyptus largiflorens*), and highly varying vegetation cover, usually without shrubs. The second riverine woodland (RWII, ~80 × 25 m) was characterized by sandy clay with only slightly dispersed black box eucalypts. The herb-layer coverage varied strongly among years, and the shrub layer was dominated to varying extends by black blue bush (*Maireana pyramidata*), black rolypoly (*Sclerolaena muricata*), cannonball burr (*Dissocarpus paradoxus*), and ruby saltbush (*Enchylaena tomentosa*). While the RWI got almost entirely flooded during each flood, the RWII remained just above flood level in all floods that occurred throughout our study. The Kinchega field station (hereafter station, ~50 × 40 m) consisted of seven huts in 1986/1987 and eight huts since 1991 made of corrugated iron and surrounded by sandy soil occasionally covered by single shrubs and low and patchy herbs. During the 30 yr, park rangers and

Table 1. Overview on the eight most abundant lizard species.

Species	Study plot	Activity	Habitat	Capture method	Prey	Foraging mode	Predators	SVL (cm)	Longevity (yr)	CT _{max} (°C)	N
MB	RWII	d	t	Focal search; pitfall traps	Arthropods	Widely foraging	d	4.2	4	41.6	704
CR	RWII	d	t	Pitfall trap	Arthropods/vertebrates	Widely foraging	d a.f. cannibal.	6.0	1	45.1	116
HB	RWI, RWII, Station	n	t	Transect; pitfall traps	Arthropods	Widely foraging	n	4.35	3	40.6	135
DT	RWI	n	t	Transect	Arthropods	Sit-and-wait	n	4.7	3	43.5	316
LP	RWII	n	s	Pitfall traps	Fossorial arthropods	Widely foraging	n, <i>Varanus</i>	8.2	2	43.1	88
LX	RWII	n	s	Pitfall traps	Fossorial arthropods	Widely foraging	n, <i>Varanus</i>	4.5	1	40.9	47
ER	RWI, RWII, Station	n	s	Transect; pitfall traps	Arthropods/vertebrates	Widely foraging	n a.f. cannibal.	8.2	3	42.0	71
GV	RWI, Station	n	a	Focal search	Arthropods	Sit-and-wait	n	5.15	28	45.6	1676 3740

Notes: The main study plot used for analyses is shown in bold. All data stem from our own analyses and Henle (1989a, b, c, 1990a, b) except CT_{max} (see Appendix S1: Table S1). MB, *Morethia boulengeri*; CR, *Ctenotus regius*; HB, *Heteronotia binoei*; DT, *Diplodactylus tessellatus*; LP, *Lerista punctatovittata*; LX, *Lerista xanthura*; ER, *Eremiascincus richardsonii*; GV, *Gehyra variegata*; SVL, mean adult snout-vent lengths; CT_{max}, critical thermal maximum; N, sample size across all years (without recaptures); d, diurnal; n, nocturnal; t, terrestrial; s, subterranean; a, arboreal; and a.f. cannibal., apart from cannibalistic. Longevity refers to minimal longevity as individuals can only be aged when they were captured before adulthood. RWI, first riverine woodland; RWII, second riverine woodland.

individual researchers have used the huts to a varying extent. The minimum distance from the station to RWI and RWII and between the two riverine woodlands were 60, 130, and 230 m, respectively. As no individual was observed in several study plots, they can be considered to be independent.

Monitoring took place at the end of the reproductive season in February or March from 1986 to 2016 except for 1988–1991, 1993, 1995, and 2008–2011. Each species was caught by hand or in pitfall traps for at least five days per plot per season (Table 1; see Appendix S1 for details). Every individual caught was measured, weighted, sexed and aged (if possible), and individually identified by its pattern or toe clipping (Appendix S1).

The eight most abundant lizard species and their functional traits are summarized in Table 1. We divided species into four functional groups based on two traits (activity time and habitat use) that we assumed most important for hot desert reptiles: two diurnal, terrestrial skinks (*Morethia boulengeri*, *Ctenotus regius*); two nocturnal, terrestrial geckos (*Heteronotia binoei*, *Diplodactylus tessellatus*); three nocturnal, subterranean

skinks (*Lerista punctatovittata*, *Lerista xanthura*, *Eremiascincus richardsonii*); and the nocturnal, arboreal gecko *Gehyra variegata*. Species names follow Cogger (2014), except for following Greer (1990) who showed that *Lerista aericeps* is a synonym of *L. xanthura*. We considered a species as habitat specialist if it had only been found in one study plot and as habitat generalist otherwise.

Body condition was calculated for each captured individual using the scaled mass index, which accounts for individual growth (Peig and Green 2009; Appendix S1). Annual occupancy (i.e., the probability that a randomly selected site in a study plot is occupied) for each species per plot was calculated using multi-season occupancy modeling based on the 30-yr species-specific capture histories (MacKenzie et al. 2006). We assumed year-dependent colonization, extinction, and detection and considered the years as yearly site covariates (see Appendix S1 for the details).

During each monitoring season, we recorded plot-specific proxies for vegetation (% cover, mass, or foliage) and species-specific indices for prey abundance, potential predators, and the station usage (Table 2; Appendix S1). The plot-specific methodologies for quantifying these proxies

did not affect our statistical methodology because for each species, network analyses were based on data originating from main study plots only (Appendix S2).

Climate data

Climatic data from the weather station closest to Kinchega (station 047019 Menindee Post Office; Bureau of Meteorology, Australian Government) matched the local conditions very well (Grimm-Seyfarth et al. 2018). We chose climatic parameters that likely affect the lizards and the biotic conditions in late summer (Table 2; see Appendix S2: Table S1 for details): summer mean maximum temperature; the number of days warmer than 45°C reflecting the number of days exceeding all species' critical thermal maxima (Table 1); the summed summer and the summed previous winter rainfall, both known to affect vegetation in summer (Robertson 1988); and the averaged summer and winter river heights of the adjacent Darling River at the closest weir (weir 32; Department of Primary Industries, Office of Water, New South Wales Government) since both vegetation (Shmida et al. 1986) and lizard species (Grimm-Seyfarth et al. 2018) are likely affected by floodplain dynamics. Previous analyses indicated that Darling River heights were strongly related to the

ENSO phenomenon (Grimm-Seyfarth et al. 2018) and thus represent indirect distant climatic variables acting on the local ecosystem. As flooding effects might appear with delay, we also considered the number of years after the last flooding of parts of the study area. Finally, we considered an interaction between each water parameter (summer and winter precipitation, Darling River heights) and summer temperature (Kwok et al. 2016). No collinearity occurred among climatic variables (Grimm-Seyfarth et al. 2018).

Structural equation modeling

Based on previous studies (see *Introduction*) and our own expertise, we developed a conceptual network between the climatic (temperature, precipitation, flooding) and biotic (vegetation, prey, predation) factor groups that could potentially influence the eight focal lizard species at either individual or population level (Fig. 1, Table 2; see Appendix S1 for a detailed network description). We applied this conceptual network to 9 and 8 different network analyses at individual and population levels, respectively, and separately for each focal lizard species.

Body condition measures or annual occupancy rates were used as overall response variable in the network analyses, for which we applied

Table 2. Summary of all climatic and biotic factor groups and variables, their description, and the study plots for which they apply.

Factor group	Variable	Description	Study plot
Temperature	Summer temperature	Mean maximum current summer temperature (°C)	All
	Number of days >45°C	Number of days above 45°C in the current summer	All (plot-specific)
Precipitation	Summer rain	Total rainfall in the current summer (mm)	All
	Previous winter rain	Total rainfall in the previous winter (mm)	All
Flooding	Summer Darling River height	Average Darling River height in the current summer (m)	All
	Winter Darling River height	Average Darling River height in the previous winter (m)	All
	Number of years postflood	Number of years since parts of the study area were flooded last time	All
Vegetation	Vegetation coverage	Estimated non-tree vegetation coverage, no difference between herbs and shrubs possible (%)	RWI, Station
	Herb-layer biomass	Biomass of the herb layer (kg/ha)	RWII
	Shrub coverage	Estimated shrub and bush vegetation coverage (%)	RWII
	Eucalypt foliage	Black box eucalypt foliage (five categories)	RWI
Station usage	Station usage intensity	Classification (four categories) of the number of people staying	Station
Prey	Prey index	Either arthropod abundance (three categories), or calculated small-vertebrate index	All (species-specific)
Predation	Predator index	Calculated predator index	All (species-specific)

Note: See Appendix S1 as well as Appendix S2: Table S1 for details, calculations, classifications, and references. RWI, first riverine woodland; RWII, second riverine woodland.

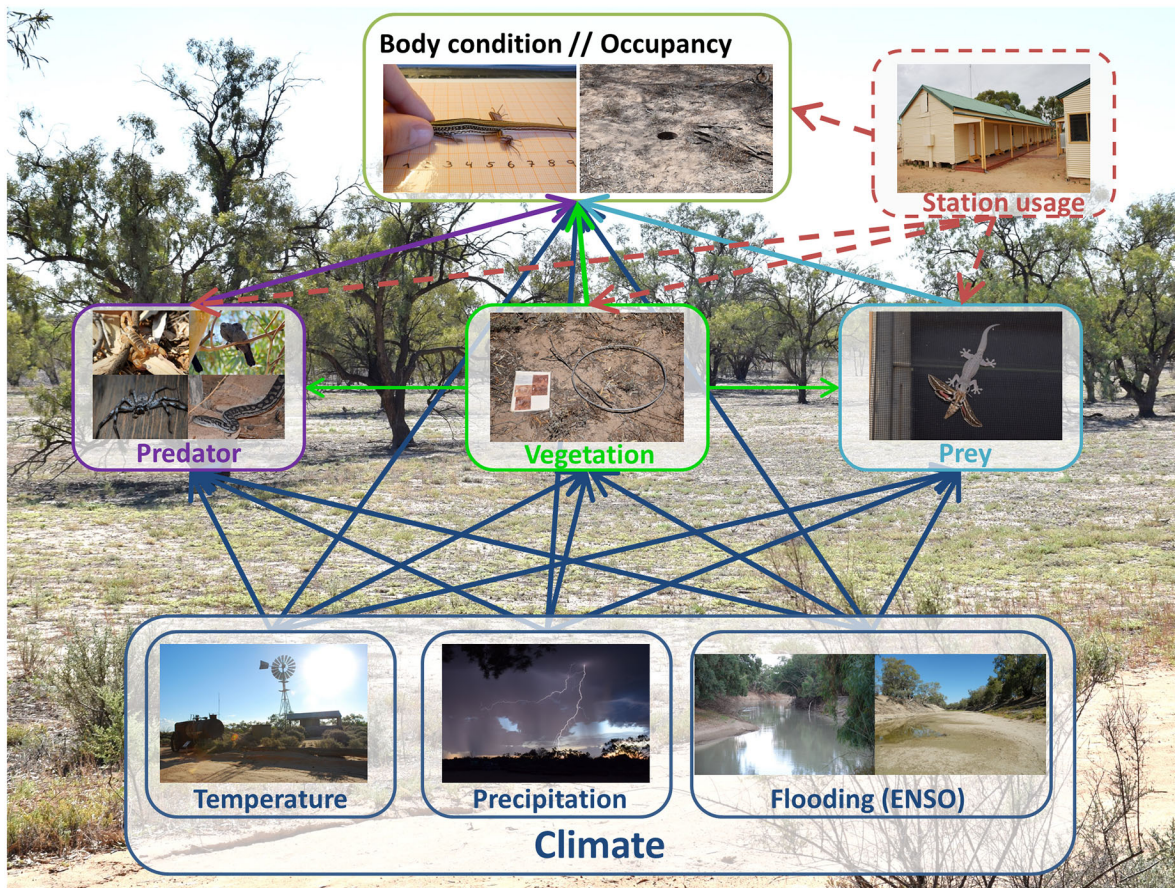


Fig. 1. Conceptual network showing climatic and biotic factor groups influencing body condition or occupancy in eight lizard species in Kinchega. The background shows the first riverine woodland study site in 2015, a year with high winter rain and high vegetation coverage. Arrows represent potential direct effects of one factor group (predictor) on another (response). The variables behind each factor group are described in Table 2.

piecewise structural equation modeling (SEM; Shipley 2009). With this method, each variable can be both a response and a predictor to other variables. We used the R-package *piecewiseSEM* (Lefcheck 2016) with year as the grouping variable accounting for potential temporal autocorrelation. It has the advantage that multiple generalized linear mixed models (GLMMs) with various random effects and variance structures can be joined into a single hierarchical SEM. Specifically, we built five different GLMMs within each SEM based on our conceptual network (Fig. 1): responses of (1, 2) two plot-specific vegetation variables to climatic variables; (3) the species-specific prey index to climatic and vegetation variables; (4) the species- and plot-specific

predator index to climatic and vegetation variables; and (5) species- and plot-specific body condition or occupancy in response to all climatic and biotic variables and additionally to station usage in all analyses at the station. Details on error distributions, control variables, and random structures are described in Appendix S2.

To reduce the number of initial paths, we performed a pre-selection on the direct relations of climatic parameters on each biotic variable (prey, predators, vegetation) as well as on lizard response using single GLMMs (Appendix S2). In the subsequent SEMs, we kept all climatic variables as paths that turned out to be potentially important for a biotic variable (within $\Delta Akaike$'s information criterion < 2) to make sure that we

do not miss potentially important paths. We then used Shipley's (2009) test of d-separation to assess the overall fit of the SEMs and to control for potential missing paths. We included missing paths when the test was significant and a plausible ecological connection could exist. We did not delete non-significant paths since these paths were important in the pre-selection and may explain additional variance (see Appendix S2: Tables S7 and S8 for an overview of all final paths).

For comparisons among predictors, we obtained scaled standardized path coefficients. We corrected the direct effect of variables that were part of an interaction by summing the estimate of the variable itself and the product of the interaction estimate with the estimate of the variable in the interaction (Whisman and McClelland 2005). We calculated the total effect of each climatic and biotic variable by multiplying all coefficients along each path and summing all paths per predicting parameter, and the overall indirect effect (i.e., the effect through paths of at least two

factors) by subtracting the direct effect from the total effect.

To assess the relative contribution of each climatic and biotic factor group (Table 2) for individual or population response per species, we set the sum of all absolute total effects to 100% and calculated the percentage taken by each factor group. Last, we analyzed which species' functional traits could influence to which factor group species were responding by means of permutational multivariate analyses of variance (pMANOVA; Mcardle and Anderson 2001) using Gower dissimilarity (Gower 1971) and the R-package vegan (Oksanen 2018). We tested different functional traits and their combinations based on eight hypotheses (Table 3): study design, foraging, morphometrics, habitat and activity, physiology, and all hypotheses except of study design together with habitat and activity since we assumed initially that habitat and activity influence desert reptiles most. All statistical analyses were performed in R 3.1.1 (R Core Team 2016).

Table 3. Functional traits that determined the relative contribution of factor groups on body condition and occupancy based on eight different hypotheses.

Hypothesis	Functional trait(s)	Body condition		Occupancy	
		<i>p</i> _{marginal}	<i>p</i> _{model}	<i>p</i> _{marginal}	<i>p</i> _{model}
Design	Study plot	0.23	0.23	0.36	0.36
Foraging	Foraging mode	0.58	0.58	0.82	0.82
	Prey	0.07	0.07	0.84	0.84
	Foraging mode × prey	0.21	0.21	0.88	0.88
Morphometrics and longevity	Snout-vent length	0.21	0.21	0.06	0.06
	Longevity	0.76	0.76	0.24	0.24
	Snout-vent length + longevity	0.29; 0.82	0.50	0.03; 0.04	0.02
Habitat and activity	Activity	0.16	0.16	0.25	0.25
	Habitat	0.21	0.21	0.28	0.28
	Habitat × activity	0.003	0.003	0.47	0.47
	Habitat specialization	0.29	0.29	0.05	0.05
	Habitat specialization + habitat × activity	0.06; 0.003	0.003	0.04; 0.18	0.08
Physiology	CT _{max}	0.66	0.66	0.87	0.87
Foraging + habitat and activity	Foraging mode + habitat × activity	0.3; 0.005	0.01	0.36; 0.35	0.43
	Prey + habitat × activity	0.6; 0.05	0.06	0.38; 0.48	0.40
	Foraging mode × prey + habitat × activity	0.54; 0.1	0.10	0.30; 0.23	0.32
Morphometrics + habitat and activity	Snout-vent length + longevity + habitat × activity	0.97; 0.62; 0.1	0.20	0.27; 0.96; 0.75	0.59
	Snout-vent length + longevity + habitat specialization	0.08; 0.55; 0.09	0.21	0.03; 0.11; 0.08	0.01
Physiology + habitat and activity	CT _{max} + habitat × activity	0.64; 0.05	0.04	0.85; 0.66	0.70

Notes: *p*_{marginal} and *p*_{model} refer to obtained *P*-values of the pMANOVAs for each functional trait separated by semicolon, and overall *P*-values, respectively. Significant (*P* < 0.05) and marginally significant (*P* < 0.1) overall *P*-values are highlighted in italic boldface and italic, respectively.

RESULTS

Both body condition (Appendix S1: Fig. S6) and occupancy (Appendix S1: Fig. S7) were highly variable among years. Body condition measures strongly varied among but less within species. Occupancy was high for *G. variegata* (usually >0.7) and *M. boulengeri* (~0.5) and did not vary much but spanned the whole range between 0 and 1 for the remaining species. Confidence intervals were highly variable across time, with high intervals being typically associated with low capture rates.

Vegetation measurements differed among years but showed a strong synchrony in temporal variations among plots (Appendix S1: Fig. S8). In RWI, vegetation coverage and eucalypt foliage were positively correlated, while in RWII, herb-layer biomass and shrub coverage were negatively correlated. At the station, vegetation coverage increased with station usage (Appendix S2: Table S7). Both prey and predator abundance varied strongly over time (Appendix S1: Figs. S9, S10). Except eucalypt foliage, increasing vegetation proxies usually facilitated arthropod abundance. Herb-layer biomass at RWII decreased abundance of prey lizard species for *E. richardsonii*. Vegetation coverage facilitated predatory species in all plots but the station. Eucalypt foliage decreased predator abundance at RWI and herb-layer biomass facilitated nocturnal but suppressed diurnal predators at RWII (Appendix S2: Tables S7, S8).

Individual and population responses were highly variable among species, but two common response patterns could be identified. Body condition increased with prey availability in all species but decreased when predators became more abundant, except *G. variegata* for which predator abundance was positively correlated with body condition (Fig. 2; Appendix S2: Table S7). Likewise, occupancy of all species increased with prey abundance except for diurnal terrestrial skinks where occupancy decreased (Fig. 3; Appendix S2: Table S8).

All final SEMs showed a good fit (Fisher's C test, $P > 0.9$) and completeness without missing paths (Shipley's test of d-separation, $P > 0.1$). All models fulfilled the requirements that the ratio of the total sample size to the number of paths was larger than five (Grace et al. 2015).

Diurnal, terrestrial lizards

Body condition of the two diurnal skink species was mainly driven by biotic factors, followed by flood parameters (Fig. 4). Specifically, herb-layer biomass was overall positive through reducing predators. The effect of shrub coverage was entirely negative for *M. boulengeri*, whereas positive direct and negative indirect (through facilitating predators) effects compensated each other in *C. regius*. Winter Darling River height increased body condition of *M. boulengeri* but decreased it in *C. regius*, while summer Darling River height only facilitated the latter (Fig. 2; Appendix S3: Tables S1, S2).

Occupancy was most impacted by flood parameters (Fig. 4). It increased mainly with the number of years postflooding for both species and with winter and summer Darling River heights for *C. regius* and *M. boulengeri*, respectively. Herb-layer biomass and predator abundance directly increased occupancy of *C. regius*. Despite its direct positive effect, shrub coverage overall decreased occupancy of *M. boulengeri* mainly through predator facilitation (Fig. 3; Appendix S3: Tables S10, S11).

Nocturnal, terrestrial lizards

Temperature and rainfall contributed most to both gecko species' body condition (Fig. 4), which directly increased with increasing summer temperature and winter rain but decreased with the number of days above 45°C. Summer rain only favored *H. binoei* indirectly through both increasing vegetation coverage, which in turn increased prey abundance, and decreasing predator abundance. Vegetation coverage was directly negative for *D. tessellatus* but balanced by stronger indirect positive effect through increasing prey and decreasing predator abundance. Two site-specific parameters were also relevant: *H. binoei* was negatively affected by the intensity of the station usage and *D. tessellatus* was slightly positively influenced by increasing eucalypt foliage (Fig. 2; Appendix S3: Tables S3, S4).

Flood parameters were most important for both species' occupancy, followed by vegetation parameters (Fig. 4). While occupancy of *H. binoei* was highest in flooded years and decreased subsequently, occupancy of *D. tessellatus* increased the longer the study site was not flooded.

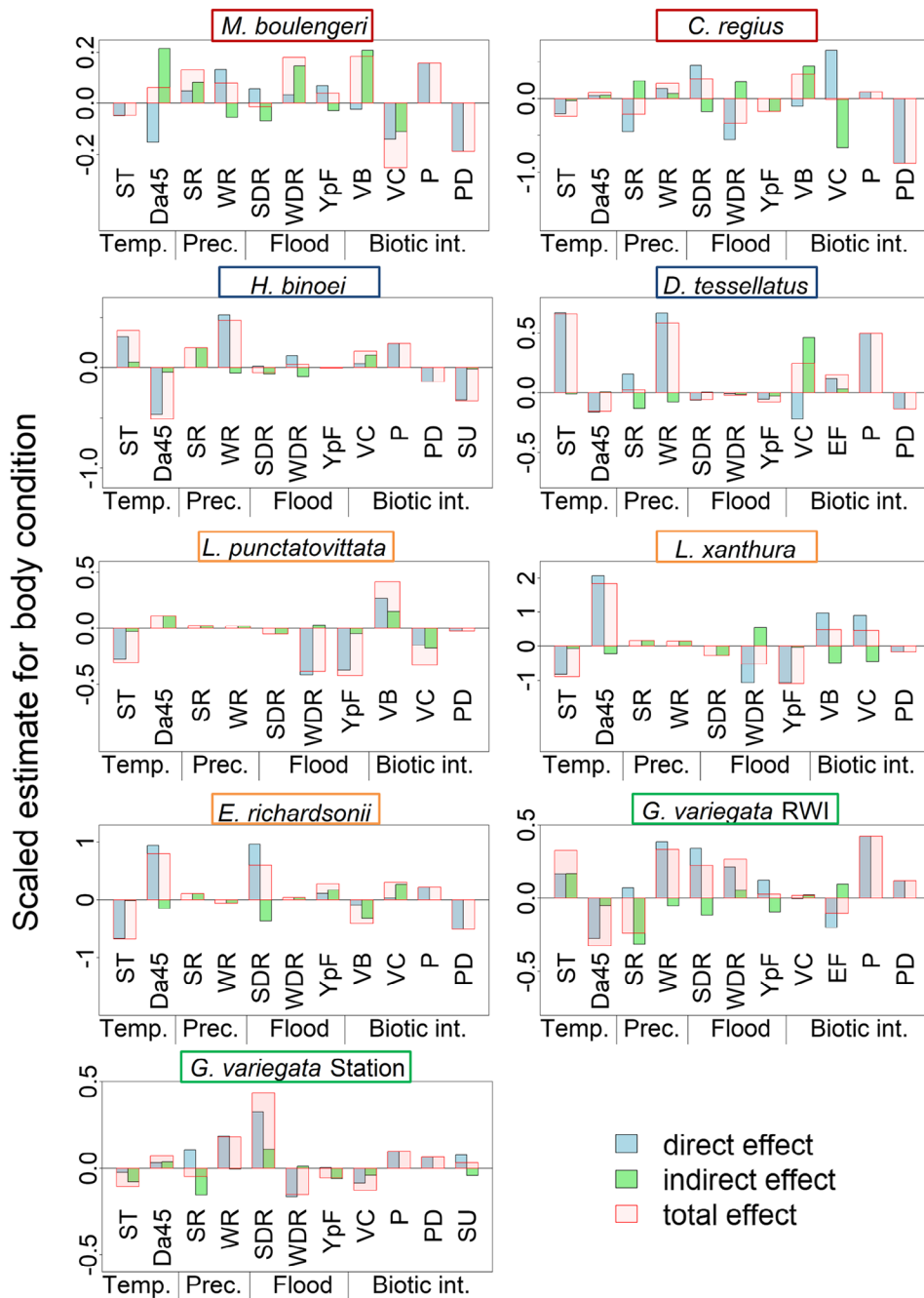


Fig. 2. Direct (blue), indirect (green), and total (transparent red) scaled estimates of structural equation models for body condition. Species names are color-coded according to their functional groups: red, terrestrial, diurnal; blue, terrestrial, nocturnal; orange, subterranean, nocturnal; green, arboreal, nocturnal. Variables and factor groups have been abbreviated as follows: ST, summer temperature; Da45, number of days above 45°C; SR: summer rain; WR, winter rain; SDR, summer Darling River height; WDR, winter Darling River height; YpF, number of years postflood; VB, vegetation biomass; VC, vegetation coverage; EF, eucalypt foliage; P, prey index; PD, predator index; SU, station usage intensity; Temp., temperature; Prec., precipitation; Flood, flooding; Biotic int., biotic interaction.

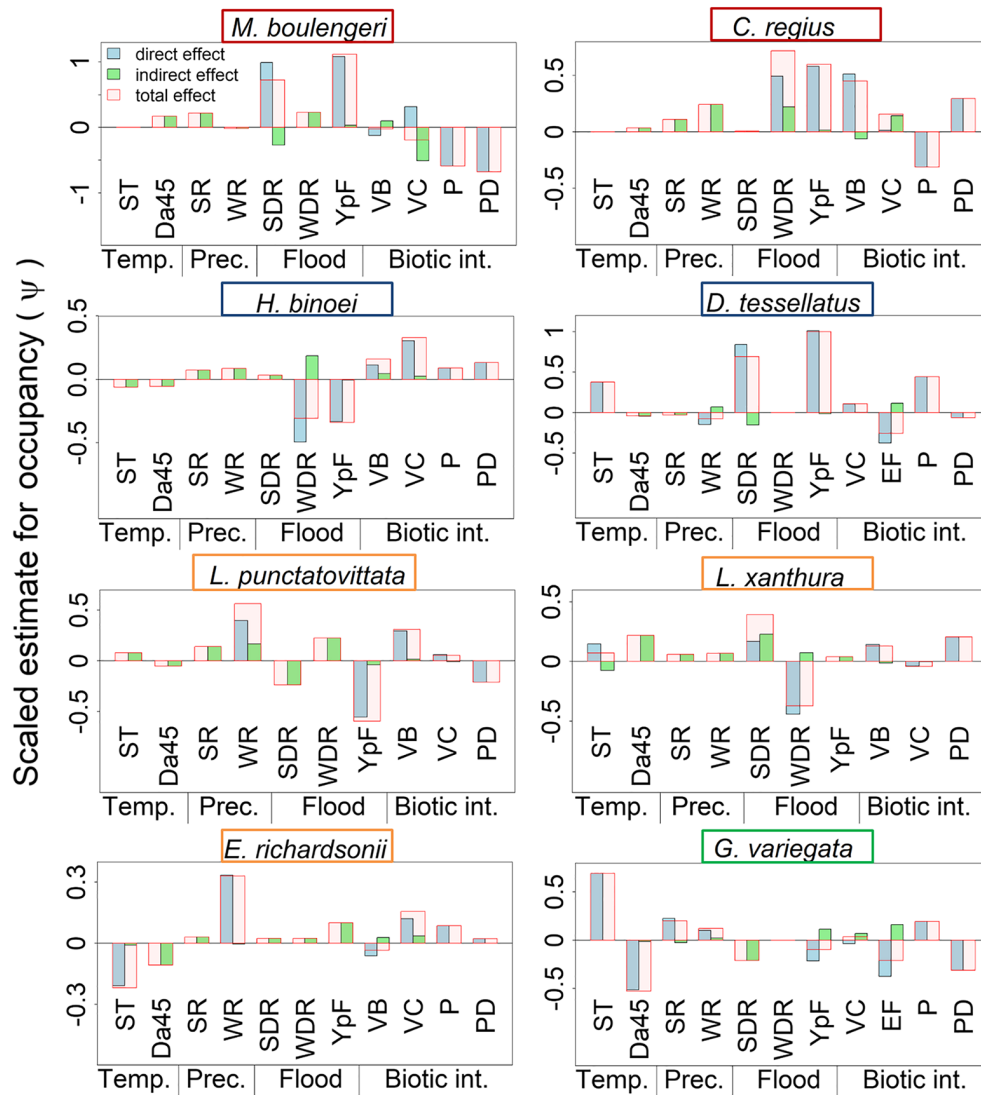


Fig. 3. Direct (blue), indirect (green), and total (transparent red) scaled estimates of structural equation models for occupancy. Species names are color-coded according to their functional groups red, terrestrial, diurnal; blue, terrestrial, nocturnal; orange, subterranean, nocturnal; green, arboreal, nocturnal. Variables and factor groups have been abbreviated as follows: ST, summer temperature; Da45, number of days above 45°C; SR: summer rain; WR, winter rain; SDR, summer Darling River height; WDR, winter Darling River height; YpF, number of years postflood; VB, vegetation biomass; VC, vegetation coverage; EF, eucalypt foliage; P, prey index; PD, predator index; SU, station usage intensity; Temp., Temperature; Prec., Precipitation; Flood, Flooding; Biotic int., Biotic interaction.

Whereas winter Darling River heights decreased occupancy of *H. binoei*, summer river heights increased occupancy of *D. tessellatus*. Vegetation coverage increased occupancy of both species, but herb-layer biomass only that of *H. binoei*, whereas eucalypt foliage decreased occupancy of

D. tessellatus (Fig. 3; Appendix S3: Tables S12, S13).

Nocturnal, subterranean lizards

Body condition of the three skink species was most affected by temperature and flood

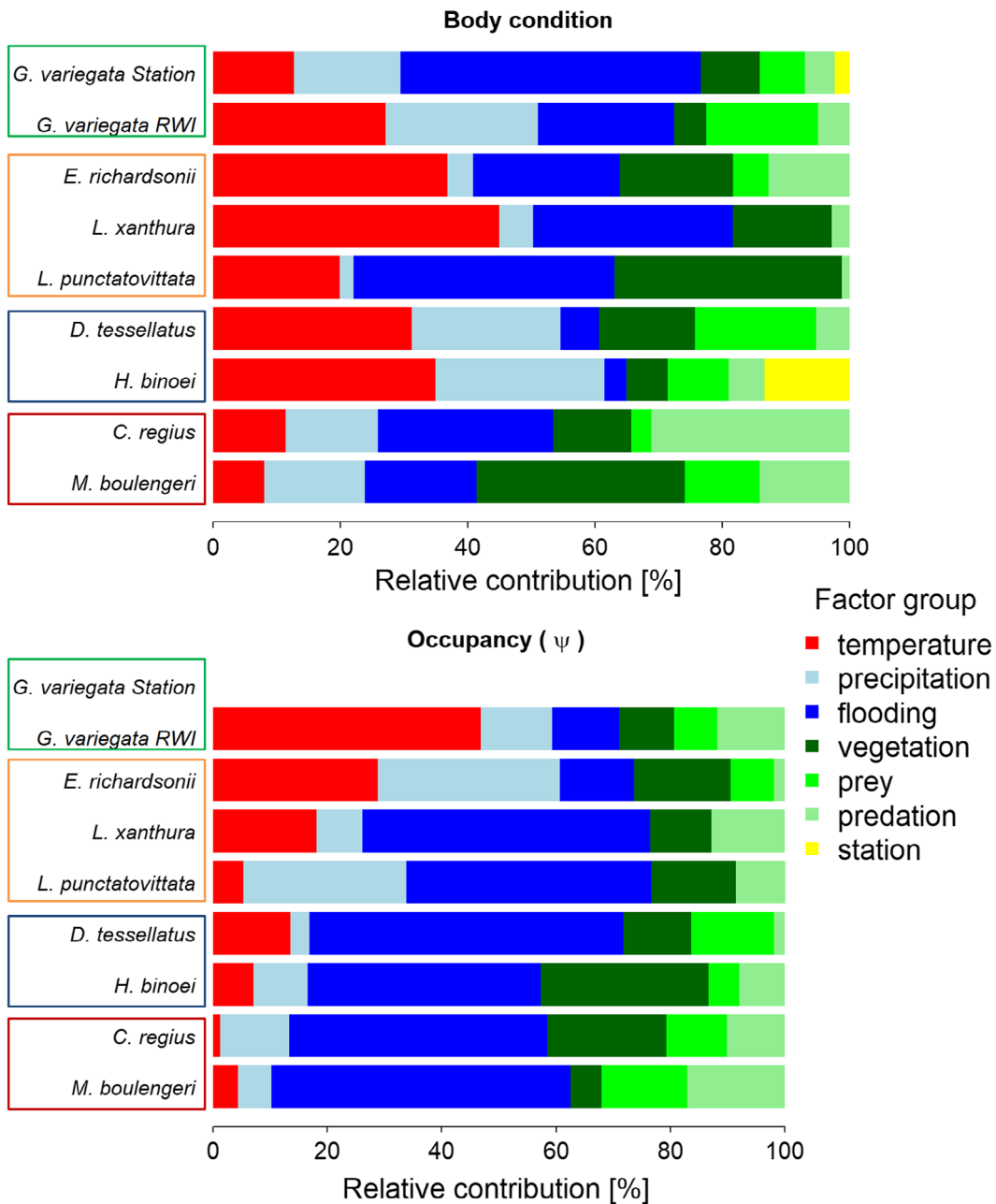


Fig. 4. Relative contribution of each factor group to the variability on body condition (left) and occupancy (right). Species names are color-coded according to their functional groups: red, terrestrial, diurnal; blue, terrestrial, nocturnal; orange, subterranean, nocturnal; green, arboreal, nocturnal.

parameters (Fig. 4). It decreased with summer temperature but increased with a higher number of days above 45°C. Both *Lerista* species suffered from high Darling River heights in winter and with increasing number of years after flooding.

Contrarily, *E. richardsonii* strongly profited from high summer Darling River heights. Responses to vegetation were highly species-specific. Both *Lerista* species directly profited from increasing herb-layer biomass, while *L. punctatovittata*

suffered but *L. xanthura* profited from increasing shrub coverage. Vegetation only indirectly affected *E. richardsonii* since increasing herb-layer biomass decreased prey abundance but favored predators, whereas increasing shrub coverage facilitated prey abundance (Fig. 2; Appendix S3: Tables S5, S6, S7).

Responses of species' occupancy differed among species with flood being most important for both *Lerista* species (Fig. 4). Occupancy of *L. punctatovittata* decreased with time after the study area adjacent to the study plot had been flooded. In *L. xanthura*, occupancy increased with summer but decreased with winter river heights. All species increased in occupancy with increasing winter rain. In *E. richardsonii*, occupancy decreased with increasing summer temperature but increased with winter rain (Fig. 3; Appendix S3: Tables S14, S15, S16).

Nocturnal, arboreal lizards

In contrast to the previous functional groups, we focus here on among study plot comparisons within a single species. While at the station body condition of *G. variegata* was mostly driven by flood parameters, in RWI temperature, rain and flood parameters were similarly important (Fig. 4). Body condition increased with summer Darling River height and winter rain at both sites, while a positive direct influence of summer rain was suppressed by a strong indirect negative effect through reduction of prey abundance. Differences were found for winter Darling River heights, which increased body condition at the RWI but decreased it at the station, and for temperature, with higher temperatures increasing but a high number of days above 45°C decreasing body condition at the RWI site (Fig. 2; Appendix S3: Tables S8, S9).

We could only examine occupancy in RWI with temperature being the most important parameter (Fig. 4). Occupancy increased with summer temperature, but decreased with an increasing number of days above 45°C. It further increased with rainfall but decreased after the area was flooded as well as with increasing eucalypt foliage (Fig. 3; Appendix S3: Table S17).

Functional traits in relation to species responses

Functional traits significantly determined the factor groups to which species responded

(Table 3). The response of body condition was mainly driven by the interaction of activity and habitat (pMANOVA, $P = 0.003$, Fig. 5a), as summarized above. To a lesser extent, species-specific prey also contributed (pMANOVA, $P = 0.07$) with arthropod feeding species responding to prey and rainfall but species feeding on fossorial arthropods to vegetation and flood (Fig. 5b). In all other model combinations, the interaction between habitat and activity remained the only significant functional trait (Table 3).

Occupancy was mainly driven by the combination of mean adult snout-vent length, minimal longevity, and habitat specialization (pMANOVA, $P = 0.01$; Table 3). Specifically, species responded more to rainfall but less to flooding with increasing body size, semelparous species responded most to predation, and habitat specialists responded more to flooding but habitat generalists to temperature and vegetation (Fig. 5c-f). The foraging mode and CT_{max} did not determine any responses, nor did the study plot.

DISCUSSION

Responses to biotic and climatic factors at both individual and population levels were species-specific, partially demonstrated opposite responses, and no single overarching factor group influenced all species. Despite those species-specific responses, we identified some consistency in terms of the factor groups to which species responded based on their functional traits. While responses of body condition were clearly determined by their activity and habitat, responses of occupancy were less clearly separated by single functional traits, with subterranean and arboreal species together being different from terrestrial species independent of their activity. Lizard body size determined responses to rainfall and flooding, longevity to predation, and habitat specialization to flooding, temperature, and vegetation.

Our findings contradict the general assumption that precipitation is the overall driver framing the ecology of species in arid ecosystems (McCluney et al. 2012, Deguines et al. 2017). We even observed some unexpected results through indirect interdependencies. Exemplarily, summer rain had a direct positive effect on body condition of *D. tessellatus* and *G. variegata*. However, increasing summer rain decreased prey, possibly

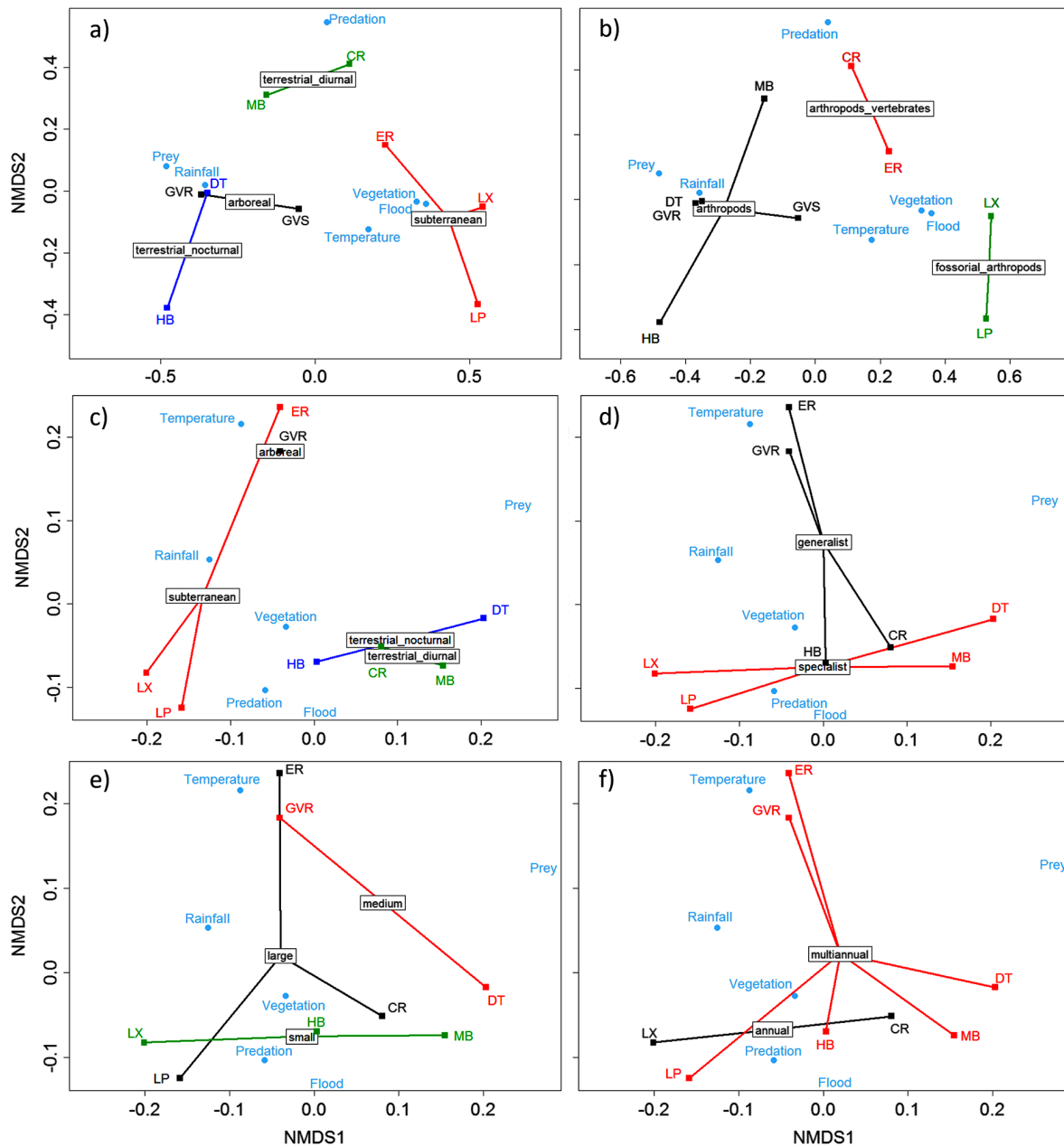


Fig. 5. Significant functional traits determining species responses in body condition (a–b) and occupancy (c–f) to biotic and abiotic factor groups: *habitat and activity* (a), *prey* (b); *habitat and activity* (c), *habitat specialization* (d), *snout–vent length* (e), and *longevity* (f). Nonmetric multidimensional scaling was used for visualization (Oksanen 2018). Species names are abbreviated using the capital letters of the genus and the species and are colored according to their functional group. Factor groups are highlighted in light blue.

due to an earlier abundance peak in early summer (Shmida et al. 1986), while simultaneously increasing predator abundance, together canceling or even reversing the direct effect in both

species. On population level, abundance of desert lizards often shows contrasting responses to rainfall. Exemplarily, Dickman et al. (1999) found that the agama *Ctenophorus nuchalis* was

most abundant in dry years with little vegetation cover, while *C. isolepis* was most abundant in wet years with high vegetation cover. Other observations showed differences among functional groups with some nocturnal gecko species being most abundant in wet years but the diurnal, terrestrial *Ctenotus leonhardii* being most abundant in dry years (Read et al. 2012). In this study, rainfall was most important for larger species and more important for subterranean and arboreal species than for terrestrial species, with increasing rainfall increasing occupancy.

In support to previous studies (Flesch et al. 2017), we identified prey availability as an important driver for desert lizards, with increasing prey abundance always increasing body condition corroborating that food availability and food intake are positively correlated (Henle 1989a, 1990b). Increasing prey abundance further increased occupancy in all nocturnal species, presumably through increasing lizard abundances, as shown for *G. variegata* (Henle 1990a). The opposite response pattern was observed for diurnal lizards. This may result from differences in habitat selection rather than from variations in abundance since high prey abundance was highly associated with shrub coverage, which could lead to aggregations of diurnal lizards around bushes (Shmida et al. 1986).

While prey abundance was more important than predator abundance for some species (bottom-up forces), predation pressure had greater importance for others (top-down forces). Pianka (1986) stated that desert lizard communities, particularly in Australia, are to a large extent shaped by predation. We found that increasing predation pressure diminished body condition, presumably due to increasing energetic costs with predator avoidance strategies (Pianka 1986) since lizards face trade-offs between feeding and fleeing (Cooper and Pérez-Mellado 2004) or hiding (Amo et al. 2007). The only species which showed a positive correlation of body condition with predator abundance was *G. variegata*. While this seems unexpected at first glance, it is in line with previous findings showing that adult mortality increased with decreasing body condition (Henle 1990a), suggesting that predators presumably have primarily caught individuals with lower body condition, increasing the average body condition among surviving individuals.

Predator abundance further decreased occupancy of iteroparous but increased that of semelparous species. It has been shown before that predation increased mortality for the iteroparous species *G. variegata* (Henle 1990a), *M. boulengeri* (Henle 1989a), and nocturnal, terrestrial geckos (Henle 1990b), and, thus, decreased occupancy. For semelparous species, changes in occupancy are more likely through changes in reproductive success. In an experiment with fish species, Magnhagen (1990) could show that under predation pressure, semelparous species, which have a pressure to reproduce in their first season, reproduced equally well, while iteroparous species did not reproduce as they might benefit more from delaying reproduction by one year. To our knowledge, this has not yet been investigated in lizard species. However, we assume similar responses as lizards have adjustable reproductive strategies in relation to mortality risks like predation pressure (Amat 2008). Our results indicate that semelparous lizards might even increase their reproduction rate under predation pressure resulting in increased occupancy.

For terrestrial lizards, temperature was recently called the limiting factor (Kearney et al. 2009, Gunderson and Stillman 2015). However, in this study temperature has not been the main factor affecting lizards at individual or population level. At the individual level, temperature was affecting nocturnal but not diurnal lizard species, with reverse effects on skinks and geckos, presumably due to different evolution of nocturnality (Huey and Bennett 1987, Huey et al. 1989, Autumn et al. 1999). Increasing summer temperatures declined body condition of skinks but increased that of geckos, whereas an increasing number of days above 45°C increased it in skinks but declined it in geckos. High temperatures are a prerequisite for body growth (Greer 1989). Geckos may grow extremely fast during hot periods (i.e., many days above 45°C), while body mass might not increase in the same intensity (Autumn and De Nardo 1995) leading to lower body condition. At the population level, the effects of temperature were weaker and evident only for four of the six nocturnal species, while there was no effect on diurnal species. Higher summer temperatures usually increased occupancy, suggesting potential strategies on individual level that compensate effects on

population level (Adolph and Porter 1993, Grimm-Seyfarth et al. 2018). *Eremiascincus richardsonii* was the only species that declined in occupancy with increasing temperature, but it was also the only habitat generalist whose favorite habitat, an adjacent sand dune, was not included in the three study plots (Henle 1989c).

Fluctuations in lizard occupancies were most related to temperature in iteroparous habitat generalists, but to the flooding regime of the bordering Darling River otherwise. Specifically, flooding at RWI destroyed arthropod burrows and condensed the soil making the habitat unsuitable for *D. tessellatus* and recolonization necessary. During or immediately after adjacent floods at RWI, the edges of the sandy clay became sandier and with more leaf litter (photograph comparison) and thus more favorable for *L. punctatovittata* and *H. binoei*, whereas the two diurnal skinks *M. boulengeri* and *C. regius* probably avoid high soil moisture (Briggs et al. 2000). Rivers of highly variable flow regimes, such as the Darling River, are components of many desert systems (Kingsford and Thompson 2006). They may transport the effects of climate change taking place at distant regions over considerable distances strongly impacting the local desert reptile community. However, despite river heights themselves being strongly related to La Niña events (Grimm-Seyfarth et al. 2018), the subsequent flooding is regulated for water supply and irrigation (Murray-Darling Basin Authority 2015). If flooding of the area would be decreased in duration or even prevented in the future, it would prevent the lizard community from natural fluctuations and also affect the well-adapted vegetation (Roberts and Marston 2000), changing important habitat requirements (Grimm-Seyfarth et al. 2017). Flooding might be a disturbance on the first look (McCluney et al. 2012), but it is an important component of the unique arid-zone lizard community.

With advancing climate change, hot deserts will become hotter and dryer (Noble and Gitay 1996). Even small changes in temperature or precipitation could change desert species' composition (Sala 2000). However, due to species-specific differences in the trophic and climatic interrelationships, we may accurately predict future changes in species abundance and occurrence only if these interdependencies are understood

and accounted for (Walther 2010). Our results suggest that robust predictions of future distributions of species under climate change require consideration of such mechanisms. Regrettably, we often lack the relevant information for many species (Urban 2016). Since one might never get all necessary information to accurately calibrate mechanistic models for all species, modeling species and community response through functional groups instead of true species might offer a promising solution. This study gives an indication how to identify relevant functional groups at different ecological levels, which could be important for both fieldwork targeted at determining relevant mechanistic processes and for conservation. Further field data of other species are necessary to obtain more robust functional grouping, especially on population level. This should lead to adjusted management strategies for the conservation of desert ecosystems and to prevent impacts of climate change in desert reptile communities.

ACKNOWLEDGMENTS

Research was carried out under permit numbers SL100593, 10935, and A478 of the NSW National Parks and Wildlife Service. This licence covered all animal ethics considerations as well as a permit to capture the animals. Our special thanks are due to their staff at Kinchega National Park for access to their field station, the Department of Zoology and Botany, Australian National University, and the Institute for Applied Ecology, University of Canberra, for support with logistics. Research in 2012 and 2015–2016 was funded by the German National Academic Foundation and the German Research Foundation (DFG), respectively. All authors conceived the ideas, designed the general methodology, and collected field data. AGS analyzed the data, performed the modeling, and led the writing of the manuscript. All authors contributed critically to the drafts and gave their final approval for publication.

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DATA ACCESSIBILITY

All abiotic data are available online: Climate data: Bureau of Meteorology, Australian Government (<http://www.bom.gov.au/climate/data/stations>). Darling River level at weir 32: Department of Primary Industries, Office of Water, New South Wales Government; http://realtimedata.water.nsw.gov.au/water.stm?ppbm=DAILY_REPORTS&dr&3&drkd_url). Species data: Data for *Gehyra variegata* are available through DRYAD: <https://doi.org/10.5061/dryad.j0j2b70/1>. Data for the remaining species are available upon request through the Department of Conservation Biology, Helmholtz-Centre for Environmental Research – UFZ. Monitoring data of all species have been provided to National Parks & Wildlife Service NSW / Atlas of Living Australia (<https://regions.ala.org.au/feature/5749748>).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2865/full>

Appendix S1: Overview on underlying field and analytical methods to derive indices for vegetation, prey and predators for the structural equation models

Appendix S2: Structural equation modelling; pre-analyses and paths selection

Appendix S3: Summary results of structural equation models (SEMs)