



Successional changes in trophic interactions support a mechanistic model of post-fire population dynamics

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Abstract

Models based on functional traits have limited power in predicting how animal populations respond to disturbance because they do not capture the range of demographic and biological factors that drive population dynamics, including variation in trophic interactions. I tested the hypothesis that successional changes in vegetation structure, which affected invertebrate abundance, would influence growth rates and body condition in the early-successional, insectivorous gecko *Nephurus stellatus*. I captured geckos at 17 woodland sites spanning a succession gradient from 2 to 48 years post-fire. Body condition and growth rates were analysed as a function of the best-fitting fire-related predictor (invertebrate abundance or time since fire) with different combinations of the co-variables age, sex and location. Body condition in the whole population was positively affected by increasing invertebrate abundance and, in the adult population, this effect was most pronounced for females. There was strong support for a decline in growth rates in weight with time since fire. The results suggest that increased early-successional invertebrate abundance has filtered through to a higher trophic level with physiological benefits for insectivorous geckos. I integrated the new findings about trophic interactions into a general conceptual model of mechanisms underlying post-fire population dynamics based on a long-term research programme. The model highlights how greater food availability during early succession could drive rapid population growth by contributing to previously reported enhanced reproduction and dispersal. This study provides a framework to understand links between ecological and physiological traits underlying post-fire population dynamics.

Keywords Disturbance · Fire management · Functional traits · Habitat accommodation model · Pyrodiversity

Introduction

Temporal population dynamics depend on a range of interacting demographic, biological and environmental factors (Hodges et al. 2006) including predator–prey cycles (Radchuk et al. 2016), climatic fluctuations (Letnic and Dickman 2010) and density-dependent competition for resources (Forero et al. 2002). In fire-prone ecosystems, periodic disturbance and subsequent habitat succession add additional

layers to the already complex suite of factors driving population dynamics (Burgess and Maron 2016; Davies et al. 2012). However, changes in post-fire population density are often interpreted as responses to changing habitat complexity with time since fire (e.g. Nimmo et al. 2012; Smith et al. 2013b), following the habitat accommodation model of animal succession (Caughley 1985; Fox 1982). Few studies consider the interacting biological and demographic mechanisms which drive population dynamics and how the mechanisms themselves change with time since fire. This means we still lack the ability to predict how ecological communities respond to variation in fire regimes, such as increases in fire frequency or changes in the spatial configuration of fires (Kelly et al. 2011; Westgate et al. 2012). This predictive capacity is essential to plan and implement fire management strategies that will conserve biodiversity (Driscoll et al. 2010). It also underpins our knowledge of how ecosystems will respond to the rapid changes in fire regimes that are

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occurring with climate change (Moritz et al. 2012; Silvério et al. 2013).

Models based on functional ecological traits have proven valuable in understanding plant responses to varying fire regimes (e.g. Keith et al. 2007; Pausas 2015), but have limited power in predicting disturbance responses in animal communities (Bargmann et al. 2016; Hu et al. 2013; Kelly et al. 2011; Santos et al. 2014). One reason is that these models do not capture the complex interactions that affect animals during post-fire succession such as rainfall (Greenville et al. 2016), grazing (Driscoll et al. 2012), soil type (Davies et al. 2012) and inter-specific interactions (St. Clair et al. 2016). For example, Nimmo et al. (2014) showed that regional differences in fire–vegetation relationships obscured generalisable patterns of post-fire abundance in animal species. Another reason is the severe lack of ecological and life-history data for the majority of animal species targeted by these studies. Coarse ecological trait groups such as ‘low’ or ‘high mobility’ are often used (necessarily, given scarce data, e.g. Santos et al. 2014) which might not provide enough resolution to detect complex ecological responses. In other cases, so little is known about some species that they cannot be assigned to even coarse groups (Smith et al. 2013b). Improved ecological data for a range of species in the community are needed. At the individual species level, data showing how ecological traits and demographic rates change during succession will provide deeper insight into the mechanisms underlying post-fire population dynamics.

A range of processes might contribute to post-disturbance population dynamics within animal species including changes in dispersal rates (Templeton et al. 2011), survival and reproductive rates (Sanz-Aguilar et al. 2011) and intraspecific social interactions (Banks et al. 2012). Trophic interactions are another potentially important driver (Bowman et al. 2016). For example, increasing reproduction and local abundance of plant species after fire can be partially driven by disrupted interactions with antagonistic herbivores (García et al. 2016; St. Clair et al. 2016). Much of the work on post-fire trophic interactions has focussed on plant–herbivore relationships (e.g. Caut et al. 2014; Cherry et al. 2016) or predation of native mammals by exotic carnivores (e.g. Leahy et al. 2016; McGregor et al. 2014). Knowledge of interactions at a wider range of trophic levels is needed to develop a general understanding of how this process contributes to post-fire population dynamics (Di Stefano et al. 2014). Furthermore, understanding how successional changes in trophic interactions relate to other mechanisms driving population dynamics is necessary to advance basic ecological knowledge and to develop better predictive models for biodiversity conservation.

In this study, I tested the hypothesis that successional changes in vegetation structure which influence invertebrate abundance would be reflected in variation in growth

rates and body condition in a disturbance specialist, insectivorous gecko *Nephrurus stellatus*. The gecko species has a strong and regionally consistent response to fire: population density increases for 10–15 years after fire then declines sharply to less than 10% of peak density 30 years or more after fire (Driscoll and Henderson 2008; Driscoll et al. 2012; Smith et al. 2013b). This reflects variation in population density, not detectability (Smith et al. 2012). At the same study sites, invertebrate abundance is higher in the first 5 years after fire, compared with habitat that has not burned for over 30 years (Teasdale et al. 2013). As burrowers, *N. stellatus* can probably survive fire and recently burnt habitat might allow them to forage more efficiently in open, sandy spaces (Smith et al. 2013b) although direct evidence for this is currently lacking. Successional changes in factors such as predation pressure (Hawlena et al. 2010), parasitism (McCoy et al. 2012) and thermal specialisation (Hossack et al. 2009) might also drive changes in body condition and growth rates. However, links between invertebrate abundance and growth trajectories in geckos would provide support for the hypothesis that changes in trophic interactions influence post-fire population dynamics.

Long-term mechanistic studies of single species have greatly advanced ecological knowledge of temporal population dynamics [classic examples include studies of voles (Radchuk et al. 2016), lemmings (Therrien et al. 2014) and snowshoe hares (Hodges et al. 2006)]. The fire ecology of *N. stellatus* has now been studied for over a decade (Driscoll and Henderson 2008; Driscoll et al. 2012; Smith et al. 2012, 2013a, b) and the species could make a valuable contribution to our understanding of post-fire population dynamics. As population density increases after fire, survival rates are low while reproductive rates almost double, offsetting the lower survival and contributing to the rapid increase in population density (Smith et al. 2012). Spatial genetic structure is greatest during very early succession, probably reflecting rapid population expansion from a very small number of individuals at the time of the fire (Smith et al. 2016b). As population density declines, genetic diversity and rates of dispersal and movement also decline (Smith et al. 2016b). Given this detailed body of knowledge, the second aim of the current study was to integrate the new findings about body condition and growth rate into a general conceptual model of mechanisms behind post-fire population dynamics. This in-depth investigation of a single species provides a framework to understand linkages between ecological and life-history traits which underlie temporal population dynamics. This will help guide future mechanistic research in animals, improving our ability to predict animal responses to variation in fire regimes.

Materials and methods

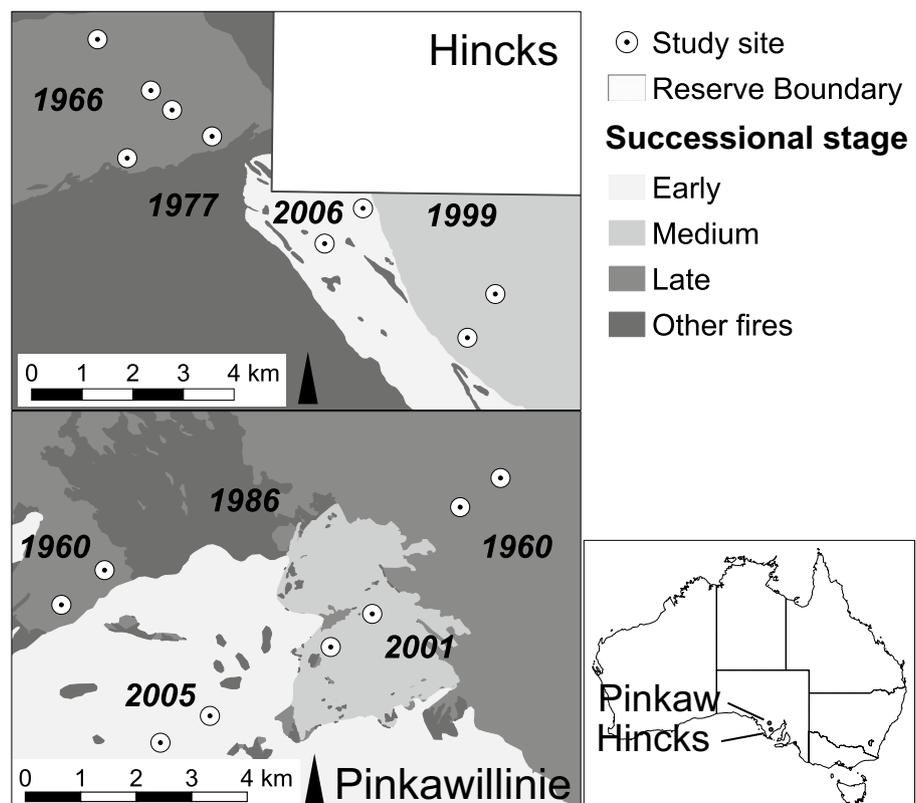
Study system and design

The study was conducted in two large reserves in the semi-arid (average annual rainfall: 296–361 mm), Mediterranean-type ecosystem of the Eyre Peninsula, South Australia: Hincks Wilderness Area (67,000 ha) and Pinkawillinie Conservation Park (132,000 ha) (Fig. 1). *Nephrurus stellatus* is largely restricted in its distribution to the Eyre Peninsula region. The dominant vegetation is ‘mallee’ woodland, characterised by short (< 6 m), multi-stemmed *Eucalyptus* trees, with a shrubby midstorey and *Triodia* grass ground-layer (Smith et al. 2012). Large, severe wildfires, commonly ignited by summer lightning, occur on a 10- to 100-year time scale (Gibson et al. 2015). Fire history was characterised using spatial data on the number of years since the most recent fire (South Australian Department for Environment, Water and Natural Resources). Previous mark recapture studies showed that fire and subsequent habitat succession affected abundance, survival, reproduction (Smith et al. 2012) and movement rates (Smith et al. 2016b) in *N. stellatus*. The current study is based on data collected during those surveys and examines whether morphology and growth rates are related to post-fire succession.

I established 17 sites and broadly classified them into three fire categories based on time since last fire (Fig. 1): ‘early’ [2–3 years since fire at the time of first data collection (2008)], ‘medium’ (7–9 years) and ‘late’ (42–48 years). Marked differences in vegetation structure occur among these categories (Smith et al. 2012). Other factors at the sites were similar, including the presence of sandy soil and *T. irritans*, an important habitat plant for many reptiles (Pianka 1969). At each reserve, two sites were sampled in the early and medium fire categories. Four and five sites were sampled in the late fire category at Pinkawillinie and Hincks, respectively, in anticipation of low capture rates (Driscoll and Henderson 2008). At each site, geckos were captured in pitfall traps over two spring–summer sampling seasons (November 2008–February 2009 and November 2009–February 2010) (trapping details in Smith et al. 2012). Three trapping sessions were conducted during each season with traps open for 5–15 (mean = 8) days per session. There were 0.5–2 months between sessions within seasons and 8–9 months between seasons (Smith et al. 2012). During each session, traps at all sites within reserves were opened and closed at the same times.

Snout–vent length (mm) and weight (g) (measured using a 30 g Pesola scale) were recorded for each captured individual. I recorded age as adult or juvenile based on size to sexual maturity (male = 55 mm, female = 70 mm, Smith et al. 2012). Adult sex was determined by external

Fig. 1 The insectivorous gecko *Nephrurus stellatus* was sampled in two conservation reserves in southern Australia at 17 sites representing a range of fire histories. Sites were broadly classified into three successional stages (early, medium and late) based on the time since last fire (the actual year of the last fire is shown in italics). Invertebrate abundance varied among these successional stages (Fig. S1)



hemipenial bulges, obvious in males but not females. Sex was known for some juveniles in the data because they were later captured as adults (males reach maturity in their first year and females in their second, Smith et al. 2012). More males were captured than females (Table S1), but I previously found no effect of fire category on the age or sex structure of the population and little support for sex, age or fire effects in detectability (Smith et al. 2012). Adult females were scored as gravid when well developed eggs were visible. Previous work showed that post-fire succession affected the reproductive condition of females (57% of females were gravid in the medium fire category vs. 94% in the early fire category, Smith et al. 2012). Thus, to avoid biasing growth rate and body condition estimates with fire-related variation in reproductive condition, I removed gravid individuals from the current data set. Visible Implant Elastomer (Northwest Marine Technology) was used to mark geckos and reliably identify individuals upon recapture (Smith et al. 2012). All geckos were released at their capture location within 24 h of processing.

To quantify food abundance, I used data from a previous study of the effect of post-fire succession on the invertebrate fauna, in which invertebrates were sampled from the same sites as the geckos in the current study (Teasdale et al. 2013). Three different sampling methods were used: (1) small and (2) large pitfall traps which generally sampled small and large ground-dwelling invertebrates, respectively, and (3) sweep nets which sampled invertebrates on bare ground, in low vegetation (e.g. grasses and shrubs) and in the shrub and tree canopy. There was little overlap in community composition among these methods (Teasdale et al. 2013), suggesting they each sampled a different subset of the invertebrate fauna.

Analysis

For the metric of body condition, I used the residuals from a linear regression of $\log(\text{weight})$ as a function of $\log(\text{snout-vent length})$ (Naulleau and Bonnet 1996). Only the first observation from each captured individual was included in the body condition analysis. Variation in body condition was analysed in two separate data sets: all individuals (433 observations, Data set 1) and adult individuals (261 observations, Data set 2) (Table S1). Growth rates were calculated as the change in weight (Data set 3) and snout-vent length (Data set 4) between captures, divided by the time between captures (mean = 62 days, median = 23, range = 2–435) (Campos et al. 2013; Jarvie et al. 2015; Webb and Shine 1998). The growth rate data included only individuals that were captured more than once (300 observations of 159 individuals, Table S1). Each growth record was included as a separate observation, e.g. geckos captured

twice had one observation while those captured three times had two observations.

I used linear mixed-effects models in the R (R Core Team 2017) package ‘lme4’ (Bates et al. 2013) to analyse variation in body condition and growth rates. Models were fitted using the maximum likelihood criterion to enable model comparison (Zuur et al. 2009). In the first stage of analysis, I investigated seven different fire-related variables separately to determine the best predictor of body condition and growth rate (Table S2). Four of these were measures of invertebrate abundance: sweep net, small pitfall, large pitfall (Fig. S1) and all invertebrates (the summed abundance from the three methods). I also tested linear and unimodal forms of time since fire (the number of years since the most recent fire at a given sample site) and fire category, a three-level factor describing post-fire succession as ‘early’, ‘medium’ and ‘late’ (described above and shown in Fig. 1). All numeric predictors (i.e. all except fire category) were standardised prior to analysis ($(x - \text{mean}(x))/\text{SD}(x)$). In this stage of the analysis, I kept the fire-related predictor and reserve in all models and, for growth rates, also included age. I ranked models by AICc in the ‘AICcmodavg’ package (Mazerolle 2012) and used the top-ranked predictor in the main analysis. Invertebrate abundance from sweep nets was the best fire-related predictor of body condition in all individuals and adults (Table S2). The linear form of time since fire was the best predictor of growth rate in weight (Table S2). Invertebrate abundance from small pitfall traps was the best fire-related predictor of growth rate in snout-vent length. However, the null model ranked highest, suggesting little evidence of fire-related variation in growth in length (Table S2).

My overarching aim was to determine if there were successional changes in body condition and growth rates, thus I kept the fire-related variable in all models as the primary design variable. I used model selection primarily to determine which co-variables to include with the fire-related variable because data limitations prevented me from fitting a full model. For comparison, I also fitted a null model for each data set with no variation in fixed effects. For body condition, I considered all additive and two-way interaction models with the co-variables age and reserve (all individuals) and sex and reserve (adult individuals). Preliminary analysis showed that three-way interaction models (e.g. fire \times sex \times reserve) were ranked lower than all other models and were overparameterised, thus I did not include them in the final analysis. Season (a two-level factor indicating the two spring-summer sampling seasons) was included in preliminary analysis but was never significant ($P > 0.05$), so was not included in the final models. I initially fitted site nested within ‘fire’ (a factor naming individual fire events) as a random effect. However, variation in the site random term in all models was approximately zero so I removed it

to reduce model complexity. This did not influence model rankings or estimates of fixed effects, indicating that the fire random effect adequately accounted for spatial clustering of individuals and repeated sampling of the same fire event (Fig. 1).

Each observation in the growth rate data included an age at time 0 and an age at time 1. To account for age-specific growth rates, common in reptiles (e.g. Wright et al. 2013), I fitted a two-level factor (adult/juvenile) to all models, based on the age at time 0. Preliminary analysis showed that this age variable explained more variation in growth rate than a three-level factor which included a small number transitions (6% of observations) between juvenile and adult in the time between captures (juvenile:juvenile/juvenile:adult/adult:adult). Multiple recaptures were included (e.g. an individual captured three times had two observations in the data). I initially fitted individual nested within site, within fire as a random effect. However, variance on the individual and site random terms was zero in all models and removing these terms did not affect rankings or parameter estimates. Thus, the final models included the fire random effect only. I ranked models by AICc and, to incorporate model uncertainty into the conclusions, I evaluated the effect sizes of all

models within $\Delta\text{AICc} < 4$ (Hegyi and Garamszegi 2011; Smith et al. 2016a).

To determine if there was spatial autocorrelation in the residuals of the first-ranked models for each data set, I produced variograms using the geoR package (Ribeiro and Diggle 2001) in R for each response variable at each reserve. The data were divided into 11 distance classes and visually assessed for spatial autocorrelation. There was no evidence of a sill that would indicate spatial autocorrelation in the model residuals (Liebhold and Sharov 1998) (Fig. S2).

Results

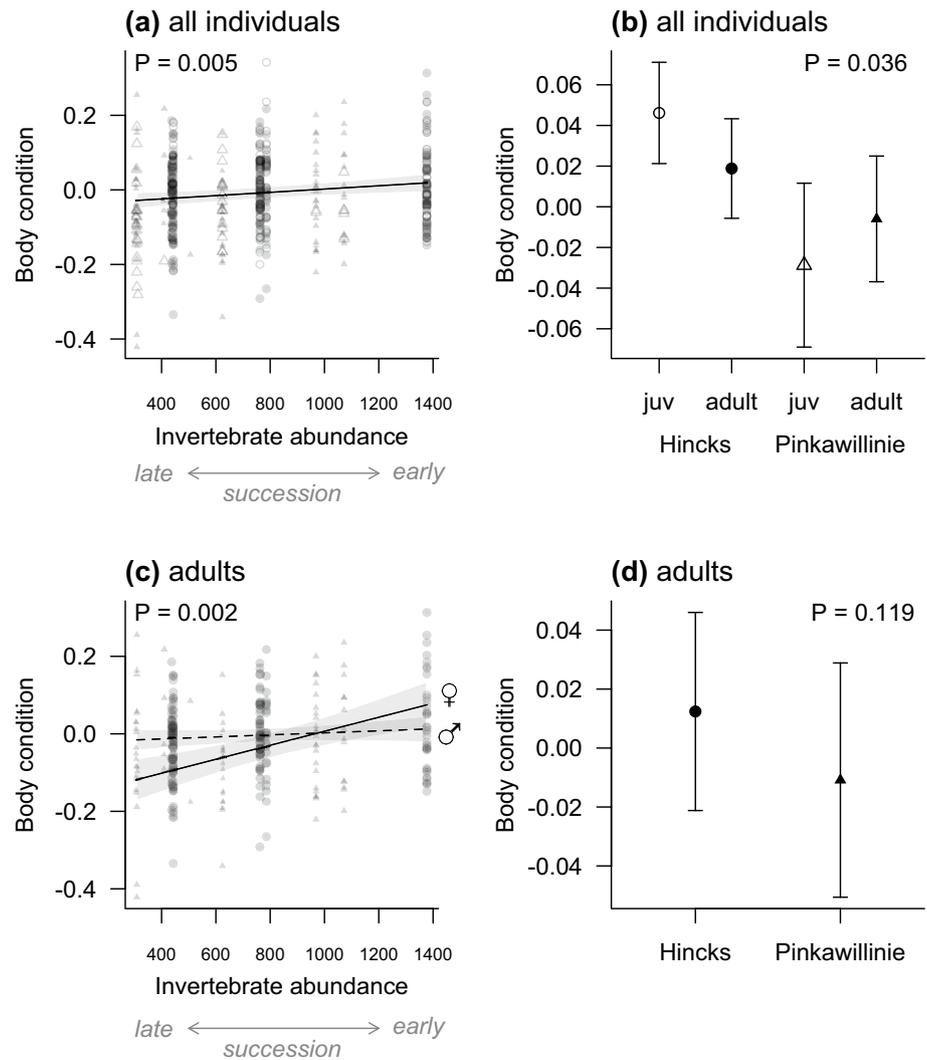
Models ranked within $\Delta\text{AICc} < 4$ are shown in Table 1 and Fig. S3, full model rankings are in Table S3 and coefficients for all models are in Supplementary Material 1. The first-ranked model for body condition in all individuals (AICc weight = 44%) included invertebrate abundance and an interaction between age and reserve (Table 1). Body condition increased with increasing invertebrate abundance (Fig. 2a) and was higher in juveniles than adults at Hincks (Fig. 2b). There was also support for a main effect of reserve

Table 1 Model selection results from analysis of body condition (all individuals and adult individuals) and growth rates (weight (g/day) and snout–vent length (mm/day)) in *Nephrurus stellatus*

Data and model	df	Log-likelihood	AICc	ΔAICc	AICc weight	Cumulative weight
<i>Data set 1: body condition all individuals</i>						
Invertebrate abundance + age \times reserve	7	344.83	− 675.40	0.00	0.44	0.44
Invertebrate abundance + reserve	5	341.93	− 673.73	1.67	0.19	0.63
Invertebrate abundance + reserve + age	6	342.65	− 673.10	2.30	0.14	0.77
Invertebrate abundance \times reserve	6	342.22	− 672.25	3.15	0.09	0.86
Invertebrate abundance \times reserve + age	7	343.09	− 671.92	3.48	0.08	0.93
<i>Data set 2: body condition adults</i>						
Invertebrate abundance \times sex + reserve	7	198.70	− 382.95	0.00	0.50	0.50
Invertebrate abundance \times sex	6	197.49	− 382.64	0.31	0.43	0.94
<i>Data set 3: growth weight</i>						
Time since fire \times age	6	186.95	− 361.54	0.00	0.36	0.36
Time since fire + age	5	185.24	− 360.21	1.32	0.18	0.54
Time since fire \times age + reserve	7	187.02	− 359.55	1.99	0.13	0.68
Time since fire + age + reserve	6	185.24	− 358.12	3.42	0.06	0.74
Time since fire \times age + sex	8	187.30	− 357.97	3.57	0.06	0.80
<i>Data set 4: growth snout–vent length</i>						
Null model	3	3.09	− 0.07	0.00	0.50	0.50
Invertebrate abundance + age	5	4.15	1.95	2.02	0.18	0.68
Invertebrate abundance \times age	6	4.48	3.39	3.46	0.09	0.77

The best-fitting fire-related predictor (invertebrate abundance and time since fire) was determined in the first stage of analysis and varied among data sets (Table S2). Invertebrate abundance refers to samples from sweep nets for body condition in all and adult individuals and to samples from small pitfall traps for growth rate in snout–vent length. Models that differed in AICc from the top model (ΔAICc) by < 4 are shown (see Table S3 for rankings of all models and Supplementary Material 1 for coefficients and standard errors from all models)

Fig. 2 Results from the first-ranked models of body condition in *Nephrurus stellatus* for all (**a**, **b** Data set 1) and adult (**c**, **d** Data set 2) individuals. In all individuals there was **a** a main effect of invertebrate abundance on body condition (model estimates and 95% confidence intervals shown for adults at Hincks) and **b** an interaction between age and reserve (estimates shown for maximum invertebrate abundance). In adults there was **c** an interaction between invertebrate abundance and sex (estimates shown for Hincks) and **d** a main effect of reserve (estimates shown for males at maximum invertebrate abundance). The raw data are plotted in panels **a** and **c** and the symbols correspond to those in panels **b** and **d**. Invertebrate abundance was greater in early-successional habitats (see Fig. S1)



on body condition, being overall lower at Pinkawillinie than Hincks (second-ranked model AICc weight = 19%; Fig. S3). The first-ranked model for body condition in adults (AICc weight = 50%) included an interaction between invertebrate abundance and sex and a main effect of reserve (Table 1). Body condition increased with increasing invertebrate abundance in females but not males (Fig. 2c) and was higher at Hincks than Pinkawillinie (Fig. 2b). Models of adult body condition without this interaction had little support (AICc weight < 1%, Table S3) indicating the effects of invertebrate abundance were stronger for adult females than males.

The first-ranked model for weight growth rate included an interaction between time since fire and age (AICc weight = 36%, Table 1). Growth rate declined with increasing time since fire in adults and increased for the first 10 years after fire in juveniles (Fig. 3). There were no juvenile re-captures from late-successional vegetation, so the growth rate trajectory beyond 10 years for juveniles could not be reliably modelled. The second-ranked model

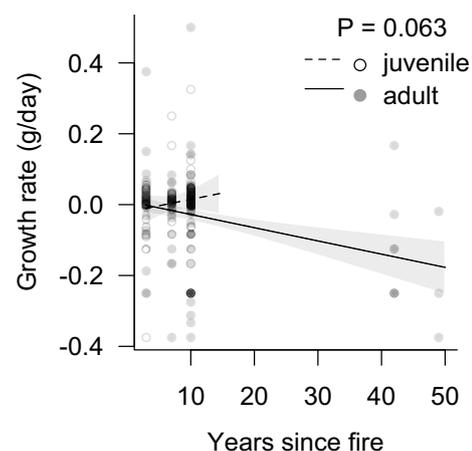


Fig. 3 The first-ranked model of weight growth rate (g/day) in *Nephrurus stellatus* (Data set 3) included an interaction between age and the linear form of time since fire. Model estimates and 95% confidence intervals are shown over the raw data. Estimates for juveniles are only presented up to 15 years post-fire as there were no growth rate data for juveniles in late-successional habitat

(AICc weight = 18%, Table 1) indicated an overall decline in weight growth rate with time since fire, regardless of age (Fig. S3). This main effect was strong in all models within $\Delta\text{AICc} < 4$ (Fig. S3), thus the general decline in weight growth rate with time since fire was well supported by the data. There were no important effects of reserve or sex on weight growth rate (Fig. S3). For growth rate in snout–vent length, none of the models ranked higher than the null model (Table 1) and none of the terms in second or third ranked models were important (Fig. S3).

Discussion

This study points to changes in body condition and growth rates as one of several mechanisms related to post-fire population dynamics in the disturbance specialist gecko *Nephurus stellatus*. Geckos inhabiting recently burnt vegetation where invertebrate abundance was highest had enhanced body condition and the highest rates of growth in weight, compared to long-unburnt vegetation. Thus, previously reported increases in invertebrate abundance after fire (Teasdale et al. 2013) might have filtered through to a higher trophic level, with physiological benefits for insectivorous geckos. This could arise through a combination of increased food availability (Teasdale et al. 2013), increased foraging efficiency in more open vegetation after fire (Vernes and Haydon 2001) and/or increased food nutrient levels (Ferran and Vallejo 1992; Joern et al. 2012). In late-successional vegetation (> 30 years since fire) where *N. stellatus* is rare, growth rates were negative showing that individuals were losing weight between captures. This reveals a potential mechanism underlying the decline in population density with time since fire: geckos might have a reduced ability to find and consume invertebrate prey, leading to declines in weight and possibly population-level fitness (Chamaillé-Jammes et al. 2006; Wikelski and Wrege 2000).

In the adult population, early-successional invertebrate abundance had a positive influence on body condition in females but not males. This was unlikely influenced by reproductive status, since gravid females were not included in this study. However, if small, developing eggs remained undetected, they could have contributed to the effect on female body condition since fecundity in *N. stellatus* is higher during early succession (Smith et al. 2012). A more likely explanation is that investment in body mass is more critical for females than males given the importance of female body condition on reproductive success (Wang et al. 2017). In the common wall lizard *Podarcis muralis*, females adapted reproductive investment to environmental change quickly, while males lagged behind (MacGregor et al. 2017). In *N. stellatus*, females might also be better equipped than males to exploit increased post-fire food abundance given

they are larger [mean (SD) adult mass $g = 13.49$ (4.48) vs. 8.63 (2.42) in males] and show evidence of female-biased dispersal (Smith et al. 2016b). The lack of successional changes in growth in length, when weight growth rates did change, is unlikely due to measurement error. Care was taken to measure length precisely and three repeat measurements of three *N. stellatus* individuals suggested reasonable precision [mean (SD) = 73.0 (0.0), 50.0 (1.0), 78.7 (0.6) mm]. It is possible that body weight responds more strongly to ecological factors (including feeding and movement patterns) than body length in *N. stellatus*, as has been found in lizards more generally (Meiri 2010).

Variation in body condition and growth rates can reflect factors other than food availability, food quality and foraging success. For example, high predation risk can also drive weight loss because stress hormones accelerate gluconeogenesis, even when food availability is high (Hodges et al. 2006). In *N. stellatus* however, growth rates and body condition were highest in recently burnt vegetation where survival rates are low (Smith et al. 2012) probably partly due to high predation pressure in more open vegetation (Hawlena et al. 2010). Increasing investment in reproduction can also decrease body condition (Cox et al. 2010), but body condition in *N. stellatus* was highest in recently burnt habitat where reproductive investment is also high (Smith et al. 2012). High predation risk and reproductive investment at the population level have not limited the physiological benefit of greater food resources. When resources are not limiting, increased body condition and growth rates can enhance reproductive success (Ruffino et al. 2014) and dispersal (Phillips 2009). Thus, exploitation of greater food availability during early succession might contribute to the rapid increase in population density after fire by driving previously reported successional changes in reproduction (Smith et al. 2012) and dispersal (Smith et al. 2016b) in *N. stellatus* (Fig. 4). Successional variation in parasite prevalence might also affect lizard physiology (McCoy et al. 2012) but very little work has addressed this.

The decline in population density that begins 10–15 years after fire might be driven by absolute declines in food availability but also by density-dependent competition for food and space (Forero et al. 2002). At approximately 10 years after fire, growth rates in juveniles were higher than in adults (Fig. 3) suggesting that density-dependent competition might be strongest among adults. Reproductive rates are also likely to be density dependent as the ability to find mates would decline with time since fire (Allee effects, Gascoigne et al. 2009) (Fig. 4). Overall, the demographic and inter-specific mechanisms that drive population dynamics must be viewed in the context of broader environmental factors. For *N. stellatus*, the population density response to time since fire is relatively consistent, but the response of many other reptile species varies regionally (Driscoll and

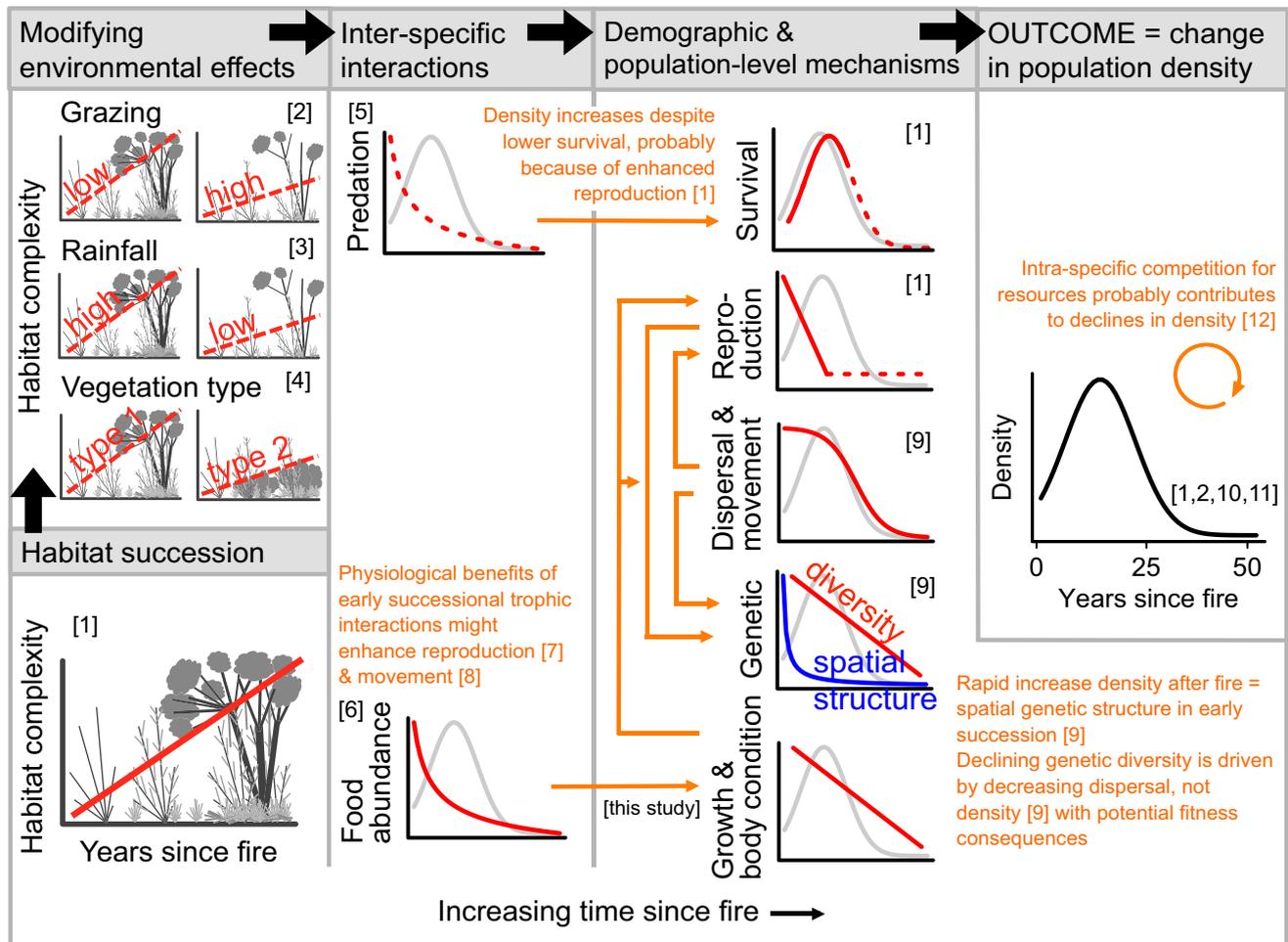


Fig. 4 Mechanisms underlying post-fire population dynamics. The grey lines on each plot show how population density changes with time since fire in the disturbance specialist gecko *Nephrurus stellatus*. The solid lines indicate mechanisms contributing to the change in population density that have been directly studied in *N. stellatus*. Dashed lines were inferred from other studies or estimated where data on *N. stellatus* was limited. The thick black arrows indicate how different types of mechanisms are related. For example, changes in habitat complexity with time since fire can be modified by regional-scale environmental drivers such as rainfall, grazing and vegetation type which will influence how in inter-specific interactions affect popula-

tion processes during succession. Demographic factors can influence population density directly or by influencing other population-level mechanisms, indicated by the arrows connecting the plots. Competition among species at the same trophic level also drives population dynamics (Cunningham et al. 2009), but has not been directly studied in this system beyond basic data on abundance in other reptiles (Smith et al. 2013b). References: [1] Smith et al. (2012), [2] Driscoll et al. (2012), [3] Greenville et al. (2016), [4] Nimmo et al. (2014), [5] Hawlena et al. (2010), [6] Teasdale et al. (2013), [7] Ruffino et al. (2014), [8] Phillips (2009), [9] Smith et al. (2016b), [10] Driscoll and Henderson (2008), [11] Smith et al. (2013b), [12] Forero et al. (2002)

Henderson 2008; Nimmo et al. 2014). Considering how rainfall (Greenville et al. 2016), grazing (Driscoll et al. 2012), and vegetation type (Nimmo et al. 2014) modify demographic processes after fire will be important in studies of other species (Fig. 4).

Few species will respond to fire in the same way as *N. stellatus* given the complex interplay between post-fire habitat succession, demography, inter-specific interactions and environment. However, by synthesising knowledge about this species, some key ecological and life-history traits that underlie post-fire population dynamics have become apparent, including important linkages among these mechanisms

(Fig. 4). This study suggests that changes in trophic interactions following disturbance might contribute to changes in population density after fire and to successional changes in dispersal and reproduction. Factors which enhance reproduction are likely to be critical because reproductive rates must be especially high to drive a rapid increase in population density at times of lower survival (Fig. 4). Future studies of post-fire community dynamics will benefit from grouping species based on their dispersal ability, food requirements and post-fire reproductive rates, in addition to their habitat requirements. This functional approach should provide greater power to predict post-fire responses at the community

level than models based predominantly on habitat complexity. At the population level, continued mark–recapture and genetic studies across post-fire succession gradients will help to understand how life history variation affects disturbance responses. Shifting the focus of fire ecology from patterns in population density to the demographic mechanisms underlying the patterns will improve our ability to predict the response of animal species to changing fire regimes.

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Author contribution statement ALS conceived, designed and executed this study and wrote the manuscript. No other person is entitled to authorship.

Compliance with ethical standards

Ethical approval All applicable institutional and national guidelines for the care and use of animals were followed. I followed the *Australian code for the care and use of animals for scientific purposes* and worked under scientific (S25589 Government of South Australian) and animal ethics (E256 Flinders University) permits.

Data accessibility Data supporting this article have been uploaded as part of the Electronic Supplementary Material.

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