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What predicts the richness of seeder and resprouter species in fire-prone Cape fynbos: Rainfall reliability or vegetation density?

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Abstract In ecosystems subject to regular canopy fires, woody species have evolved two general strategies of post-fire regeneration. Seeder species are killed by fire and populations regenerate solely by post-fire recruitment from a seed bank. Resprouter species survive fire and regenerate by vegetative regrowth from protected organs. Interestingly, the abundance of these strategies varies along environmental gradients and across regions. Two main hypotheses have been proposed to explain this spatial variation: the gap dependence and the environmental-variability hypotheses. The gap-dependence model predicts that seeders are favoured in sparse vegetation (vegetation gaps allowing effective post-fire recruitment of seedlings), while resprouters are favoured in densely vegetated sites (seedlings being outcompeted by the rapid crown regrowth of resprouters). The environmental-variability model predicts that seeders would prevail in reliable rainfall areas, whereas resprouters would be favoured in areas under highly variable rainfall that are prone to severe dry events (leading to high post-fire seedling mortality). We tested these two models using distribution data, captured at the scale of quarter-degree cells, for seeder and resprouter species of two speciose shrub genera (*Aspalathus* and *Erica*) common in fire-prone fynbos ecosystems of the mediterranean-climate part of the Cape Floristic Region. Contrary to the predictions of the gap-dependence model, species number of both resprouters and seeders increased with values of the Normalized Difference Vegetation Index (a widely used surrogate for vegetation density), with a more marked increase for seeders. The predictions of the environmental-variability hypothesis, by contrast, were not refuted by this study. Seeder and resprouter species of both genera showed highest richness in environments with high rainfall reliability. However, with decreasing reliability, seeder numbers dropped more quickly than those of resprouters. We conclude that the environmental-variability model is better able to explain the abundance of woody seeder and resprouter species in Southern Hemisphere fire-prone shrublands (fynbos and kwongan) than the gap-dependence model.

Key words: *Aspalathus*, *Erica*, gap dependence, post-fire recruitment, rainfall reliability.

INTRODUCTION

Fire has played a key evolutionary role in many ecosystems, shaping the form and function of plants (Bond & van Wilgen 1996). Woody plants in fire-prone ecosystems can be categorized into two types of post-fire regeneration responses that confer population resilience to recurrent fires, namely *seeders* and *resprouters* (Keeley 1986; Bond & van Wilgen 1996; Bond & Midgley 2003; Ojeda *et al.* 2005; Altwegg *et al.* 2015). Seeders are fire-sensitive (killed by fire = R−) and populations regenerate solely by post-fire recruitment (P+) from a seed bank (R−P+ or

‘obligate seeders’ *sensu* Pausas *et al.* 2004). Resprouters are fire-resistant (survive fire = R+) and regenerate by vegetative regrowth from protected organs, with or without fire-cued seed germination (R+P+ or ‘facultative species’ and R+P− or ‘obligate resprouters’, respectively; *sensu* Pausas *et al.* 2004).

Recently, Pausas and Keeley (2014) integrated demographic factors, environmental variables and fire regime to propose a conceptual model to explain the evolution and ecological correlates of seeders and resprouters in fire-prone ecosystems. They argued that in vegetation with reliable canopy fires, resprouting is selected for in ‘fertile competitive environments’ with ‘more reliable water’ and ‘denser vegetation’. Under such conditions, seedlings would be outcompeted in the post-fire environment by the

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rapid canopy regrowth of resprouters. Seeders, however, are favoured in areas with ‘stronger oscillations in water availability’ and ‘stressful site conditions (such as low soil fertility and severe water deficits)’, resulting in more ‘open vegetation’ (Pausas & Keeley 2014). These latter conditions would favour longer fire intervals and hence more intense fires causing high mortality in resprouter adults and creating vegetation gaps as low-competition, open sites for seedling growth. This, in turn, favours effective post-fire recruitment of seeders, which typically produce seedlings capable of withstanding intense seasonal water stress (Pausas & Keeley 2014; Keeley *et al.* 2016). This hypothesis is termed ‘the gap-dependence model’.

Based on the distributions of four seeder and resprouter subspecies pairs within the shrub genus *Arctostaphylos* in mediterranean-climate California, Keeley *et al.* (2016) found empirical support for Pausas and Keeley’s (2014) gap-dependence model. They showed that the seeder congeners were consistently associated with sites with high values (medians of 20–50%) of bare ground, whereas for resprouters, bare ground was 5% or less. Keeley *et al.* (2016) concluded that ‘obligate seeding appears to be selected when fuel structure is broken up by bare ground and resprouting selected when vegetation is denser’.

Although Pausas and Keeley (2014) assumed population dynamics of seeders to be semelparous-like, as Ojeda *et al.* (2005) and Higgins *et al.* (2008) had done before, they downplayed the effects of temporal environmental variability (e.g. post-fire rainfall variability; Cowling *et al.* 2005) on post-fire recruitment success and, hence, fitness of seeder populations. Although they pointed out that reliable rainfall had a positive effect on post-fire seedling survivorship (see fig. 2 in Pausas & Keeley 2014), they implicitly assumed that seedlings of seeders are tolerant of moisture stress across the whole aridity gradient, while resprouters (seedlings and adults) are not. However, this latter assumption conflicts with previous work, which demonstrate that, although seedlings of seeder species might have at least two-fold higher survival rates than resprouter seedlings under mild seasonal moisture stress, severe or extended dry events dramatically increase and equalize seedling mortality rates in both seeders and resprouters (Zammit & Westoby 1987; Thomas & Davis 1989; Enright & Lamont 1992a; Richards & Lamont 1996).

Temporal environmental variability, manifested as post-fire rainfall variability, has been identified as a key factor selecting for regeneration strategies (Cowling *et al.* 2005; Ojeda *et al.* 2005; Higgins *et al.* 2008). Variable or unreliable rainfall increases the risk of severe, extended seasonal dry events and results in high post-fire recruitment variability,

favours resprouters over seeders, as seeder populations are more sensitive to occasional bouts of low effective recruitment (Enright & Lamont 1992b; Lamont & Markey 1995; Higgins *et al.* 2000; Ojeda *et al.* 2005). This hypothesis (which we term ‘the environmental-variability model’) has been invoked to explain the geographical pattern of abundance of seeder and resprouter species of *Erica* in South Africa’s Cape Floristic Region (CFR) (Ojeda 1998; Ojeda *et al.* 2005), as well as the relative abundance of these two regeneration strategies in mediterranean-climate vegetation globally (Cowling *et al.* 2005).

The gap-dependence model has not been tested in the fire-prone mediterranean-type shrubland ecosystems of the CFR and the Southwest Floristic Region of Western Australia, both dominated by fire-prone shrublands (fynbos and kwongan, respectively) noted for their high incidence of seeder shrub species at all spatial scales (Kruger 1977; Cowling & Witkowski 1994; Bond & Midgley 2003; Cowling *et al.* 2004; Keeley *et al.* 2012; Groom & Lamont 2015). Here, we explore the predictions of the gap-dependence and environmental-variation models in the mediterranean-climate part of the CFR, using as focal taxa the genera *Aspalathus* and *Erica*, both shrubby genera comprising a mix of seeder (R–P+) and resprouter (mostly R+P+) species. *Aspalathus* (Fabaceae) and *Erica* (Ericaceae) are the largest genera in the megadiverse CFR flora (Goldblatt & Manning 2002) and both have featured in the literature on post-fire regeneration (Schutte *et al.* 1995; Ojeda 1998; Bond & Midgley 2003). Both genera have geographical distribution patterns typical of speciose Cape genera, namely a massive concentration of species in the southwest, with declining richness northwards and eastwards (Appendix S1; Levyns 1964; Cowling *et al.* 2017). The extraordinary diversity of the two genera is largely the product of relatively recent (Plio-Pleistocene) diversification (Edwards 2006; Pirie *et al.* 2016), *Erica* mainly in montane habitats, whereas *Aspalathus* has also speciated intensively in the lowlands of the CFR (Cowling *et al.* 2017).

The gap-dependence model, as formulated by Pausas and Keeley (2014), predicts that seeders should dominate in environments that have large areas of bare ground resulting in large post-fire gaps, whereas resprouters should dominate in areas of dense vegetation where post-fire gaps are small and quickly filled. We tested this model by assessing richness of seeder and resprouter species of *Aspalathus* and *Erica* in relation to patterns of the Normalized Difference Vegetation Index (NDVI), a widely used surrogate for vegetation density (Tucker & Sellers 1986; Pettorelli *et al.* 2005; Wilson *et al.* 2015). To test the environmental-variability model within the mediterranean-climate part of the CFR, we modelled richness of seeder and resprouter species in response to

the coefficient of variation of annual rainfall (CVR), a surrogate for the likelihood of periods of much more intense summer water deficit than average (Cowling *et al.* 2005). Owing to their reliance on post-fire seedling recruitment for persistence, we predicted a strong negative relationship between CVR and richness of seeders. In environments subject to stochastic, severe dry events in association with low seasonal (winter) rainfall, seeders would be disadvantaged relative to resprouters (Ojeda *et al.* 2005). However, since resprouters of both *Aspalathus* and *Erica* are facultative (R+P+ *sensu* Pausas *et al.* 2004), and some adults do succumb to fire and severe moisture stress (Marais *et al.* 2014; Slingsby *et al.* 2017), we also predict a negative relationship between resprouter richness and CVR, but with a shallower slope than that of seeders.

METHODS

We restricted our analysis to the western part of the CFR that receives at least 65% of its rainfall in the winter months (April to September), that is, having a mediterranean-type climate (the eastern CFR receives non-seasonal or bimodal rainfall). This western part of the CFR is also the most species rich (Appendix S1, Cowling *et al.* 1992; Cowling & Lombard 2002). Our delimitation ensured comparability with the other four mediterranean-climate ecosystems of the world (Bradshaw & Cowling 2014), including California, the locus of Keeley *et al.*'s (2016) study. With the exception of small areas of the extreme northwest, our study area is subject to regular fires of similar intensity and frequency; therefore, variation in disturbance regime can be discounted as a factor influencing the incidence of the two regeneration strategies (cf. Bond & Midgley 2003).

We used the number of seeder and resprouter species per unit area in *Aspalathus* and *Erica* as the response variable in our analyses. To do so, we were able to classify as seeders or resprouters 149 species of *Aspalathus* (54.6% of total) and 438 species of *Erica* (64.4% of total) based on field observations, examination of herbarium specimens, and communication with colleagues (see also Ojeda 1998). When restricted to the mediterranean-climate part of the CFR, numbers were reduced to 111 species in *Aspalathus* (76 seeders and 35 resprouters) and 319 species in *Erica* (294 seeders and 25 resprouters). We used PRECIS (Germishuizen & Meyer 2003), a flora data set managed by the National Herbarium in Pretoria, South Africa, to access spatial data for our focal taxa, provided as lists of species per quarter-degree cell (QDC). We, thus, generated 758 records for *Aspalathus* and 2047 for *Erica*. We acknowledge that patterns of species number may be uncoupled from patterns of ecological dominance of these two strategies (Bouchenak-Khelladi *et al.* 2014). However, collecting data on the ecological dominance of the two strategies for both species at the QDC scale was beyond the scope of this paper.

We used spatial patterns Normalized Difference Vegetation Index (NDVI) as a surrogate for vegetation density or openness. NDVI data were obtained from the long-term

average of the MODIS Terra and Aqua 16-day composites (MOD13Q1 and MYD13Q1) compiled over the period between February 2000 and October 2017 (extracted from Climate Engine on the 17th October 2017 at a resolution of 500 m; Huntington *et al.* 2017; <http://clim-engine.appspot.com/>). Values range from 0 (bare ground) to 1 (complete cover of dense, green vegetation). The gap-dependence hypothesis predicts a negative relationship between richness of seeders, and a positive relationship of resprouters, with increasing NDVI.

We used the coefficient of variation of annual rainfall (CVR) as a surrogate for environmental variability, specifically the variability of seasonal soil moisture conditions that would impact on post-fire seedling mortality (Ojeda 1998; Cowling *et al.* 2005). Framed thus, the environmental-variability hypothesis predicts negative relationships with CVR for both seeders and resprouters, but with a steeper slope for seeders. The precipitation data were sourced from Schultze (1997).

The relationships between the number of species for each genus per regeneration strategy and the two explanatory variables underpinning the two hypotheses (NDVI for gap dependence and CVR for environmental variability; both resampled to the PRECIS resolution of the species dataset) were investigated using generalized linear models, with linear and/or quadratic relationships and a stepwise AIC-based variable selection (Akaike 1974). Goodness-of-fit of models were quantified with R^2 measures corrected by the number of degrees of freedom of the models. We tested for significant differences in the intercept and slopes of these regressions with analyses of covariance (ANCOVA). All analyses were performed with the software R v.3.4 (R Development Core Team 2017; <http://www.R-project.org/>).

RESULTS

Patterns

Areas with large cover of bare ground are concentrated in the north-eastern, northern and north-western fringes of the winter-rainfall CFR (Fig. 1); these are also the drier areas, receiving <350 mm annual rainfall (Bradshaw & Cowling 2014). The densest vegetation is associated with the southeast of the region on the rugged landscapes of the Cape Fold Mountains, where annual rainfall can be as high as 3000 mm. The region also has the lowest values of CVR; values increase dramatically westwards on the lowlands, and northwards of 33°S on the Fold Mountains (the Cederberg), and on the semi-arid north-western coastal plain.

Irrespective of genus or regeneration strategy, areas of highest species richness were in the extreme south (Cape Peninsula, Hangklip to Hottentots Holland mountains), followed by the remainder of the Cape Fold Mountains northwards to the Cederberg (Fig. 2). However, in the case of *Aspalathus* and

resprouter *Erica* species, hotspots extended further north than for seeder *Erica* species that were massively concentrated in the extreme south. Overall, more cells were dominated by seeders in *Erica* than *Aspalathus* (Fig. 3). However, for both genera, areas dominated by seeders were the north-trending Cape Fold Mountains, whereas the western lowlands and the northern mountains (Gifberg-Bokkeveld) had several areas where resprouters dominated.

Models

Contrary to the predictions of the gap-dependence model, although resprouter species numbers increased with increasing NDVI, they were not accompanied by a concomitant decrease in seeder species numbers. Instead, for both *Aspalathus* and *Erica*, there was a significant positive relationship between NDVI and richness of seeder and resprouter

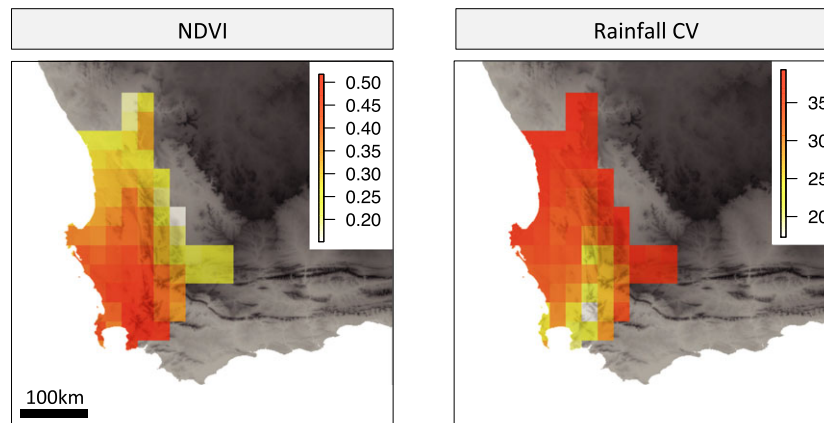


Fig. 1. Patterns of Normalized Vegetation Difference Index (NDVI) and coefficient of variation of annual rainfall (Rainfall CV) at the quarter-degree scale in the winter-rainfall part of the Cape Floristic Region.

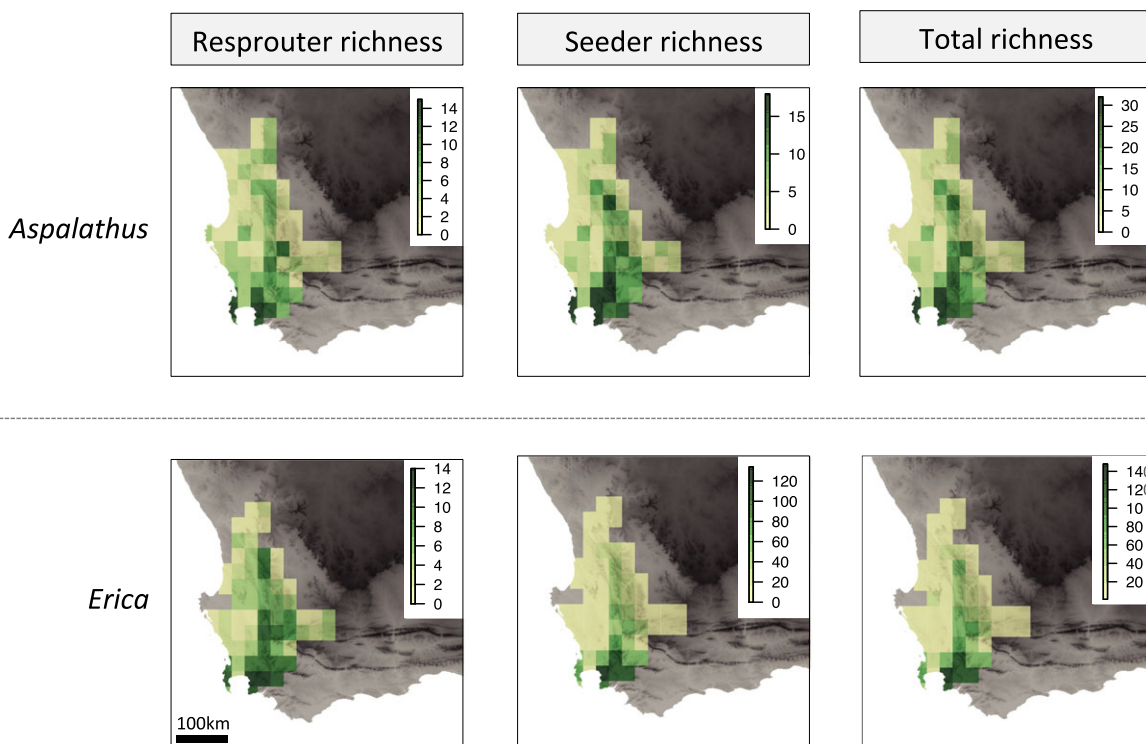


Fig. 2. Richness of resprouter, seeder and total species of *Aspalathus* and *Erica* in quarter-degree cells across the winter-rainfall part of Cape Floristic Region, South Africa.

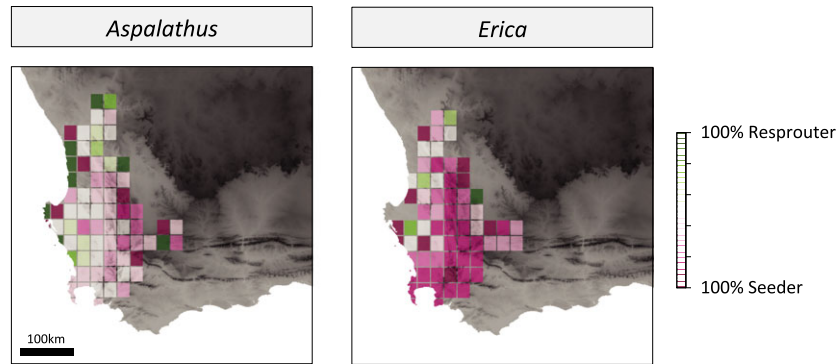


Fig. 3. Patterns in the ratio of resprouter:seeder species of *Aspalathus* and *Erica* species per quarter-degree cell in the winter-rainfall part of the Cape Floristic Region, South Africa.

species (Fig. 4, see Table 1 for model parameters). This relationship was stronger for *Aspalathus* (R^2 of 0.30 for seeders and 0.39 for resprouters; both the slopes and intercept did not significantly differ between seeders and resprouters) than for *Erica* (R^2 of 0.30 for seeders and 0.25 for resprouters; with significantly greater intercept and slopes for seeders than resprouters: $P < 0.0001$ and $P < 0.001$, respectively).

The relationships between richness and the CVR were consistent with the predictions of the environmental-variability model (Fig. 4). Species richness of all genus-regeneration strategy combinations showed strong and significant negative relationships with annual rainfall reliability (R^2 values ranging from 0.51 to 0.72; see Table 1). As predicted, the slope (and intercept) of this relationship was steeper for seeders than for resprouters, but only significantly so for *Erica* ($P < 0.01$ for both slope and intercept).

DISCUSSION

Our results refute the predictions of Pausas and Keeley's (2014) gap-dependence model. For both *Aspalathus* and *Erica*, richness of both seeders and resprouters was highest in areas of highest vegetation density. The densely clad slopes of the southern Fold Mountains (Hottentots Holland-Franschhoek-Jonkershoek) (van Wilgen 1982; McDonald 1988; Mucina & Rutherford 2006), which registered the highest NDVI values, do not harbour the lowest richness of seeders, as predicted by the gap-dependence hypothesis (Pausas & Keeley 2014; Keeley *et al.* 2016). Nor do the open shrublands of the north (northern Cederberg-Gifberg-Bokkeveld) (Taylor 1996) and northwest (Sandveld) (Richard M. Cowling pers. obs.) support the highest richness of seeders.

We acknowledge that the scale (quarter-degree cells) of our study may be too coarse to discern the finer-scale patterns of species replacement that

characterize Cape vegetation (e.g. Richards *et al.* 1995; Simmons & Cowling 1996). Thus, seeder-resprouter habitat discrimination might indeed occur at finer scales (e.g. in the dry north where resprouting ericas are often associated with mesic microsites; Taylor 1996; Ojeda 1998). Also, differences in species numbers (i.e. richness) do not necessarily parallel differences in ecological dominance between the two strategies (e.g. Bouchenak-Khelladi *et al.* 2014). However, in most habitats throughout the region, seeders dominate in terms of both richness and ecological dominance (McDonald 1988; Taylor 1996; Mucina & Rutherford 2006). In some areas of the north and northwest of the CFR, resprouters outnumber seeders in terms of species richness (Appendix S1; Ojeda 1998) but perhaps not in terms of ecological dominance. Only in the extreme southeast of the CFR, where fire-return intervals are shorter (Kraaij & van Wilgen 2014) due to more rapid post-fire regrowth associated with a high amount of warm-season precipitation (Wilson *et al.* 2015), are resprouters often the dominant shrubs, both in terms of species richness (Appendix S1) and ecological dominance (Cowling 1984; Le Maitre & Midgley 1992). Interestingly, this is not the case for some shrubby legume lineages (Podalyriaceae and Liparidaceae), where seeders are richer than resprouters in the south-eastern CFR (Schutte *et al.* 1995).

In the CFR, many resprouters associated with forest and thicket dominate in areas of low fire exposure throughout the region (Campbell 1986; Geldenhuys 1994). These formations are largely of tropical affinity and comprise lineages with few species in the CFR (Bergh *et al.* 2014), and only a few have invaded fire-prone habitats (e.g. *Colpoon phoenix* and *Euclea acutifolia*). Most of the component species are 'obligate resprouters' (i.e. R+P-, *sensu* Pausas *et al.* 2004) with vertebrate-dispersed, fleshy fruits whose seedling establishment is not fire-dependent (Manders 1990; Cowling *et al.* 1997). Indeed, these

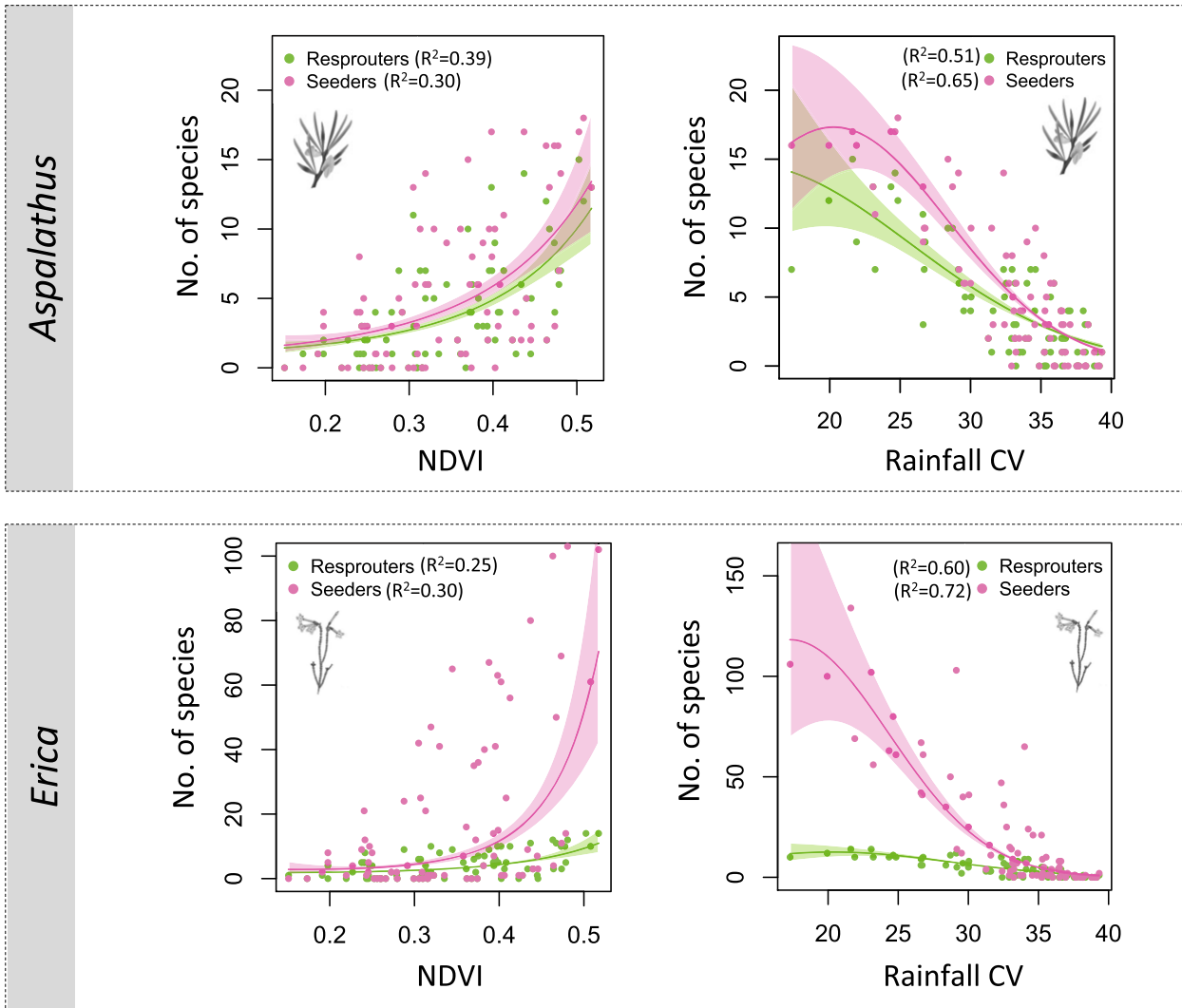


Fig. 4. Relationships between number of resprouter and seeder species of *Aspalathus* and *Erica* and the Normalized Difference Vegetation Index (NDVI) values (as a measure of vegetation density) and coefficient of variation of annual rainfall (Rainfall CV) (as a measure of post-fire moisture variability).

communities probably have the highest biomass of resprouters in the CFR, and they also occupy the most fertile sites, measured in terms of soil nutrient and organic matter content (Cowling & Potts 2015). Might these be the 'fertile competitive environments' referred to by Pausas and Keeley (2014) that favour resprouters? We think not. First, forest and thicket vegetation do not support regular canopy fires (Manders 1990; Geldenhuys 1994), and second, the high soil fertility is a consequence rather than a cause of forest and thicket distribution (Cowling 1984; Coetzee *et al.* 2015).

In contrast to the gap-dependence hypothesis, the predictions of the environmental-variability hypothesis were not refuted by this study. Both seeder and resprouter species of *Aspalathus* and *Erica* showed highest richness in environments with high rainfall

reliability (i.e. low CVR), which would favour obligate seeders but also facultative species, since seedling establishment is also important for the maintenance of resprouter populations (Thuiller *et al.* 2007; Marais *et al.* 2014; Slingsby *et al.* 2017). However, given that resprouters are more resilient to occasional bouts of high post-fire seedling mortality that would characterize areas of low rainfall reliability, their numbers decline less steeply with increasing CVR than seeders. In other words, seeders are more sensitive than resprouters to an increase in the likelihood of a severe, seasonal moisture stress (Lamont & Markey 1995; Ojeda *et al.* 2005). Under these conditions, resprouters may even dominate the species complement (Ojeda *et al.* 2005).

It is interesting to note that in *Aspalathus*, seeders are able to penetrate less reliable environments,

Table 1. Relationships between numbers of seeder and resprouter species of *Aspalathus* and *Erica* and the Normalized Difference Vegetation Index (NDVI) values and coefficient of variation of annual rainfall (CVR). In all cases, the best model (based on AIC score selection) included both linear and quadratic terms.

	Intercept	Linear coef	Quadratic coef	R ²
NDVI				
<i>Aspalathus</i>				
Resprouters	1.30***	4.60***	0.46	0.39
Seeders	1.47***	4.65***	0.37	0.30
<i>Erica</i>				
Resprouters	1.24***	4.01***	0.92	0.25
Seeders	2.06***	7.35***	1.95	0.30
CVR				
<i>Aspalathus</i>				
Resprouters	1.31***	-5.14***	-0.93	0.51
Seeders	1.49***	-6.51***	-1.94**	0.65
<i>Erica</i>				
Resprouters	1.26***	-6.09***	-1.83**	0.60
Seeders	2.09***	-11.41***	-2.61**	0.72

Significance codes: $P < 0.05$ (*), < 0.01 (**), < 0.001 (***); coef = coefficient.

probably because they possess relatively large seeds and more robust seedlings than *Erica* which has small seeds and drought-sensitive seedlings (V. Wilman, pers. comm, 2012). However, no research has been done on the moisture stress tolerance of seedlings of these, or any other Cape genera. Among adults, there is some indication that seeder and facultative resprouters do not differ in their water relations (Lamont & Bergl 1991; Pratt *et al.* 2012).

Is there a 'silver bullet' hypothesis to explain patterns in the abundance, however measured, of seeders and resprouters in vegetation subject to recurrent canopy fires? We doubt it. However, the environmental-variability model is a likely candidate in mediterranean-climate ecosystems. This hypothesis explains global patterns of shrub seeder dominance subject to canopy fires: in the two regions with the highest rainfall reliability, the CFR and Australia's Southwest Floristic Region (Cowling *et al.* 2005), seeders prevail in the woody flora, sometimes overwhelmingly so (Cowling & Lamont 1998), whereas this regeneration strategy is less prominent in California and the Mediterranean Basin (Pausas *et al.* 2004) that experience much lower rainfall reliability. Within Australia, the kwongan shrublands of the warmer and more moisture-stressed northern sandplains support the highest richness of resprouters in *Banksia* and *Hakea* (Proteaceae), while seeder richness is higher on the more mesic southern sandplains (Lamont & Markey 1995; Groom & Lamont 1996). While these patterns are similar to those for the mediterranean-climate part of the CFR, they have

yet to be modelled using explanatory variables appropriate for testing the gap-dependence and environmental-variability hypotheses.

In conclusion, our study indicates that environmental variability, manifested as rainfall reliability, is an important determinant of the landscape-scale patterns in the richness of seeder and resprouter species of the two largest genera in the megadiverse CFR. However, our research has but scratched the surface of an interesting topic. More work is required on finer-scale habitat discrimination between seeders and resprouters, and on the moisture stress tolerance of seedlings, ideally of closely related congeners with different regeneration strategies, sourced along a gradient of rainfall reliability. Finally, recent research has shown that facultative species (resprouters with post-fire seedling establishment) can show high mortality of adults in relation to fire and prolonged moisture stress (Marais *et al.* 2014; Slingsby *et al.* 2017). Thus, the assumption of the environmental-variability model of high survival of resprouting individuals irrespective of rainfall variability may not hold for many cases. More research is required on the mortality of resprouters in relation to disturbance regimes.

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SUPPORTING INFORMATION

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

Appendix S1. Richness of resprouter, seeder and total species of *Aspalathus* (149 spp.) and *Erica* (438 spp.) per quarter-degree cell in the Cape Floristic Region, South Africa.