Modeling rates of life form cover change in burned and unburned alpine heathland subject to experimental warming

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Abstract

Elevated global temperatures are expected to alter vegetation dynamics by interacting with physiological processes, biotic relationships and disturbance regimes. However, few studies have explicitly modeled these interactions on rates of vegetation change, despite such information being critical to forecasting temporal patterns of vegetation. In this study, we build and parameterize rate-change models for three dominant alpine life forms using data from a 7-year warming experiment. These models allowed us to examine how the interactive effects of experimental warming and the abundance of bare ground (a measure of past disturbance) and neighboring life forms (a measure of life form interaction) affect rates of cover change in alpine shrubs, graminoids and forbs. We show that experimental warming altered rates of life form cover change by reducing negative effects associated with other life forms and reducing positive effects associated with bare ground. Furthermore, we show that these models can predict the observed direction and rate of life form cover change at burned and unburned long-term monitoring sites. Model simulations revealed that warming in unburned vegetation is expected to result in increases in forb and shrub cover but decreases graminoid cover. By contrast, in burned vegetation, warming is likely to slow post-fire regeneration in both graminoids and forbs and allow for rapid expansion in shrub cover. These findings highlight the applicability of modeling rates of vegetation change from experimental data and the need to account for both the abundance of other life forms and disturbance when examining and forecasting vegetation dynamics under climatic change.

Keywords: Bayesian, Fire, Open-Top-Chamber, Plant-Climate interactions, vegetation dynamics

Introduction

Warming experiments have improved our understanding of how higher temperatures affect vegetation at individual, population and community scales. In high mountain and high latitude ecosystems, warming experiments have linked elevated temperatures to changes in plant phenology (Hoffmann et al. 2010), leaf morphology (Hudson et al. 2011), growth (Arft et al. 1999) and genetics (Jay et al. 2012). The results of these experiments have provide insights into the mechanisms governing recent shifts in species ranges (Pauli et al. 2007, Gottfried et al. 2012), local extinctions (Dullinger et al. 2012) and changes in community composition and structure (Myers-Smith et al. 2011).

All biological systems change in state over time. The state observations that researchers make are snapshots in time that arise from the product of multiple processes (e.g. growth and decay, birth and death, colonization and dispersion, extinction and speciation). Although studies using repeated sampling from warming experiments have provided invaluable information on the broad direction and magnitude of warming effects, they have done so via differences or ratios of state variables for control and manipulated groups observed at some point in time(s). For example, most experimental warming studies (e.g. Hoffmann et al. 2010; Elmendorf et al. 2012; Wahren et al. 2013) have analyzed temporal observations via repeated measures ANOVA or GLMs that include random effects for time. While such analyses account for the non-independence of observations through time by computation of appropriate F-ratios (Sokal and Rohlf 1995; Gelman and Hill 2007), they do not estimate rates of change, and thus, are unable to forecast temporal changes in vegetation.

The importance of temporal dynamics was recently highlighted in a meta-analysis of the difference between warmed and control plots in tundra and alpine warming experiments

(Elmendorf et al. 2012). Nearly all fitted GLMs showed that time over which observations were made affected the magnitude of observed warming effects. Importantly, in those models, time commonly interacted with other covariates or displayed nonlinear effects. This suggests that warming effects on vegetation play out over time in complex ways. Because of this, a focus on how warming influences temporal dynamics is critical for predicting vegetation change under global warming.

However, to accurately predict temporal patterns in vegetation, models must also account for the effects of disturbance and biotic interactions, as well as how they may change as a consequence of global warming. Disturbance regimes and biotic interactions both play a major role in the distribution and structure of ecological communities (Grime 1977; Pickett and White 1985; Brooker and Kikvidze 2008). Both are also likely to change as a consequence of global warming (Tylianakis et al. 2008; Turner 2010). For example, recent studies have shown that climate change can modify biotic interactions (Tylianakis et al. 2008), particularly in temperature-limited ecosystems such as alpine environments (Callaway et al. 2002; Klanderud 2005). As such, their interactive effects under climate change are likely to be complex and may exacerbate or negate how warming affects vegetation dynamics (e.g. Lantz et al. 2009).

A large body of ecological theory has focused on the temporal dynamics of individuals (e.g. Richards 1959), populations (e.g. Volterra 1926; Levins 1969; Hanski 1999) and communities (e.g. Tilman 1988; Chesson 1994). Regardless of the focus or complexity of such theoretical models, they all concern rates of change. That is, at their core they contain a rate parameter that allows predictions of state at some future time step based on a set of initial values. However, as far as we know, there has been no experimental study that explicitly models rates of change as a consequence of climate change. As such, we suggest that greater value can be added to experimental studies by addressing theory about rates of change and by utilizing the predictive capacity of such models. In other words, we advocate that studies that examine the effects of climate change on vegetation dynamics use models that explicitly estimate treatment effects (and other covariates) on *rates* of vegetation change, as opposed to testing for (or estimating) differences.

In this study we build and parameterize rate-of-change models by using data from an existing 7-year warming experiment established in Australian alpine heathland. Using these models we examine how the interactive effects of warming, the abundance of neighboring plants of other life forms (a measure of life form interaction) and bare ground (a continuous measure of past disturbance) affects rates of cover change, and thus temporal trajectories, in three dominant life forms - shrubs, graminoids and forbs. We then examine whether these rate models can predict life form cover trajectories observed in burned and unburned alpine heathland long-term monitoring sites and how these trajectories may change under climatic warming.

Materials and methods

Study location

To parameterize our rate models we used four Australian International Tundra Experimental (ITEX; Molau and Mølgaard 1996) sites situated on the Bogong High Plains, in Australia's south-eastern highlands. These sites are unique in that they are the only ITEX sites established in the southern hemisphere and also the only ITEX sites that incorporates fire into the experimental design (Jarrad et al. 2008).

The Australian Alps have high conservation significance; they occupy less than 0.15% of the continent and contain high levels of invertebrate, vertebrate and plant endemism (Williams et al 2014). The alpine ‘treeless’ zone occurs over a narrow altitudinal range (ca. 1600 – 2200 m a.s.l) and contains no nival zone to which species can migrate. Consequently the ecosystem is considered highly vulnerable to climate change (Williams et al. 2014). Since 1979, mean growing season temperatures in the Australian Alps have risen by approximately 0.4°C, and annual precipitation has fallen by 6% (Wahren et al. 2013) with a consequent decline in the snow pack (Sánchez-Bayo and Green 2013). It has also been subject to recent drought (Griffin and Hoffmann 2012), and extensively burned by wildfires in 2003 (Camac et al. 2013).

The vegetation is a mosaic of Eucalyptus woodland and treeless vegetation, with the latter largely consisting of heathlands and tussock grasslands, but also herbfields and wetlands (McDougall and Walsh 2007). Invertebrates are the dominant herbivores in the Australian Alps (Nash et al. 2013; Williams et al. 2014). However, prior to 2003 and the commencement of this study, the Bogong High Plains were subject to a century of summer grazing by cattle (Wahren et al. 1994; Williams et al. 2014). This resulted in reductions in abundance of forb and palatable shrubs and increases in bare ground (Wahren et al. 1994). Long-term monitoring suggests that these changes are not permanent and that shrub and forb abundances have may recover while bare ground cover may decline (Williams et al. 2014).

Experimental design

Consistent with other ITEX sites, Open Top Chambers (OTCs; Molau and Mølgaard 1996) were used to simulate warmer conditions. In late 2003, at approximately 1750 m a.s.l, OTCs were established at four sites (Jarrad et al. 2008). Two sites were located in vegetation thought to be unburned since 1939, and two others were in vegetation burned by the fires of January 2003. Sites were a minimum of 500 m apart and burned sites were approximately 2 km away from unburned sites. In total 80 1 m^2 plots were established. Each unburned site consisted of 26 experimental plots (13 OTC; 13 control) and each burned site had 14 plots (7 OTC; 7 control). Within each site, plots were randomly located along permanent transects 10 m apart, and then randomly allocated as either a control or OTC (see Jarrad et al. 2008). All sites were floristically open-grassy-heathland (McDougall and Walsh 2007), a plant community containing approximately 20 species/8 m^2 and dominated by graminoids (e.g. *Poa hiemata, Carex breviculmis)*, dense patches of rhizomatous and rosette forbs (e.g. *Celmisia pugioniformis* & *Erigeron bellidioides*) and non-resprouting perennial evergreen shrubs (e.g. *Grevillea australis, Asterolasia trymalioides)*. Plots contained very low abundances of large (>1 m^2 or > 0.5 m high) shrub species such as *Grevillea australis* because they exceeded the scale of investigation (i.e. they were larger than the 1 m^2 plot). Instead, the dominant shrubs within plots were prostrate evergreen shrubs: *Asterolasia trymalioides* (Rutaceae), *Pimelea alpina* (Thymelaeaceae) and *Pimelea axiflora* (Thymelaeaceae). All sites were considered to have similar cattle grazing history. As a consequence, grazing history was not confounded with site differences or experimental treatment.

OTCs were hexagonal, 58 cm tall with an open-top diameter of 110 cm and base diameter of 168 cm. OTCs were placed over plots each year at the start of the snow-free period (October), where they remained until snowfall (early June). Temperature in both control and OTC plots were measured using Onset 4-channel temperature loggers (Onset Computer Corporation, Bourne, MA, USA). Loggers were randomly installed into four control and four OTC plots at each unburned site and two control and two OTC plots at each burned site. Each logger measured ambient (5 cm above ground) and soil surface (1-2 cm below ground) temperature at hourly intervals from 2004 to 2010. In 2010, following the data collection used in this study, eight Onset Micro Stations were randomly installed into four control and four OTC plots at one of the unburned sites. These Micro Stations measured volumetric soil moisture between 3 and 10 cm below ground at hourly intervals from 2010 to 2013. To ensure OTC treatment soil moisture differences were in the same direction and of similar magnitude across all sites, a Theta probe (Type ML2x, Delta-T Devices Ltd., UK) was used to take five replicate measurements of volumetric soil moisture from each plot in all four sites in November and May from 2010 to 2012. Over the duration of the experiment OTCs simulated the lower end of IPCC predictions (IPCC 2013) by passively raising daily mean growing season ambient and soil surface temperatures by 1.2ºC (± 0.1; 95% CI), and minimum and maximum ambient temperatures by 2ºC (± 0.2; 95% CI). Daily soil moisture in OTC plots was also consistently 4% (± 0.1; 95% CI) lower than controls between 2010 and 2013, a decrease that was consistent across all sites, regardless of whether or not the site had been burned. As such experimental warming induced both warmer and drier conditions.

Vegetation and ground cover measurements

Foliage projective cover of all species in each plot was estimated biennially in January from 2004 to 2010 using a 1 m^2 point-frame with 100 points in a 10 x 10 grid with 10 cm spacing (Molau and Mølgaard 1996). At each point, we recorded the presence of all species and the amount of bare ground. As our central focus was on producing a general model of vegetation cover, we assigned each species to one of three dominant life forms (shrub, graminoid or forb) and calculated the number of unique hits per life form and ground cover type for each plot. We focused on these three life forms for four reasons: 1) both experimental and natural observation studies indicate they can summarize and predict broad community trajectories under global change (Chapin and Shaver 1996; Elmendorf et al. 2012); 2) they are well understood by both land managers and the broader scientific community; 3) adding additional functional groups would greatly increased the number of parameters to be estimated; and most importantly, 4) plots contained insufficient or highly unbalanced numbers of species to estimate representative experimental warming responses in finer functional groups (e.g. exotic vs. native, annuals vs. perennials, resprouters vs. seeders), with the vast majority of species being native, perennial and resprouters.

Data Analysis

We used hierarchical generalized linear models to estimate rates of temporal life form cover change as a function of experimental warming, the abundance of neighboring life forms, and the abundance of bare ground. Hierarchical models, also known as multi-level models, are well suited to datasets that have a hierarchical structure (e.g. plots within sites) because they can account for observation error and partition both explained and unexplained variation at multiple levels of a dataset (Gelman and Hill 2007). In our models, experimentally manipulated (i.e. OTC treatment) and un-manipulated variables (i.e. the abundance of neighboring life forms and bare ground) were all treated as covariates affecting rates of cover change (Fig. 1).

Because we were interested in rates of cover change but our observations were of number of hits for each life form (an estimate of cover), Y, in each plot i and census t, we first modeled the data as a random realization from a binomial distribution by assuming each point was independently sampled:

$$Y_{i,t} \sim Binomial\big(logit(\hat{y}_{i,t}), 100\big). \qquad (1)$$

Where $\hat{y}_{i,t}$ is the predicted probability (hereon in referred to as predicted cover) that a life form occupies a given point for each plot-census combination and 100 equals the number of sample trials per plot.

Using a logit-link, $\hat{y}_{i,t}$ was modeled as the sum of the mean rate of cover change, $\lambda_{i,t}$, and $\hat{y}_{i,t-1}$, the predicted cover in a plot in the previous sampling period:

$$\hat{y}_{i,t} = \lambda_{i,t} + \hat{y}_{i,t-1}. \tag{2}$$

We used a logit-link because the underlying observations (i.e. presence of a life form at a point) were binary, but also because it implicitly allows the model to account for density dependence at both low and high abundance (i.e. via a sigmoidal curve). That is, at low cover, rates of cover change are reduced due to low recruitment potential (few occupied points), whereas at high cover, rates of change are constrained because of limited space (few unoccupied points).

The rate of cover change, $\lambda_{i,t}$ was modeled as a linear function of covariates at two spatial scales (site and plot):

$$\lambda_{i,t} = \alpha_{i[j]} + \beta\,.X_{i,t} + \varepsilon_i, \tag{3}$$

where, $\alpha_{i[j]}$ is the varying intercept for each site *j* to which plot *i* belongs (interpreted as the mean rate of cover change for each site), $\beta\,.X_{i,t}$ is a matrix of linear predictors and stationary (time invariant) coefficients for plot *i* at time *t* and ε_i is the residual plot level variation.

Varying site intercepts, α_j, were drawn from a normal distribution:

$$\alpha_j \sim N(\beta_{0,}\sigma_{site}), \tag{4}$$

where β_0 is the mean rate of cover change across all sites and σ_{site} is the associated standard deviation (estimated from uninformative priors; see Bayesian implementation). Residual plot variation, ε_i, was estimated from a normal distribution centered on zero and σ_{plot} (estimated from uninformative priors; see Bayesian implementation):

$$\varepsilon_i \sim N(0,\sigma_{plot}). \qquad (5)$$

Parameters

Plot-level covariates used to estimate rates of cover change included experimental treatment (i.e. OTC or control) as well as the cover of bare ground and cover of other life forms within the same plot (hereafter referred to as 'neighboring life forms') at the previous census, t-1. We used the cover of neighboring life forms at t-1 as a measure of life form interaction because it varied over time as well as between plots and sites. But more importantly, it provides insights into how the abundance of a life form influences the dynamics of another. Bare ground was also included as a time dependent plot level covariate because 1) it too varied between years, plots and sites, 2) it is correlated with the occurrence and severity of fire and other disturbances (e.g. frost heave and grazing) (Camac et al. 2013; Wahren et al. 2013), 3) it is a determinant of colonization opportunity (Williams 1992; Lantz et al. 2009), and 4) it is a continuous variable that is directly measurable at the plot level (i.e. the level which we observe life form cover changes). We did not fit a binary fire effect at the site level for two reasons. First, preliminary analyses showed that the level of replication (N = 2) was insufficient to estimate a burning effect. Second, and more importantly, fitting a binary (burned/unburned) parameter to a rate-change model, or analyzing burned and unburned sites separately produce biologically unrealistic models because they assume that the magnitude of burning-effects remains constant over time (i.e. a burned site never recovers to an unburned state). Instead, the effect of fire (and other disturbances that create bare ground) on rates of life form cover change was implicitly examined via changes in bare ground and neighboring life form abundance.

We were unable to include soil moisture as a covariate within our models because it was not measured at the same time as the life form abundance data, and thus, its effect on rates of change could not be assessed. However, treatment differences in soil moisture are implicitly incorporated into the OTC modeled parameter because, compared with the control treatment, the OTCs resulted in both warmer and drier conditions (see *Experimental design*). Other climate variables, such as annual rainfall and mean growing season temperature, were not included as modeled parameters because the number of censuses (N = 4) was insufficient to accurately estimate an effect on rates of change. However, with continued sampling resulting in longer time series we envisage that these variables will eventually be included and may further improve models by explaining inter-annual variation.

Cover-estimates of neighboring life forms and bare ground were logit transformed so that we could accurately estimate means and standard deviations needed for centering and scaling (see below). However, because some cover values were 0 or 100% (and thus could not be logit transformed), we first multiplied estimates by 0.995 and then added a small constant (0.004). Each covariate was then centered on zero (by subtracting the mean) and standardized by two standard deviations (see Electronic Supplementary Material S1) (Gelman and Hill 2007). Centering coefficients allows them to be interpreted more easily, with intercepts interpreted as average responses and slope terms as partial dependencies conditional on other continuous variables at their mean. Furthermore, standardizing by two standard deviations allows the magnitude of effects to be compared between binary (i.e. OTC treatment) and continuous variables (i.e. the cover of bare ground and neighboring life forms) (Gelman and Hill 2007). Because we were interested in whether experimental warming could alter the effects of neighboring life form and bare ground abundance, we included associated two-way interactions with the OTC treatment. The direction and uncertainty of covariate effects on rates of cover change was determined using 'inference by eye' (Cumming and Finch 2005). The advantage of this approach over reporting p-values is that the inference by eye approach highlights both the effect size and its associated uncertainty, allowing the reader to make his/her own decision on whether the effect is 'biologically significant'. To further aid in determining where most variation occurred we also included 80% credible intervals.

Bayesian implementation & prior distributions of parameters

We used Bayesian inference and therefore needed to specify prior distributions for all model parameters. The response (i.e. the probability of being at a point in a plot) was binary, so we used weakly informative Cauchy priors as recommended by Gelman et al. (2008). Regression coefficients, which model variation in rate of cover change for each life form (see eq. 3), were drawn from Cauchy distributions with prior mean 0 and prior scale 2.5. The mean rate across sites, β_0 (i.e. the mean hyper-parameter used to estimate the varying site intercepts) was drawn from a weaker Cauchy distribution with prior mean 0 and prior scale 10. This weaker prior acknowledges that effect sizes (i.e. regression coefficients) are more constrained than intercepts (Gelman et al. 2008). Site and plot-level variation σ_{site}, σ_{plot} respectively, were drawn from positive half Cauchy distributions truncated at 0, with prior mean 0 and prior scale 25 as recommended by Gelman (2006). We initialized the model by estimating the cover of each focal life form at t = 1 using an uninformative normal prior with a mean of 0 and a standard deviation of 100. Models were fitted using Markov chain Monte Carlo (MCMC) sampling in R 2.15.1 using package R2jags version 0.03-08 (Su and Yajima 2012) as an interface to JAGS 3.3.0 (Plummer 2011). Three chains were monitored to ensure convergence. We assessed convergence through visual inspection of chains and reference to the Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998). For all models, posterior distributions of each parameter always converged within 50,000 iterations. After discarding the first 50,000 iterations as burn-in, a further 50,000 iterations were taken from the joint posterior and thinned to every 50th sample. Sample JAGS code for the model is provided in Electronic Supplementary Material S2.

Model checks, hind-casting & simulating vegetation change

The residuals of each model were checked graphically against predicted cover and none showed any systematic pattern or severe heteroscedasticity. To ensure all parameters were identifiable we selectively removed each covariate and visually inspected whether the direction and magnitude of effects were severely altered; none were. Overall predictive fit of each life form model was examined by calculating the R-square between experimental observations and model fit without random effects.

To assess the transferability of our models beyond the four experimental sites and at a larger spatial scale (approximately 1 ha), we hind-casted temporal changes in life form cover at two nearby heathland reference sites, each within 5 km of the experimental sites. The 2003 fires burned one site and the other remained unburned. We then compared model predictions to biennial observations from 2003 to 2013. These sites were floristically similar to the experimental sites (i.e. were open-grassy-heathland), were approximately 1 ha in area and yielded a decade (2004 – 2013) of life form and bare ground cover estimates measured from point quadrats along permanent reference transects (see Wahren et al. 2013). In order to hind-cast community level changes, we merged the three life form models into a single model that used posterior parameter distributions of β_0, the mean cover across all sites, and other covariates from the three models related to unwarmed conditions (i.e. not including OTC parameters). This allowed for the model to simultaneously estimate the abundance of each life form in each year based on the cover of bare ground (supplied – see below) and the predicted cover of neighboring life forms. To initialize the model, we used 2003 observed life form covers. Because we did not have a model to predict temporal changes in bare ground, we supplied observed estimates of its cover for all years. These initial conditions were then logit transformed and centered and standardized based on experimental means and standard deviations (see Electronic Supplementary Material S1). We then simulated the model 3000 times for each year to produce a reliable estimate of the mean cover for each life form. We then plotted these predictions against observations. Lastly, to examine the potential of warmer climate resulting in compositional shifts in life form abundance we used these models to simulate warmed and unwarmed conditions for burned and unburned alpine heathland using the initial 2003 conditions obtained from the long-term monitoring sites.

Results

Observed cover changes in experimental plots

Pooling across plots and sites (i.e. ignoring variation in bare ground or life form covers) indicated that experimental warming had negligible effects on the average cover of shrubs, graminoids and forbs (Fig. 2). Instead, whether vegetation was burned or unburned appeared to have the strongest effect on cover, with shrubs increasing from 4% to 11% from 2004 to 2010 in unburned sites but remaining low (approximately 2%) in burned sites (Fig. 2a,b). By contrast, and over the same period, cover of graminoids decreased by 20% in unburned sites but increased by approximately 40% in burned sites (Fig. 2c,d). Forb cover increased regardless of burning (Fig. 2e,f). At the first census, approximately 10 months post-fire, bare ground cover was on average 2% higher and three times as variable at burned sites compared unburned sites (range: 0-33% & 0-10%, respectively; Fig. 2g,h); a difference maintained over the duration of this study. Experimental warming did not influence the temporal pattern of bare ground cover in either burned or unburned vegetation in any year.

Model fit to experimental data

Explanatory model fit (i.e. model fit without random effects) to experimental data was high for forbs (R^2 = 77%), moderate for shrubs (R^2 = 58%) and low for graminoids (R^2 = 13%). Rates of cover change varied among sites and plots, with the amount of unexplained variation at each level dependent on life form (Table 1). In graminoids, the weaker predictive fit was largely due to high levels of unexplained variation between sites, with a standard deviation nearly three times that of the standard deviation among plots (Table 1). By contrast, the magnitude of unexplained variation for shrubs and forbs was less compared to graminoids and was evenly split between site and plot levels.

Effects of experimental warming, bare ground and neighboring life forms

Effects of experimental warming on rates of cover change were small and contained 95% credible intervals that overlapped zero for all three life forms (Fig. 3). Instead, rates were strongly influenced by the abundance of other neighboring life forms (Fig. 3). The effects of neighboring life forms were predominately negative: rates of graminoid cover change decreased with increasing forb abundance and rates of forb and shrub cover change declined with increasing graminoid abundance (Fig. 3). Shrub abundance did not affect graminoids and had a marginal negative effect on forbs. Thus, the abundance of neighboring life forms tended to reduce the rates of cover expansion, and in some sites (e.g. graminoid cover in site 2; Fig. 3) exacerbated life form declines. Bare ground, an indicator of both disturbance and recruitment opportunity, had predominately negative (90% of credible interval is negative) effects on rates of shrub cover change, but positive effects on rates of graminoids and forbs cover change (98% of credible interval is positive for both life forms; Fig. 3).

Experimental warming interactions

Experimental warming affected rates of life form cover change by reducing the negative effects associated with neighboring life forms and the positive effects associated with bare ground (Fig. 3). For example, forbs growing in OTCs exhibited higher rates of cover change compared to those growing in control plots because the positive warming-graminoid interaction negated the negative direct effect of graminoid abundance (see Fig. 3). By contrast, in graminoids, experimental warming increased negative effects associated with shrub abundance and negated the positive effect of bare ground, but not the negative effect of forb abundance. As a consequence, warming exacerbated declines in graminoid cover in unburned vegetation (via more negative rates) and decreased recovery rates in burned vegetation relative to graminoids growing under control conditions. A summary of modeled changes in bare ground and life form interactions under control and OTC conditions is supplied in Fig. 4 a and b, respectively.

Hindcasting – comparing model predictions against long-term monitoring observations

Our rate change models, based on the warming experiment, predicted the overall trajectory of life form cover change in both burned and unburned long-term heathland monitoring sites, though not in detail (Fig. 5). Specifically, the model was predictive of the lack of shrub cover change in both burned and unburned vegetation with mean predictions falling between the 2.5th and 95th observed percentile for all years (Fig. 5a,b). The model was also predictive of graminoid post-fire regeneration (Fig. 5d), but failed to account for its sharp decline (and subsequent regeneration) in unburned sites during the severe drought between 2007 and 2009

(Fig. 5c). Forb predictions captured general trajectories but slightly overestimated forb cover in unburned vegetation (Fig. 5e) and underestimated cover in burned vegetation (Fig. 5f).

Simulating warming effects in burned and unburned alpine heathland

Simulated changes in life form composition for unburned alpine heathland suggested that cover of shrubs and forbs is likely to increase at a higher rate under warmer conditions (Fig. 6a). This was predominately due to graminoid cover substantially decreasing under warmer conditions as a product of increased negative effects associated with shrub abundance and decreased positive effects associated with bare ground (Fig. 3 & 4). These same warming effects were also predicted to reduce graminoid post-fire regeneration, which allowed for increased rates of shrub regeneration, which in turn, decreased rates of forb recovery (Fig. 6b).

Discussion

In this study, we built and parameterized rate change models using data from a 7-year warming experiment. These models allowed us to examine how experimental warming and the abundance of bare ground and neighboring life forms interact to affect rates, and thus trajectories, of cover change in three dominant life forms - shrubs, graminoids and forbs. We showed that experimental warming altered rates of life form cover change by reducing negative effects associated with neighboring life form abundance and positive effects of bare ground. These models also predicted broad directions and rates of past life form cover trajectories at burned and unburned alpine heathland sites. Furthermore, model simulations suggest that warming in unburned vegetation would decrease graminoid cover and increase the rates of forb and shrub cover growth. By contrast, in burned vegetation, warming is expected to slow post-fire regeneration in both graminoids and forbs while allowing for the rapid expansion in shrub cover.

The lack of direct experimental warming effect

The muted direct effect of experimental warming on rates of cover change in all three life forms may be due to idiosyncratic responses of species within life forms (Dormann and Woodin 2002). However, in all cases the uncertainty around the OTC parameter was small, indicating that idiosyncratic responses are unlikely to be large. Instead, it may be that photosynthesis and respiration are not significantly altered by the 1.2°C temperature rise during the growing season when the OTCs are on the plots. Chapin (1983) and Körner (2003) suggested that, for alpine and polar plants, a negligible growth response to warmer spring and summer months may be because photosynthesis is not limited by growing season temperatures. This is because many cold-adapted plants require lower temperatures (~15°C) for optimum rates of photosynthesis compared to temperate species (~25°C). Moreover, alpine and arctic plants have wide temperature response-curves, allowing substantial rates of photosynthesis even at 0°C (Chapin 1983; Körner 2003). Microclimate data collected from our plots suggest mean growing season temperatures experienced at the plant level (10 cm above ground) are 9-12°C which is already close to optimum for photosynthesis in alpine plants. Thus, increasing temperatures by 1.2°C during the growing season may not necessary elicit a strong physiological response that is ultimately expressed as altered rates of cover change. However, winter warming, which was not examined in this study, may have significant effects on vegetation dynamics by increasing snowmelt and exposing plants to more frequent low-temperature extremes (Wipf et al. 2009).

Life form interactions & experimental warming

Bertness & Callaway (1994) proposed that low temperatures in alpine and arctic ecosystems 'stress' plants and allow positive instead of negative plant-plant interactions to predominate. As such, an expectation is that experimental warming should reduce low temperature stress and increase the strength of negative interactions. Such responses have been observed in several experimental warming studies (e.g. Klanderud 2005; Olsen and Klanderud 2013). Yet, contrary to these expectations, we found that life form interactions were mostly negative and that experimental warming decreased, rather than increased, these negative effects. One possible explanation is that OTCs increased plant stress by reducing soil moisture during a period when plant available water is limited. Water availability is known to be a major determinant of vegetation change in alpine and arctic environments (le Roux et al. 2013) and can alter the magnitude of experimental warming effects (Elmendorf et al. 2012). In the meta-analysis by Elmendorf et al. (2012), our sites were considered warmer and drier relative to most other alpine and arctic experimental sites examined. Furthermore, the data used in this study was collected during part of the driest 13-year period (1996 – 2009) on record for south-eastern Australia since the late 1880s (Wahren et al. 2013). This drought has been correlated with a 25% reduction in alpine grass cover at long-term monitoring sites on the Bogong High Plains (Wahren et al. 2013) and significant mortality in both shrubs (Morgan 2004) and grasses (Griffin and Hoffmann 2012). Our microclimate data suggest that from 2003 to 2010 OTCs were likely to have on average 4% less soil moisture than control plots (see *Experimental design*). Studies of arid and semi-arid vegetation have shown that lower water availability increases the importance of positive plant-plant interactions (Pugnaire et al. 2009). However, in alpine and arctic ecosystems, water is often considered not limiting and hence few studies have assessed whether it influences alpine plant-plant interactions (e.g. Cavieres et al. 2006). We suggest that the shift from negative to neutral interactions with neighboring life forms may reflect the drier conditions experienced within OTCs. Here a decrease in soil moisture, particularly during drought, may shift the net effect of neighboring plants from negative to neutral as neighbor protection from both drying winds and high temperature extremes becomes more important.

Effects of bare ground

Disturbance at various temporal and spatial scales affects vegetation dynamics in all plant communities (Pickett and White 1985; Turner 2010). In the Australian Alps vegetation cover is high (> 95%) and the total area suitable for seedling colonization is low (Williams et al. 2014). However, disturbances such as frost heave, herbivory and fire can rapidly facilitate colonization by creating bare ground and reducing competition from surrounding vegetation (Williams 1992). In the present study, bare ground had a positive effect on rates of graminoid cover change. However, this effect was negated in warmed plots by a negative bare ground-OTC interaction. A possible explanation for this is that experimental warming may increase the frequency and duration of high lethal temperatures experienced in bare ground patches (which have been observed to reach up to 80°C (Williams 1985)), and thereby inhibit the colonization and survival of graminoid seedlings. However, further research is required to quantify the actual mechanisms behind such an effect.

Simulating temporal changes in life form abundance in burned and unburned heathland

Fire activity is projected to increase in many ecosystems worldwide (Westerling et al. 2011, Turetsky et al. 2011). In south-eastern Australia, the severity of fire weather has increased in recent decades (Clarke et al. 2013) resulting in increased fire activity in the Australian alpine bioregion (Bradstock et al. 2014). Future warming and drying is likely to exacerbate this trend. Thus, to accurately forecast rates and trajectories of vegetation change it is crucial to understand how climate affects vegetation dynamics in both burned and unburned conditions. Using bare ground as a continuous measure of past disturbance, our models predict that the cover of shrubs and forbs in unburned heathland will increase at a higher rate under warmer conditions. This occurs because warmer conditions substantially decrease graminoid cover by increasing negative effects associated with shrub abundance and decreasing positive effects associated with bare ground. This prediction is consistent with long-term monitoring observations across the unburned sections of the Bogong High Plains, with temperatures increases (0.4°C) and precipitation declines (6%) since 1979 being correlated with a 25% decline in graminoids and a 20% and 9% increase in shrubs and forbs, respectively (Wahren et al. 2013). Our simulations also suggest that these same warming effects will reduce the rate of graminoid post-fire regeneration, which in turn will allow for faster shrub regeneration (via decreased graminoid abundance), and consequently, slower forb regeneration (via increased shrub abundance).

The findings of this study highlight that models of vegetation change need to account for both direct and indirect effects of warming. Furthermore, we suggest that current and future experimental warming studies focus on modeling rates of change, as opposed to differences or ratios of state variables for control and treatment groups observed at some time. We also believe that, with continued sampling and longer time-series, these rate-models can be extended to incorporate inter-annual variability in temperature and moisture, further improving predictive capacity. By modeling rates, the utility of experimental work will be greatly extended, particularly for forecasting vegetation dynamics under climatic change.

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References

Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jónsdóttir, K. Laine, E. Lévesque, G. M. Marion, U. Molau, P. Mølgaard, U. Nordenhäll, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenström, M. Stenstrom, Ø. Totland, P. L. Turner, L. J. Walker, P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Responses of Tundra plants to experimental to experimental warming: meta-analysis of the International Tundra Experiment. Ecological Monographs 69:491–511

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology & Evolution 9:191–193

Bradstock, R., T. Penman, M. Boer, O. Price, and H. Clarke. 2014. Divergent responses of fire to recent warming and drying across south-eastern Australia. Global Change Biology 20:1412–1428

Brooker, R. W., and Z. Kikvidze. 2008. Importance: an overlooked concept in plant interaction research. Journal of Ecology 96:703–708

Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455

Callaway, R., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, F. I. Pugnaire, B. A. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–848

Camac, J. S., R. J. Williams, C.-H. Wahren, W. K. Morris, and J. W. Morgan. 2013. Post-fire regeneration in alpine heathland: Does fire severity matter? Austral Ecology 38:199–207

Cavieres, L. A., E. I. Badano, A. Sierra-Almeida, S. Gómez-Gónzález, and M. A. Molina-Montenegro. 2006. Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. New Phytologist 169:59–69

Chapin, F. S., III. 1983. Direct and indirect effects of temperature on arctic plants. Polar Biology 2:47–52

Chapin, F. S., III, and G. R. Shaver. 1996. Physiological and growth responses of Arctic plants to a field experiment simulating climatic change. Ecology 77:822

Chesson, P. 1994. Multispecies Competition in Variable Environments. Theoretical Population Biology 45:227–276

Clarke, H., C. Lucas, and P. Smith. 2013. Changes in Australian fire weather between 1973 and 2010. International Journal of Climatology 33:931–944

Cumming, G., and S. Finch. 2005. Inference by eye - Confidence intervals and how to read pictures of data. American psychologist 60:170–180

Dormann, C. F., and S. J. Woodin. 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. Functional Ecology 16:4–17

Dullinger, S., A. Gattringer, W. Thuiller, D. Moser, N. E. Zimmermann, A. Guisan, W. Willner, C. Plutzar, M. Leitner, T. Mang, M. Caccianiga, T. Dirnböck, S. Ertl, A. Fischer, J. Lenoir, J.-C. Svenning, A. Psomas, D. R. Schmatz, U. Silc, P. Vittoz, and K. Hülber. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Climate Change 2:619–622

Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Bjorkman, T. V. Callaghan, L. S. Collier, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, A. M. Fosaa, W. A. Gould, J. Grétarsdóttir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jónsdóttir, F. Keuper, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J. Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post, C. Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenström, A. Tolvanen, Ø. Totland, T. Troxler, C.-H. Wahren, P. J. Webber, J. M. Welker, and P. A. Wookey. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecology Letters 15:164–175

Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. Bayesian Analysis 1:515–533

Gelman, A., A. Jakulin, M. Pittau, and Y.-S. Su. 2008. A weakly informative default prior distribution for logistic and other regression models. The Annals of Applied Statistics 2:1360–1383

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press Cambridge

Gottfried, M., H. Pauli, A. Futschik, M. Akhalkatsi, P. Barančok, J. L. Benito Alonso, G. Coldea, J. Dick, B. Erschbamer, M. A. R. Fernández Calzado, G. Kazakis, J. Krajči, P.

Larsson, M. Mallaun, O. Michelsen, D. Moiseev, P. Moiseev, U. Molau, A. Merzouki, L. Nagy, G. Nakhutsrishvili, B. Pedersen, G. Pelino, M. Puscas, G. Rossi, A. Stanisci, J.-P. Theurillat, M. Tomaselli, L. Villar, P. Vittoz, I. Vogiatzakis, and G. Grabherr. 2012. Continent-wide response of mountain vegetation to climate change. Nature Climate Change 2:111–115

Griffin, P. C., and A. A. Hoffmann. 2012. Mortality of Australian alpine grasses (*Poa* spp.) after drought: species differences and ecological patterns. Journal of Plant Ecology 5:121–133

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169–1194.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press

Hoffmann, A. A., J. S. Camac, R. J. Williams, W. A. Papst, F. C. Jarrad, and C.-H. Wahren. 2010. Phenological changes in six Australian subalpine plants in response to experimental warming and year‑to‑year variation. Journal of Ecology 98:927–937

Hudson, J. M. G., G. H. R. Henry, and W. K. Cornwell. 2011. Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. Global Change Biology 17:1013–1021

IPCC. 2013. *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Page 1535 (T. F. Stocker, D. Qin, G. K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, Eds.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Jarrad, F. C., C.-H. Wahren, R. J. Williams, and M. A. Burgman. 2008. Impacts of experimental warming and fire on phenology of subalpine open-heath species. Australian Journal of Botany 56:617–629

Jay, F., S. Manel, N. Alvarez, E. Y. Durand, W. Thuiller, R. Holderegger, P. Taberlet, and O. François. 2012. Forecasting changes in population genetic structure of alpine plants in response to global warming. Molecular Ecology 21:2354–2368

Klanderud, K. 2005. Climate change effects on species interactions in an alpine plant community. Journal of Ecology 93:127–137

Körner, C. 2003. Alpine plant life. Second edition. Springer, Berlin

Lantz, T. C., S. V. Kokelj, S. E. Gergel, and G. H. R. Henry. 2009. Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps. Global Change Biology 15:1664–1675

le Roux, P. C., J. Aalto, and M. Luoto. 2013. Soil moisture's underestimated role in climate change impact modelling in low-energy systems. Global Change Biology 19:2965–2975.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240

McDougall, K. L., and N. G. Walsh. 2007. Treeless vegetation of the Australian Alps. Cunninghamia 10:1–57

Molau, U., and P. Mølgaard. 1996. ITEX Manual. Pages 1–85. Danish Polar Centre, Copenhagen

Morgan, J. W. 2004. Drought-related dieback in four subalpine shrub species, Bogong High Plains, Victoria. Cunninghamia 8:326–330

Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. Tape, M. Macias-Fauria, U. Sass-Klaassen, E. Lévesque, S. Boudreau, P. Ropars, L. Hermanutz, A. Trant, L. S. Collier, S. Weijers, J. Rozema, S. A. Rayback, N. M. Schmidt, G. Schaepman-Strub, S. Wipf, C. Rixen, C. B. Ménard, S. E. Venn, S. Goetz, L. Andreu-Hayles, S. C. Elmendorf, V. Ravolainen, J. M. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6:045509

Nash, M. A., P. C. Griffin, and A. A. Hoffmann. 2013. Inconsistent responses of alpine arthropod communities to experimental warming and thermal gradients. Climate Research 55:227–237

Olsen, S. L., and K. Klanderud. 2013. Biotic interactions limit species richness in an alpine plant community, especially under experimental warming. Oikos 123:71–78

Pauli, H., M. Gottfried, K. Reiter, C. Klettner, and G. Grabherr. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA* master site Schrankogel, Tyrol, Austria. Global Change Biology 13:147–156

Pickett, S. T. A., and P. A. White. 1985. The ecology of natural disturbance and patch dynamics. Pages 1–472. Academic Press

Plummer, M. 2011. JAGS Version 3.1.0 user manual

Pugnaire, F. I., C. Armas, and F. Valladares. 2009. Soil as a mediator in plant-plant interactions in a semi-arid community. Journal of Vegetation Science 15:85–92

Richards, F. J. 1959. A flexible growth function for empirical use. Journal of experimental Botany 10:290–300

Sánchez-Bayo, F., and K. Green. 2013. Australian snowpack disappearing under the influence of global warming and solar activity. Arctic Antarctic and Alpine Research 45:107–118

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third Edition. W.H Freeman and Company, New York

Su, Y.-S., and M. Yajima. 2012. R2jags: A package for Running jags from R. R package version 0.03-06. Pages 1–12. http://CRAN.R-project.org/package=R2jags

Tilman, D. 1988. Plant strategies and the structure and dynamics. Princeton University Press

Turetsky, M. R., E. S. Kane, J. W. Harden, R. D. Ottmar, K. L. Manies, E. Hoy, and E. S. Kasischke. 2011. Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. Nature Geoscience 4:27–31

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363

Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118:558–560

Wahren, C.-H., J. S. Camac, F. C. Jarrad, R. J. Williams, W. A. Papst, and A. A. Hoffmann. 2013. Experimental warming and long-term vegetation dynamics in an alpine heathland. Australian Journal of Botany 61:36–51

Wahren, C.-H., W. A. Papst, and R. J. Williams. 1994. Long-term vegetation change in relation to cattle grazing in sub-alpine grassland and heathland on the Bogong High-Plains: an analysis of vegetation records from 1945 to 1994. Australian Journal of Botany 42:607–639

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century 108:13165–13170

Williams, R. J. 1985. Aspects of shrub-grass dynamics on the Bogong High Plains (subalpine), Victoria. PhD thesis. The University of Melbourne

Williams, R. J. 1992. Gap dynamics in subalpine heathland and grassland vegetation in south-eastern Australia. Journal of Ecology 80:343–352

Williams, R. J., W. A. Papst, K. L. McDougall, I. M. Mansergh, D. A. Heinze, J. S. Camac,

M. A. Nash, J. W. Morgan, and A. A. Hoffmann. 2014. Alpine Ecosystems. Pages 167–212 *in* D. B. Lindenmayer, E. Burns, N. Thurgate, and A. Lowe, editors. Biodiversity and Environmental Change: Monitoring, Challenges and Directions. CSIRO Publishing, Melbourne

Wipf, S., V. Stoeckli, and P. Bebi. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. Climatic Change 94:105–121

Tables

Table 1 Estimated mean rate of cover change across sites (β_0) and estimated plot and site residual variation for each life form. Data are logit means for β_0 and median point estimates of residual standard deviations for site and plot levels. Upper and lower bounds in parentheses are 95% Bayesian Credible Intervals (BCI)

Model	Data level	β_0 (95% BCI limits)	Standard deviation (95% BCI limits)
Shrub	Site	0.28 (-0.20,0.76)	0.33 (0.03,1.24)
	Plot		0.30 (0.21,0.41)
Graminoid	Site	-0.01 (-1.35,1.43)	1.16 (0.37,4.11)
	Plot		0.39 (0.31,0.48)
Forb	Site	0.33 (0.06,0.55)	0.18 (0.01,0.72)
	Plot		0.15 (0.12,0.19)

Figures legends:

Fig. 1 Diagram summarizing hierarchical structure of rate model. Subscripts *i*, *j* and *t* refer to plots, sites and sampling census, respectively. OTC = Open-Top-Chamber

Fig. 2 Foliage projective cover in experimental plots unburned (left) and burned (right) by the 2003 wildfires. Values are means ± 95% confidence intervals and do not account for either site or plot level variation or how these may interact. OTC = Open-Top-Chamber; CTL = Control

Fig. 3 Logit mean coefficients ± 95 (thin line) and 80% (thick line) Bayesian Credible Intervals for each life form model. Site intercepts (S1 to S4) are mean site rates of cover change for control plots when OTC = 0 and all other covariates are at their mean. To determine the expected rate of cover change for a control plot at particular site, add the relevant site intercept and effects of bare ground and neighboring life forms (light grey). To determine the expected rate of cover change in OTC plots, add the relevant intercept, OTC coefficient and all other covariate (light grey) and two-way interaction effects (dark grey). BG = bare ground; OTC = Open-Top-Chamber

Fig. 4 Summary of life form and bare ground interactions as estimated by rate models in a) Control and b) OTC treatment. Width of arrow signifies relative strength of relationship as determined by coefficient mean (see Fig. 3). BG = bare ground, OTC = Open-Top-Chamber

Fig. 5 Comparison between model predictions of temporal life form cover changes from control treatment and observations in long-term alpine heathland monitoring sites that were unburned (left) and burned (right) by the 2003 wildfires. Points are observed mean cover estimates with 2.5th and 97th quantiles. Grey shading indicates the model uncertainty (± 95% Bayesian Credible Intervals). Model simulations were initialized using mean observed covers in 2003. Bare ground (g,h) was included in the models as a known entity for all years and was not explicitly modeled

Fig. 6 Simulated changes in life form cover over a decade for a) long-unburned and b) recently burned open heathland sites growing under control and OTC treatment. The model was initialized with data on life form covers typically observed in long-term monitoring sites burned and unburned by the 2003 wildfires. Bare ground was included in the models as a known entity for all years (based on observations in Fig. 5g,h). OTC = Open-Top-Chamber; CTL = Control; Gram = Graminoids

Figure 1:

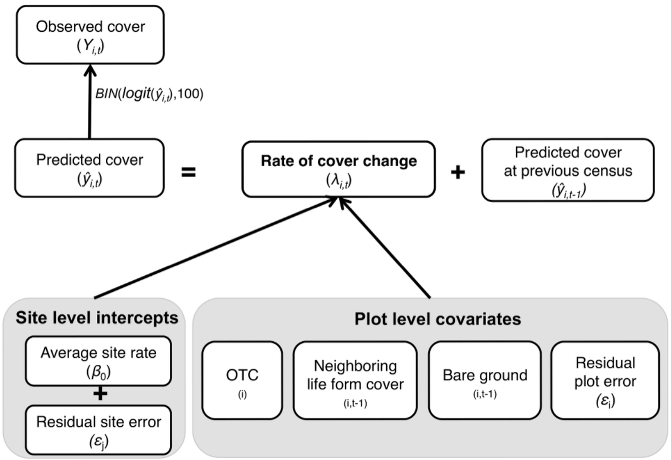

Observed cover
($Y_{i,t}$)
$BIN(logit(\hat{y}_{i,t}),100)$
Predicted cover
($\hat{y}_{i,t}$)
=
Rate of cover change
($\lambda_{i,t}$)
+
Predicted cover
at previous census
($\hat{y}_{i,t-1}$)
Site level intercepts
Average site rate
(β_0)
+
Residual site error
(ε_j)
Plot level covariates
OTC
(i)
Neighboring
life form cover
(i,t-1)
Bare ground
(i,t-1)
Residual
plot error
(ε_i)

Figure 2:

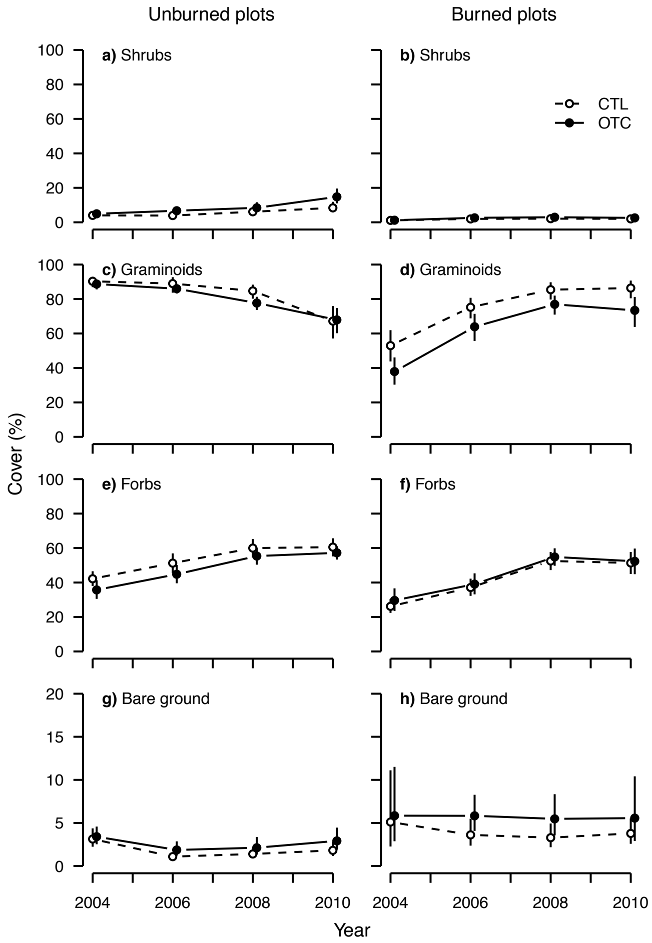

Unburned plots
Burned plots
a) Shrubs
b) Shrubs
CTL
OTC
c) Graminoids
d) Graminoids
e) Forbs
f) Forbs
g) Bare ground
h) Bare ground
Cover (%)
0
20
40
60
80
100
0
5
10
15
20
2004
2006
2008
2010
Year

Figure 3:

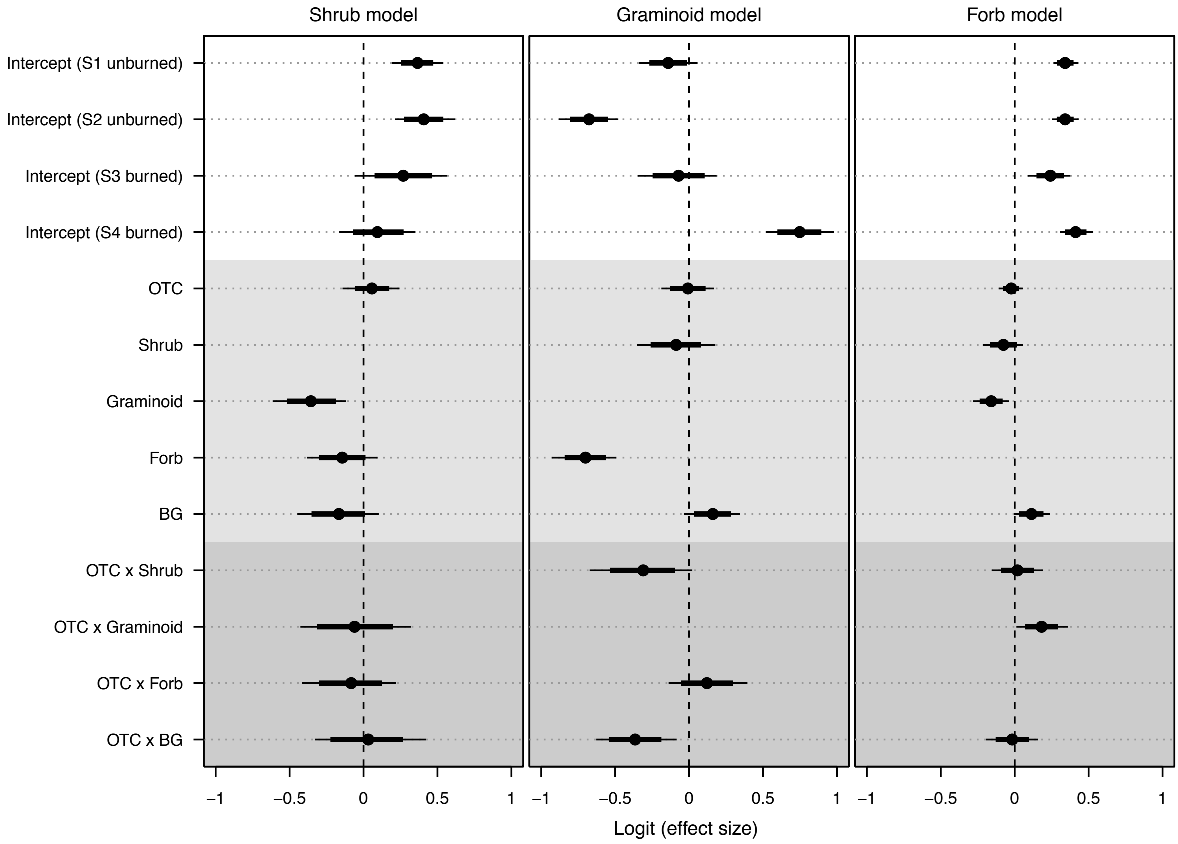

Shrub model
Graminoid model
Forb model
Intercept (S1 unburned)
Intercept (S2 unburned)
Intercept (S3 burned)
Intercept (S4 burned)
OTC
Shrub
Graminoid
Forb
BG
OTC x Shrub
OTC x Graminoid
OTC x Forb
OTC x BG
−1
−0.5
0
0.5
1
Logit (effect size)

Figure 4:

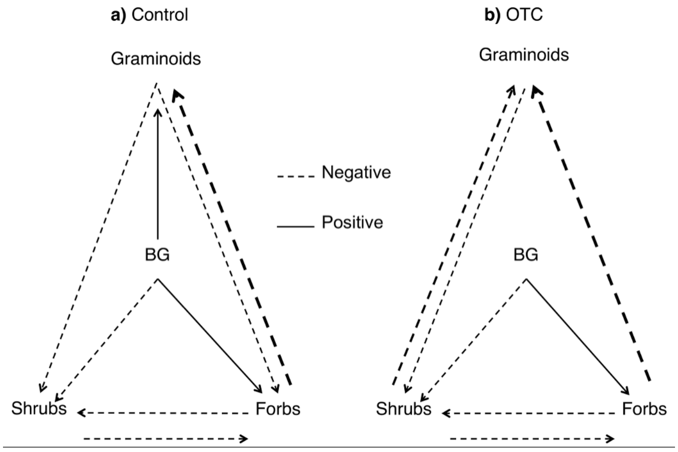

a) Control
Graminoids
BG
Shrubs
Forbs
Negative
Positive
b) OTC
Graminoids
BG
Shrubs
Forbs

Figure 5:

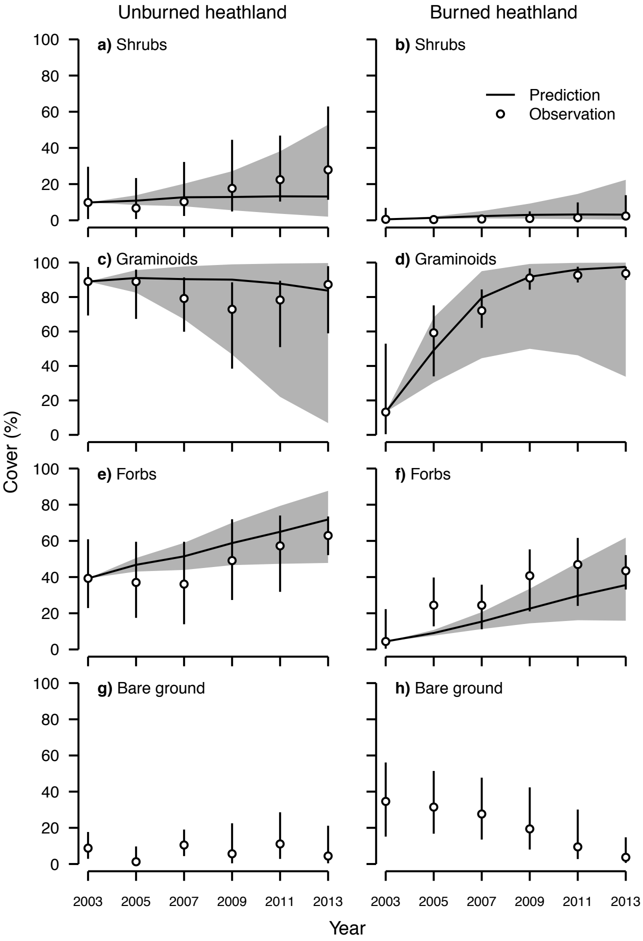
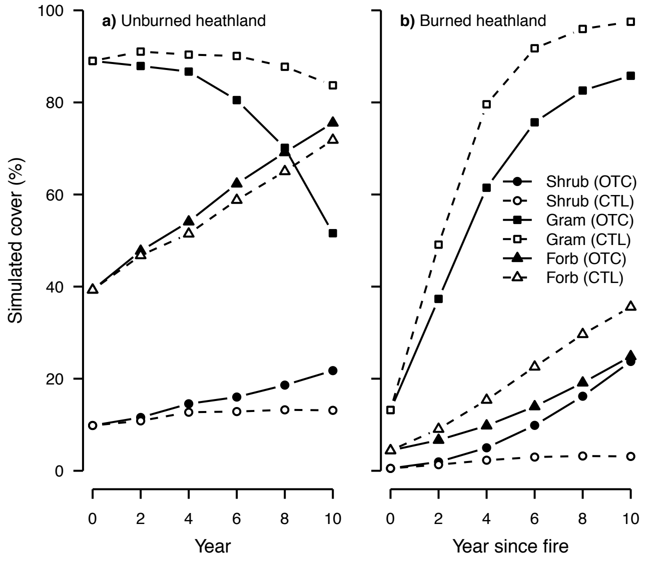

Unburned heathland
Burned heathland
a) Shrubs
b) Shrubs
Prediction
Observation
c) Graminoids
d) Graminoids
e) Forbs
f) Forbs
g) Bare ground
h) Bare ground
Cover (%)
0
20
40
60
80
100
2003
2005
2007
2009
2011
2013
Year

Figure 6:



100
80
60
40
20
0
Simulated cover (%)
a) Unburned heathland
b) Burned heathland
Shrub (OTC)
Shrub (CTL)
Gram (OTC)
Gram (CTL)
Forb (OTC)
Forb (CTL)
0
2
4
6
8
10
Year
Year since fire