Contribution of disturbance to distribution and abundance in a fire-adapted system

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Species distribution modeling (SDM) is an essential tool in understanding species ranges, but models haven't incorporated disturbance-related variables. This is true even for regions where long histories of disturbance have resulted in disturbance-adapted species. Therefore, the degree to which including disturbance-related variables in SDMs might improve their performance is unclear. We used hierarchical partitioning to determine how fire patterns contribute to variation in species abundance and presence, examining both the total variation disturbance-related variables explained, and how much of this variation is independent of soil and climate variables. For 27 Proteaceae species in the fire-adapted Cape Floristic Region of South Africa , we found that fire variability, frequency, and area burned tended to have explanatory power similar in size to that of soil and climate variables. Importantly, for SDMs of abundance, fire-related variables explained additional variation not captured by climatic variables, resulting in markedly increased model performance. In systems with high disturbance rates, species are less likely to be in equilibrium with their environment, and SDMs including variables describing disturbance regimes may be better able to capture the probability of a species being present at a site. Finally, the differential effect of fire on species abundance and presence suggests functional differences between these responses, which could hamper attempts to make predictions about species abundances using models of presence.

There is long-standing interest among ecologists in the relationship between species distributions and environmental factors. The importance of climate as an explanatory variable has long been recognized (McArthur 1972, Box 1981, Woodward 1987), and species distribution models (SDMs) are one approach to quantifying the relationship between species ranges and the environmental factors defining a species' niche (Guisan and Zimmermann 2000). They are an increasingly common tool, with applications that include prediction of the effects of climate changes on species ranges, land management and reserve planning, assessment of species invasion potential, and tests of ecological and biogeographical theory (Midgely et al. 2002, Peterson et al. 2002, Guisan and Thuiller 2005, Broennimann et al. 2007).

SDMs are usually constructed with climatic and abiotic variables, and the ability of these models to account for the effects of disturbance without explicitly including disturbance-related variables has rarely been examined (but see Moretti et al. 2006). There is some evidence in the literature that models built for species in ecosystems where the effects of disturbance are strong but not explicitly accounted for are less accurate (White 1979, Guisan et al. 1999, Austin 2002). Whether this reduced accuracy is due to the violation of the assumption of equilibrium or the importance of the effects of disturbance in shaping range limits (or both) is unclear. In the absence of data regarding pertinent disturbances in a

region, modellers may incorporate climatic or abiotic variables correlated with the disturbance of interest (Guisan et al. 1999, Dirnbock et al. 2002). However, the importance of accounting for disturbance on SDM accuracy has not been rigorously tested (but see Moretti et al. 2006).

Where disturbance is common, it may be an important determinant of community composition, since disturbance and disturbance regimes can act as selective filters which limit local membership based on species traits that mediate species' responses to disturbance (White 1979, Diaz et al. 1998). For example, species in fire-prone regions exhibit clear patterns of response to recurrent fire regimes, showing differential recruitment and persistence strategies (Bond and van Wilgen 1996, Pausas 2001): the relative fitness of a particular set of adaptations depends on fire regime, and so response to disturbance could be considered an important niche dimension (Grubb 1977).

Despite their usefulness, species distribution models have been criticized for a number of issues (Davis et al. 1998, Araujo and Guisan 2006, Austin 2007). For example, those using regression-based statistical frameworks are complicated by the issues of non-independence, multicollinearity between explanatory variables, and the retention of explanatory variables which are not ecologically relevant, (Mac Nally 2000, Graham 2003). Species presence and abundance patterns are determined by numerous factors, including average

climatic conditions and the variability or extremes of climate conditions, spatial heterogeneity and habitat conditions at finer scales, competition, predation, etc., and collinearity is almost inevitably an issue when choosing model variables to describe these factors (Mac Nally 2000, Graham 2003). Understanding the unique contribution of environmental and disturbance-related variables and their ecological importance requires the use of statistical methods which focus on explanatory power rather than predictive ability (Graham 2003). Statistical methods such as hierarchical partitioning focus on understanding the importance of different explanatory variables by distinguishing the proportion of variation in the dependent variable that can be uniquely attributed to each explanatory variable from the proportion of variation that is shared between several explanatory variables (Chevan and Sutherland 1991). This makes it useful for understanding whether disturbance-related variables contribute additional, unique information in understanding species abundances or presences, compared to climatic and abiotic variables alone.

In this paper, we examine the relative importance of variables accounting for environment and disturbance (fire regime) in explaining the abundances of 27 Proteaceae species in the Cape Floristic Region (CFR) of South Africa. The fire regime in the CFR – the combination of fire frequency, intensity, size and seasonality, as well as other factors (Gill 2008) – plays an acknowledged role in determining the likelihood of colonization and persistence among species (Cowling 1992, Bond and van Wilgen 1996). Fire regime plays an important role in determining the probabilities of species survival and recruitment in the Fynbos ecosystem in the CFR (Cowling 1992), and we expect the contribution of variables related to fire regime to species' presence and abundance to be significant. However, since climate strongly influences fuel load, fire area, and intensity (McKenzie et al. 2004), we hypothesize that the effects of fire regime are strongly collinear with those of climate, and so mostly accounted for even in the absence of explicit data on fire occurrence. We also incorporated spatial autocorrelation as an explanatory variable, given its relationship with environmental gradients and driven by biotic processes such as dispersal (Legendre and Legendre 1998).

Using hierarchical partitioning, we examined how much variation in species' presence and abundance could be independently explained by different fire, environmental and spatial variables. We addressed the questions: 1) how much variation in the presence and abundance of CFR Proteaceae species is independently explained by the effects of fire-related variables and 2) to what extent does the inclusion of fire-related variables increase the explanatory ability of species distribution models for Proteaceae species?

Methods

Study region and species

The study region was the Cape Floristic Region (CFR) on the Western Cape of South Africa, which is notable for its floral diversity (Goldblatt and Manning 2002), and high endemicity. Projections for the CFR (Midgely et al. 2002) suggest that the region is particularly vulnerable to climate change, making it a global conservation priority (Cowling et al. 2003, Lombard et al. 2003).

The CFR is generally characterized by cool, wet winters and hot, dry, drought-prone summers: it includes regions of Mediterranean-type climate in the southwest, as well as regions of summer rainfall in the east, and winter rainfall in the west (Schultze 1997). Soils are generally nutrient-poor (Cowling 1992). Most of the CFR is covered with fynbos: open shrubland dominated by sclerophyllous species (Moll et al. 1984, Midgley et al. 2003). The frequency of fire is a major structuring force in the Fynbos biome and Fynbos species are adapted to frequent (10–20 yr) fires, and in many cases require fire for successful reproduction (Bond et al. 1984, Pierce and Moll 1994).

Proteaceae species are an important component of Fynbos communities, and over 330 species are endemic or near endemic to the region. We examine the importance of various predictors of Proteaceae geographic distributions of presence and absence (hereafter: 'presence') and of the geographic distributions of abundances (hereafter: 'abundance'). Data regarding Proteaceae (or 'protea') species presence and abundance in the Fynbos is available from the Protea Atlas Project (PAP) with over 250 000 species records available; abundance data is an estimate of numerical abundance, with four possible categories: <10 individuals, between 10 and 99, between 100 and 9999, or >10000 (<http://protea.worldonline.co.za/default.htm>). Species presence is a binary variable recording presence or absence at each site. We selected twenty-seven Proteaceae species for analysis, based on their sufficient records of presence (>60 records) in areas for which climate and fire data were also available. These species represent seven genera and a variety of life history traits (Supplementary material Appendix 1). To ensure that the scale of species abundances and predictor variables matched, we treated species abundance records as point values and averaged to $1' \times 1'$ grid cells (i.e. 1 degree minute × 1 degree minute; ~1.55 × 1.85 km rectangles). We averaged abundances (rather than summing) to account for the sometimes differing numbers of Protea atlas censuses conducted within different grid cells. Analyses were also repeated using only one randomly selected abundance record per cell, but results did not qualitatively differ, so we show results for the averaged data only.

Climate, fire and spatial predictors

A wide variety of environmental data are available from the South African atlas of climate and hydrology (Schultze 1997). We retained for analysis variables understood to be of importance in determining species' survival and reproduction in the Cape Floristic Region (Cowling 1992, Mustart and Cowling 1993, Goldblatt and Manning 2002, Midgely et al. 2002): these variables reflect the importance of temperature and moisture stress, and the abiotic requirements for growth and reproduction (Table 1). We included information on soil conditions at the same scale (i.e. pH and texture; Latimer et al. 2006) since soil conditions play an important role in the ecological and evolutionary history of the Proteaceae (Pate et al. 2001). The soil variables were ordinal; pH takes values between 1 and 3, representing that the

Table 1. Summary of climatic, soil, fire, and spatial variables included in models of Proteaceae presence and abundance; values describe conditions in the study area, ~1700 km^2 of nature reserves in the Cape Floristic Region, South Africa.

Variable	Units	Minimum	Maximum	Mean	Standard deviation
Environment					
Mean annual precipitation	mm	91	3025	562	368
Frost duration	days	52.6	0.0	192.0	44.9
Growing degree days (>10°C)	degree d^{-1}	359	2968	1900	542
Soil texture	gradient from sand to clay	1	4	3	1.3
Soil pH	gradient from basic to acidic	1	3	1	0.5
Fire					
Fire frequency	fires yr^{-1}	0.04	0.44	0.09	0.06
Variability in fire frequency	fires yr^{-1}	0.000	0.537	0.044	0.082
Average fire area	no. cells	1	199	17	24
Space					
Average neighbour cell abundance (1st order)	abundance*	0.163	0.045	0.585	0.133

*Refer to Methods for description of how abundance is recorded.

grid cell consists of > 50% acidic (1), neutral (2), or alkaline soil (3); texture takes values between 1 and 4, representing that the grid cell consists of more 50% fine (1), moderately fine (2), moderately coarse (3), or coarse soil (4). Although climatic data is available for the entire CFR, we restricted analyses to those areas for which concurrent fire data was also available, see below for details.

We obtained data regarding fire occurrences in the CFR from CapeNature Scientific Services (<http://www.capenature.co.za>). Although some records exist from as early as 1927, records were not uniformly collected until the 1970s, and so we used data from between 1974 and 1995 only. Even for short periods (< 30 yr) fire history has been shown to produce recognizable effects on floristic composition in sclerophyll communities such as those in Australia and South Africa, where plants are adapted to fairly short fire cycles (Pierce and Moll 1994, Cary and Morrison 1995). Therefore we used this fire data to help characterize the average fire regime experienced by each cell. A record existed for each fire that occurred between 1974 and 1994, delineating the spatial extent of that fire (i.e. GIS shapefile). We used this data to calculate fire-related variables, namely average frequency, variability in frequency, and average fire area, for each 1′ × 1′ grid cell. The total number of fire records that included a given grid cell was used as a measure of fire frequency for that grid cell. For each grid cell, fire variability was measured as the coefficient of variation in the number of years between consecutive fire events. The area of the fires occurring in a grid cell was also recorded, and the average used as a general metric which could relate to fire characteristics such as average fire intensity (Bessie and Johnson 1995) or favourable weather conditions. Records of fire were available in reserve areas only, and for this reason, we examined only species abundances recorded within reserves managed by CapeNature within the CFR, an area covering 644 1′ × 1′ grid cells (~1700 km^2). The fire variables and species data were used at the 1′ × 1′ scale because the climate data was available only at this scale, and agreement in the scale of the three datasets was necessary for further analyses. We checked whether there was autocorrelation between the fire regimes of adjacent cells as a result of this interpolation, but in fact very few adjacent cells had identical combinations of fire frequency, area and variability.

We accounted for spatial dependence in the observed species presences/abundances using a contagion term (Araujo et al. 2002). This accounts for positive spatial autocorrelation, where individuals of a species are more likely to occur in one area if they are also present in surrounding areas, which may account for both environmental similarities and dispersal between neighbouring cells. This term accounts for the average abundance of individuals of the same species in the immediately adjacent 1′ × 1′ cells (i.e. 8 neighbouring cells) when species abundance was the response variable, or the proportion of the 8 neighbouring cells occupied when species presence was the response variable. The spatial term was constructed using values for the entire CFR, and so the boundaries of the reserve areas were not considered when calculating this term.

Hierarchical partitioning:

One of the important features of hierarchical partitioning is that it allows the contribution of a given variable to explaining variation in the dependent variable to be partitioned into the component that is shared with other explanatory variables and the component that is unique to that variable. The independent contribution of each explanatory variable is calculated by examining that variable's effect in all possible regression models that can be constructed from the set of explanatory variables (MacNally 1996). By focusing on identifying the predictive variables with the highest independent explanatory power, hierarchical partitioning can help prevent multi-collinearity in model selection.

Using hierarchical partitioning, we examined the independent and joint effect of all climate, soil and fire-related variables (Table 1) on species abundance and species presence, repeating the analysis for all 27 protea species. We used the hier.part library in the statistical package R (Hastie 2008, R Development Core Team 2009), and modeled the relationship between the explanatory variables and species abundance or presence using general linear models (GLMs). We used a binomial distribution for GLMs of presence and a Gaussian distribution for GLMs of abundance to account for differences in the distribution of presence/absence values and abundance values.

For each species, we analyzed how the total variation in the dependent variable could be partitioned among each of the 9 explanatory variables, using log-likelihoods as our measure of the goodness-of-fit. This allowed us to make direct comparisons between models of presence and abundance, despite their being modeled with different distributions. Results were averaged across all 27 species, separately for abundance and presence. The focus of this analysis is on understanding how variation in abundance or distribution is partitioned among different explanatory variables.

Species distribution models

Hierarchical partitioning provides information about how variables explain shared and independent variation in the response variable, however it relies on a monotonic relation between variables, whereas most SDMs acknowledge that there may be important non-linear relationships between species distributions and explanatory variables. As a result, we also used general additive models (GAMs) to model the presence and abundance of the 27 Protea species: this method of building SDMs tends to be accurate and robust across species and scales and has been used for models of both distribution and abundance (Pearce and Ferrier 2001, Thuiller et al. 2003, Elith et al. 2006). We examined how model deviance for GAMs containing only the environmental and spatial variables compared to model deviance for GAMs containing environmental, spatial, and fire-related variables. We used the R package gam (Hastie 2008) to construct the GAMs, using a Gaussian error distribution for models of abundance, and a binomial error distribution for models of presence. Cubic spline smoothers were used. We used model deviance, calculated as the difference between the null deviance and residual deviance (adjusted for sample size and parameter number) (Guisan et al. 1999) to describe model variation (D^2_{adj}), because it is comparable between models of presence and abundance, whereas more common measures such as AUC cannot be calculated for models of abundance.

Results

Hierarchical partitioning

Species abundances
Results from hierarchical partitioning show that the majority of the explained variation in species abundance is attributed to the spatial term, which explains 5 to 10 times as much variation as the remaining environmental and fire-related variables (Fig. 1). On average, the environmental and fire-related variables accounted for similar amounts of the explained variation, with the environmental variables explaining the most variation being the number of growing degree days and soil texture. It is worth noting that individual species varied widely in terms of the explanatory power of each variable, although these differences did not relate significantly to species traits, possibly due to the limited number of species (see Supplementary material Appendix 2 for species-level results). Fire-related variables tended to explain slightly less variation in abundance than
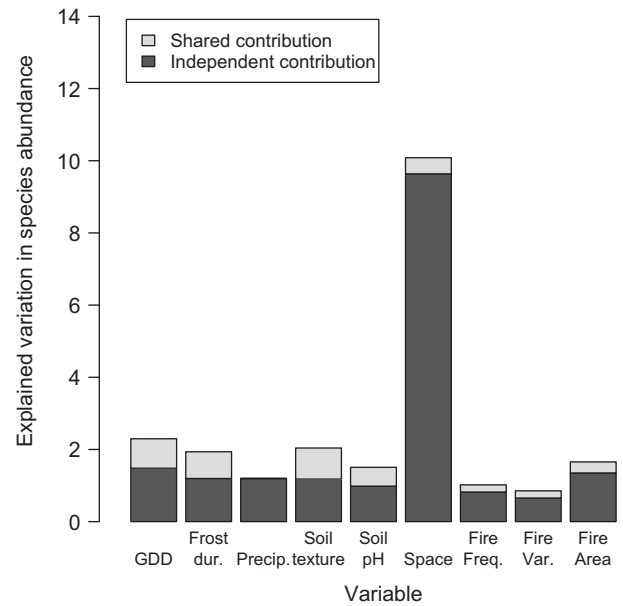

Figure 1. The variation in species abundance (log-likelihood) explained by the 9 explanatory variables, averaged across 27 Proteaceae species. Lower portions of bars represent the component of this variation that is independently explained by that variable, the upper portion of bars represent the component of variation that is explained jointly with other variables.

the environmental variables, however the majority of the variation explained by fire is independent of the other variables (74, 82, and 78% for fire frequency, fire variability, and fire area, respectively (Fig. 3)). Variation explained by environmental variables was also primarily independent (between 68 and 82% of total variation explained by a variable is contributable only to that variable).

Species presences
Hierarchical partitioning results for species presence indicated that the environmental, fire, and spatial variables explained far more of the variation in species presence than they did the variation in species abundance, although space similarly contributed the majority of the explained variation in species presence (Fig. 2). The variables with the most explanatory value for species presence were frost duration and soil pH. Fire variables, in particular fire frequency and fire variability, tended to explain less variation in presence than the climate and soil variables, although their contribution to presence is still 3–4 times higher than their contribution to abundance. The proportion of the variation explained by the environmental and fire variables that was independent was also lower, varying between 50–65% (Fig. 3). For example, the proportion of variation in species presence explained by fire frequency, fire variability, and fire area that was independent of the other variables was 58, 52, and 66%, respectively. Results for individual species are available in Supplementary material Appendix 2.

Species distribution models
Comparisons of model deviance for models of abundance and presence both showed significant increases in the proportion of explained deviance (D^2_{adj}) when fire-related variables were
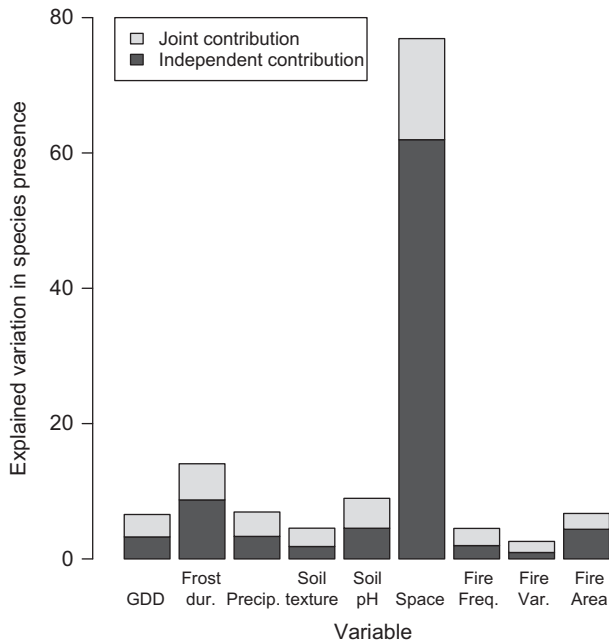
Figure 2. The variation in species presence (log-likelihood) explained by the 9 explanatory variables, averaged across 27 Proteaceae species. Lower portions of bars represent the component of this variation that is independently explained by that variable, the upper portion of bars represent the component of variation that is explained jointly with other variables.
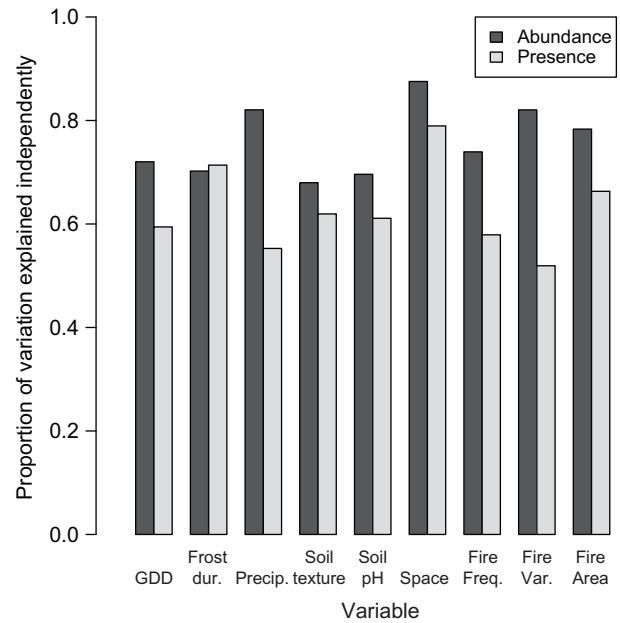

Figure 3. Proportion of the variation explained by a variable that is independent: paired bars represent a variable's independent contribution to species abundance and species presence, average across 27 Proteaceae species.

included with climate, soil and spatial variables (Fig. 4). For abundance models, the inclusion of all fire-related variables increased the average D^2_{adj} from 0.48 ($\pm$ 0.17) for the non-fire containing models, to 0.62 ($\pm$ 0.18) after its inclusion, a significant increase in the mean model deviance (t = –2.8957, p = 0.005). For models of presence, the effects of fire-related variables were smaller and not significant: model deviance increasing from 0.60 to 0.62 when the fire-related variables were included. We also looked at the difference in the AIC for the full models containing fire-related variables and the reduced models which omitted fire variables. For models of abundance, there was a Δ_{aic} = 4.8, suggesting strong support for the retention of the full, fire-containing model. Support for models of presence containing fire-related variables was also strong, with Δ_{aic} = 4.26.

Discussion

Species distribution models don't generally include disturbance-related variables (Austin 2002), and the effect of disturbance on the accuracy of SDMs is not often quantified. We hypothesized that variables relating to fire were important determinants of presence and abundance in this fire-adapted system, but that they were likely collinear with the effects of environmental variables. This proved partly true, as fire-related variables shared explanatory ability with climate and soil variables, but fire-related variables also contributed additional explanatory ability to models, particularly for species abundances. As a result, including fire-related variables greatly improved the explanatory ability of SDMs of abundance, with SDMs of presence showing lesser improvements.

The differential contribution of fire-related variables to the SDMs of Proteaceae abundance and presence was an interesting result. Bradstock et al. (1997) also found differential effects of fire regime on presence and abundance, which they suggested indicated that species abundances were more sensitive to the effects of fire regime than species presences. Among Proteaceae species, population sizes can vary highly between fires, since the likelihood of successful germination and establishment is sensitive to conditions such as the time since the last fire, fire season and intensity, and pre- and post-fire climate (Whelan et al. 2001, Auld and Scott 2004). In addition, since underground seed banks may bear little relationship to aboveground measures of abundance (Enright and Lamont 1989), populations are buffered from local extinction (Bond et al. 1984) even though recent fires have been unfavourable, maintaining species' presences in an area. As a result, fire frequency and area may affect species' density without affecting their presence: although populations may not be extirpated by too-frequent or severe fires, seedbanks or resprouting ability may be greatly reduced, making population size dependent on the fire regime. The area burnt by a given fire may effect post-fire canopy cover, competitive pressure, and the probability of establishment of seedlings.

Fire is acknowledged as one of the most important selective agents in the CFR (van Wilgen 1987). Specifically for Proteaceae species, fire is known to have effects on life history (Pierce and Moll 1994, Bond and van Wilgen 1996), population dynamics (Bond et al. 1984, Le Maitre 1987), and species interactions (Cowling 1992, Cary and Morrison 1995). Studies in Australian shrublands also show that fire and disturbance can significantly contribute to species frequency and density (Cary and Morrison 1995, Bradstock et al. 1997, Henderson and Keith 2002). Our results also found that fire-related variables help explain variation
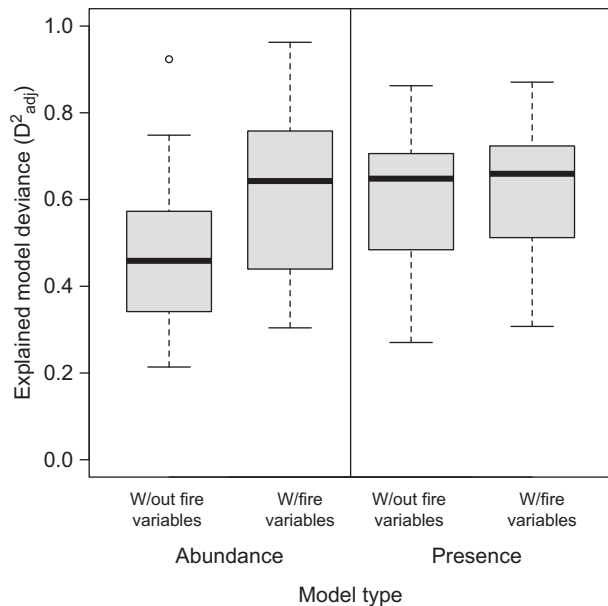
Figure 4. Change in explained model deviance, D^2_{adj} between full models including space, climate, soil and fire variables, and models excluding fire variables, for both models of abundance and presence. Results are averaged across the 27 Proteaceae species.

in species presences. However, including fire variables in SDMs of species presence did not greatly increase model deviance, due to greater collinearity or shared explanatory ability, between the fire and environmental variables. It is likely, for example, that fire frequency is directly or indirectly related to humidity, precipitation, dry season length, and fuel load present (a compound function of fertility, precipitation, temperature and age since previous fire) (McKenzie et al. 2004, Archibald et al. 2008). Fire area may relate to important aspects of the fire regime such as seasonality and weather conditions, which in turn can affect the likelihood of post-fire germination for a number of Proteaceae species (Bond et al. 1984, Enright and Lamont 1989). In contrast, hierarchical partitioning results indicated that for species abundances, there was additional contribution of fire-related variables beyond their collinear effects with environment. This meant that by explicitly including fire-related variables in models of abundance, model explanatory ability increased by nearly 30%. Given that model accuracies (even when fire regime variables were included) were fairly low for these species (average D^2_{adj} ~0.48), this additional information could be important for producing models of practical value. Of course, in systems where fire or other disturbances are less important, the inclusion of information on disturbance may be less beneficial, and the cost and effort of obtaining data on disturbance would need to be considered.

The differential contribution of the fire-related variables to abundance also hints at the difficulties that might arise when trying to scale models of presence to make predictions about abundance. The question of whether models of presence can be scaled to predict abundance is an important one, given the greater availability of presence survey data and the greater value of abundance data as an indicator of habitat value and the likelihood of species persistence (Nielson et al. 2005). The different contribution of fire to species abundance and presence suggests that these response variables

may be a function of different processes (Nielson et al. 2005). If the response variables of presence and abundance capture different processes (i.e. they do not relate in similar ways to habitat suitability), making predictions about abundance on the basis of models built using presence as the response variable will be difficult (Cingolani et al. 2007).

The fire-related variables we used for this analysis relate to interval-dependent components of fire regimes (Bond and van Wilgen 1996), which relate to variation in fire frequency and affect the ability of species to pass important life hurdles during the inter-fire interval (Cowling 1992, Bond and van Wilgen 1996, Midgley and Kruger 2000). There are also event-dependent aspects of fires, which are determined by the unique conditions of a given fire (including, season, weather and fire intensity). These can modify the interval-dependent effects of fires so that fire-return interval on its own is greatly reduced as a predictor of post-fire species composition (Whelan et al. 2001). Event-dependent components of the most recent fires may have effects on abundance and presence similar in magnitude to those of interval-dependent fire effects in some systems (Bradstock and O'Connell 1988, Bradstock 1990), although this is likely dependent on the system. If this is true, fire is even more important to patterns of Proteaceae presence and abundance than these results suggest.

The data we used came from multiple sources, and there were discrepancies between the scales of the different data sets, which could affect the relative importance of the explanatory variables. The climate variables were available at a $1' \times 1'$ scale, but fire variables were available only at a coarser resolution in the form of large-scale spatial records, and were interpolated to the scale of the climatic data. Fire tends to be highly patchy, and ideally data would have be available at a finer scale, however we treated the fire-related variables as representative of the average fire regime rather than the precise conditions experienced by a species at a site. Hence these have probabilistic relationship with species' abundances and distributions, that is, they effect the likelihood of a species being present (or abundant) at a locale. Since our data do not capture the fine-scaled features of fire events, our results are likely a conservative estimate of fire's importance. Even so, the fire-related variables were important determinants of Proteaceae presence and abundance, emphasizing how important accounting for disturbance can be.

For most species, the largest proportion of variation in species presence and abundance was explained by the spatial variable, and much of this explained variation was independent of the other model variables. In addition, the importance of this spatial term varied greatly among the 27 species (Supplementary material Appendix 2). In general, strong spatial dependence in species presence or abundances is the result of either unmeasured, spatially-autocorrelated environmental variables, or biotic processes such as competition or predation (Miller et al. 2007). We also expected that the importance of the spatial variable might relate to species traits such as seed dispersal vector, seed size, or seed bank type (serotinous versus underground), which can influence spatial structure in populations (Nathan and Muller-Landau 2000). However, there were no significant relationships between these traits and the importance of the spatial variable for either presence or abundance (results not shown). The fact that we did not find a relationship is not surprising,

since dispersal ability can interact with other species traits like height or seed shape, and dispersal ability is not the only factor determining colonization success and species persistence in a new site (Schurr et al. 2007).

We were restricted to examining results only for those species which had enough observations for models of their presence and abundance to be built. This may limit the type of species our results relate to, since species with high abundances or large range sizes may exhibit different characteristics than rare species, which can affect how easily their presence and abundance are modelled (McPherson et al. 2004, McPherson and Jetz 2007). Despite the fact that these species have traits expected to mediate species' responses to fire (post-fire regeneration ability, seedbank type, seed dispersal ability), there were not consistent patterns between species traits and the importance of accounting for fire in models of abundance or presence. However, the relatively low number of species (27) may have precluded finding significant effects of species traits.

Disturbance regimes are changing due to human actions: changes in climate are likely to result in increased fire probability and extent (Gillet et al. 2004), while conversely, suppression of fires (Frost 1998) and other human activities (Archibald et al. 2008) can also alter the frequency, size and locations of burns. Incorporating the influence of disturbance on species ranges into SDMs may be an important activity in systems where disturbance has historically been important, and/or where disturbance regimes are changing. In such regions, disturbance events mean that species are unlikely to be in equilibrium with suitable habitat conditions, a basic assumption of SDMs. Variables describing disturbance regimes may help SDMs capture differences in the probability of a species being present at a site: this could increase SDM accuracy even though the assumption of equilibrium is violated.

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Supplementary material (Appendix E6948 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.