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Title:
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Date:
2017-12-01

Citation:
Freeman, M. E., Vesk, P. A., Murphy, B. P., Cook, G. D., Richards, A. E. & Williams, R. J. (2017). Defining the fire trap: Extension of the persistence equilibrium model in mesic savannas. Austral Ecology, 42 (8), pp.890-899. https://doi.org/10.1111/aec.12516.

Persistent Link:
https://hdl.handle.net/11343/216907

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Defining the fire trap: extension of the persistence equilibrium model in mesic savannas

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Abstract

Mesic savannas are dominated by trees that are strong resprouters caught in a frequent fire trap. Persistence within this fire trap has been described by a resprout curve of SizeNext ~ f(Pre-fire size), defined by the Michaelis-Menten function. A key feature of this resprout curve is a stable persistence equilibrium that represents the size of individual plants upon which a population will converge over successive inter-fire time steps under a given fire regime. Here, we contend that such a resprout curve does not adequately describe resprout tree dynamics in frequently burnt mesic savannas because it is constrained to an asymptote. We propose a new framework for modelling the resprout curve, which recognises that local environmental stochasticity and growth patterns can interact to change the growth response function entirely, and thus more readily reflect the range of feasible resprout responses. Importantly, we define an unstable equilibrium representing the size above which individuals have escaped the fire trap. Further, we explore mechanisms that can shift an individual from persistence to escape. Through a case study from northern Australia, we confirm that our framework provides a simple yet practical approach to defining these critical aspects of savanna tree growth dynamics: persistence and escape.

Keywords

demographic bottleneck; fire trap; persistence niche; resprouting; savanna

Introduction

Topkill by fire in small tree size classes (~<5cm diameter at breast height (DBH)) is a predominant feature of woody dynamics in mesic savannas. Frequent fire can trap these small trees in a cycle of above-ground biomass loss followed by resprouting, which results in a demographic bottleneck limiting transition to the canopy (Hoffmann 1998, Higgins et al. 2000, Bond 2008, Prior et al. 2010, Bond et al. 2012, Werner and Prior 2013). This phenomenon necessitates that tree species are strong resprouters able to persist in the shrub layer, potentially for decades (Bellingham and Sparrow 2000, Bond and Midgley 2001, Higgins et al. 2007). As such, frequent fire maintains a tree community height structure that is broadly bimodal, with abundant multi-stemmed resprouts, very few saplings, and canopy tree density maintained below the site potential (Sankaran et al. 2005, Higgins et al. 2007, Bond 2008, Lehmann et al. 2009, Holdo et al. 2014). Surprisingly, despite significant interest in consequences of the demographic bottleneck on stand structure and tree species dominance (Williams et al. 1999, Ryan and Williams 2011, Bond et al. 2012, Hoffmann et al. 2012), conceptual models that describe persistence in, and escape from, the fire trap remain ill-defined.

Grady and Hoffmann (2012) proposed a stable size 'persistence equilibrium model' that describes resprout population persistence within the fire trap. It is defined by a 'resprout curve' of size in successive inter-fire time steps and features an 'equilibrial size'; an expression of the resprout persistence niche (Bond and Midgley 2001) at a given site and fire regime. This persistence model provides a basis from which to explore resprout growth dynamics as mediated by size of individuals, disturbance and environmental conditions. Here, 'resprout' refers primarily to trees <1.5m tall, but does also include all small trees up to 5cm DBH (i.e. saplings). However, in its current form the Grady and Hoffmann (2012) model does not accommodate one of the most critical aspects of savanna dynamics: escape from the fire trap. Specifically, it is constrained to an asymptotic height by the Michaelis-Menten function meaning, from a model perspective, individuals can never advance beyond a persistence equilibrium. But, for canopy trees to exist in savannas, some individuals must escape.

Here, we extend the Grady and Hoffmann (2012) persistence model to reflect the range of resprout responses feasible in savannas under different fire scenarios or species life-history strategies. We propose that species characteristics, length of fire interval, fire season and growing conditions will not only result in a shift in stable "persistence equilibrium" size, as was found by Grady and Hoffmann (2012), but can alter the response function entirely. This framework uses a data-driven approach to define the limits of the fire trap and identify mechanisms that lead to persistence or escape. We begin with an exploration of theoretical growth response models and then illustrate use of the framework through a case study from three fire experiments in northern Australia.

Beyond the Stable Size Equilibrium

The topkill-resprout cycle and environmental conditions, such as dry-season water stress, can lead to positive, negative or zero net individual growth increments within an inter-fire period (Prior and Eamus 2000, Hoffmann and Solbrig 2003, Murphy et al. 2015). In the persistence model (Grady and Hoffmann 2012), resprouts that are smaller than the equilibrium size before a fire will on average increase in size by the end of the inter-fire period, but those that are larger will decrease because there is insufficient time or resources to recover their pre-fire size (**Error! Reference source not found.**; A). This relationship between an individuals' pre-fire size and size before the next fire (SizeNext) remains consistent, regardless of whether the measure is diameter, height or total biomass (Grady and Hoffmann 2012, Schafer and Just 2014).

The persistence response curve represents species that are strong resprouters suppressed to the shrub layer in perpetuity by frequent fire. If this were the only possible growth trajectory, the system would eventually shift away from a wooded savanna toward a (grassy) shrubland as canopy trees die.

For a savanna to exist, some resprouts must pass through a 'window of opportunity' (Balke et al. 2014) (see below) that allows their periodic transition out of the fire trap at a sufficient rate to retain a level of canopy cover (Jeltsch et al. 2000). Accordingly, a model of escape includes a stable persistence equilibrium and an unstable equilibrium, above which the individual is resistant to topkill by fire (**Error! Reference source not found.**; B).

Grady and Hoffmann (2012) allude to such an extension of their model. They offer that eucalypts are able to escape because their persistence size (stable equilibrium) is very close to their escape size (unstable equilibrium), requiring only a minor shift in conditions to move an individual from persisting in the fire trap to escaping the fire trap. This may be one pathway to escape, however it is not a prerequisite. For example, Fensham and Bowman (1992) found remarkable height growth of eucalypt resprouts with overstorey removal. With such growth rates being possible, the difference between persistence and escape heights may not need to be small, but could be in the range of meters.

Two other possible resprout curve forms describe populations that are not limited by fire; where pre-fire size is always exceeded by SizeNext (Figure 1, C), and, conversely, populations where pre-fire size is never recovered; where individuals embark on a “death spiral” (Grady and Hoffmann 2012) (**Error! Reference source not found.**, D).

In all our theoretical models, we purposefully do not express response curves originating at zero. By doing so, we introduce another unstable equilibrium that represents the size below which persistence is not viable, i.e. a mortality size threshold.

Shifting between Persistence and Escape

On average, size recovery of individuals following fire converges on the stable persistence equilibrium but diverges from the unstable equilibria (mortality and escape sizes). This means that occasional bursts of size growth or shrinkage, mediated by a temporary change in conditions (“window of opportunity” sensu Balke et al. (2014)), must occur if resprouts are to pass the unstable equilibria to escape or die. Factors creating a window of opportunity to escape in savannas may include top-down mechanisms, such as milder or patchier fires (Werner and Franklin 2010, Werner and Prior 2013), and browsing removal

(Staver and Bond 2014); bottom-up mechanisms such as release from competition (Fensham and Bowman 1992) and efficient resource allocation strategies (Schutz et al. 2009); or a combination of these. The opposite may tip an individual below the lower unstable equilibrium to mortality.

The scale of the window of opportunity required to catalyse an individuals' shift from persistence at the stable size, to escape (or mortality) will depend on species' ecology and site resources (Balke et al. 2014). At the population level, as a window of opportunity closes, the resprout curve may revert from escape to persistence-only if enough individuals are affected. Because of this, the escape curve may not always be detected when modelling the average population response.

Escape size is important to estimate because it represents the ceiling to the fire trap and therefore has implications for the effects of fire on stand structure. In populations for which we observe the persistence resprout curve, an escape size is not visually evident, but this does not mean it does not exist. In these cases, the size range within which the 'true' value of escape size lies is delimited by the upper bound of uncertainty (prediction interval) around the persistence equilibrium and the maximum potential size of individuals (Figure 2). This maximum size (eg. canopy height) represents another stable equilibrium upon which populations will converge once individuals have escaped. We use the prediction interval in this framework because it encompasses individual-level variation, and is thus wider and more reflective of the range of growth responses likely to be observed than the confidence interval, which represents uncertainty around the population mean.

Applying the framework

Application of our framework to data depends on the inclusion of non-topkilled individuals for identifying escape size – the size at which a tree is no longer suppressed by fire. If all individuals are topkilled, we would expect to only detect the persistence curve, as in Grady and Hoffmann (2012). In existing field-collected datasets the level of detail that differentiates trees that were not topkilled because they were large enough to withstand burning compared to trees that were not topkilled because they were not directly impacted by fire is often not available. This doesn’t impact the utility of the framework, but should be acknowledged when interpreting results. If data consists of both locally burnt and unburnt (due to fire patchiness) individuals, the resprout curve will be more uncertain. Ideally, if the detail is available, a best-estimate of persistence and escape size would be obtained by applying the framework only to burnt individuals.

Another feature of the framework is that it can be applied to any level of fire frequency. The critical aspect is that size is measured immediately before fire and sizeNext immediately before the next fire. If applying the framework to combined data from various sources, the length of time between size and sizeNext censuses must be consistent. Accounting for fire history before the collection of census data is not a feature of our framework given that longevity of savanna resprouts in the shrub layer (Bond and Midgley 2001, Higgins et al. 2007) will generally preclude any ability to determine an individual’s pre-census history. It’s also unlikely that an understanding of fire history could resolve all observed individual-level variation. Again, such individual-level variation is accounted for in uncertainty around the resprout curve. Depending on the aim of the researcher, the data used to infer persistence and escape size could be highly localised, giving precise estimates for a given environment, or could combine datasets to yield a more accurate landscape average.

Case Studies

To demonstrate use of this framework we undertook graphical analysis of data from three fire response studies in mesic savannas of the Northern Territory of Australia. One dataset was drawn from the Kapalga fire experiment (Andersen et al. 2003, Andersen et al. 2005, Williams et al. 1999), another from an independent study of sub-adult trees in Kapalga

(Werner and Prior 2013)and third from recent work in experimental fire plots on the Tiwi Islands (Richards et al. 2012). Data collection methods for each dataset are included in Appendix S1of the Supporting Information, and, for the Kapalga data, in the original studies (Williams et al. 1999, Prior et al. 2010, Werner and Prior 2013, Werner 2012). All study areas are dominated by mesic eucalypt (*Eucalyptus* and *Corymbia* spp.) savanna characterised by highly seasonal rainfall, occurring almost entirely over the six month wet season; roughly November to April. Sub-dominant trees include a range of predominantly deciduous non-eucalypt species of pantropical affiliation, which are more likely to become caught in the frequent fire trap (Prior et al. 2010, Bond et al. 2012), and more negatively impacted by increased fire frequency and intensity, than the canopy-dominant eucalypts (Williams et al. 1999, Russell-Smith et al. 2003, Murphy et al. 2015, Scott et al. 2012).

Datasets were filtered to only include species that have the potential to become trees, which we defined as woody dicotyledons at least 6 m in height. Only the top three most common eucalypt and non-eucalypt species (across all datasets) were used in our case study (Table 1). Fire treatments and species counts for each dataset are summarised in Appendix S1. Treatments included in the case study were early dry season fires (EDS, applied in June or July) and late dry season fires (LDS, applied in November). Due to higher fuel loads and increased Forest Fire Danger Index (FFDI), LDS fires are usually more intense with more complete fuel combustion than EDS fires (Cook and Corbett 2003, Williams et al. 2003, Russell-Smith and Edwards 2006), providing a greater challenge to escape (Werner and Franklin 2010, Werner 2012). The window of opportunity to escape under LDS fires is also presumably much narrower than for EDS fires, not only due to differences in intensity, but due to lower small-scale patchiness of burns (Werner and Franklin 2010).

Each dataset did contain a fire-exclusion treatment, which was not considered here given our interest in defining the fire trap. Datasets were composed of annual height measurements of tagged individuals, taken at the start of the dry season before burning took place. Accordingly, HeightNext corresponds to pre-fire height of the following year. New recruits (pre-fire height = 0) were not included, but otherwise we include all individuals, both topkilled and not (Table 2). The studies varied in length, as detailed in Appendix S1. Accordingly, the data included in this case study were:

- “Williams”: dataset of EDS and LDS fire treatments containing trees that were unburnt for one year before the first census, and then were burnt annually for the next 5 years resulting in 5 censuses;
- “Tiwi”: dataset of EDS fire treatment only, containing trees that had experienced 6 years of annual burning before the 2 annual censuses used here;
- “Werner”: dataset of EDS and LDS fire treatments containing trees that were unburnt for one year and then were burnt once resulting in a single one-year census.

Resprout curves were modelled by Robust Locally Weighted Least Squares Regression (LOESS) using the bisquare estimation method in R (R Core Team 2016) using ggplot. This was done separately for each species, fire treatment and dataset, and repeated for each species and fire treatment combining all datasets. Each year of data was used, meaning individuals are represented more than once in both the Williams and Tiwi datasets, which comprised more than one census (Appendix S1). We used LOESS regression so as not to restrict the relationship between pre- and post-fire to a functional form that might bias our evaluation of the response curve, and bisquare estimation to reduce the influence of outliers. Curves were plotted with 95% confidence intervals.

We expected that, under these fire regimes:

1. eucalypt resprout curves would show evidence of escape and pantropical non-eucalypts would conform to the persistence resprout curve;
2. escape resprout curves would be more prevalent in the EDS fire treatment than LDS;

3. the difference between persistence height and escape height in the LDS fire treatment would be greater than EDS.

There was generally high agreement between the shapes of resprout curves for each dataset; therefore here we present single curves combining all datasets. Resprout curves for each dataset, species and fire treatment are included in Appendix S2 of the Supporting Information.

Case Study Results and Discussion

The most apparent feature of the height response field data is large individual-level variability across all size classes. Relatively minimal curvature of most resprout curves is due to almost equal numbers of individuals regressing towards the stable equilibrium and advancing in size towards escape. The individuals within each dataset had experienced different pre-census fire regimes and also different within-census fire effects, with un-accounted-for variation in local patchiness and fire intensity. Further, we did not delimit the datasets to include only individuals that were burnt by fire. Our model fits truly are population "averages", encompassing the full range of individual, site and geographic effects that may cause individual-level variation in height response. The result of this is that our resprout curves provide conservative estimates of persistence and escape under two different seasons of fire.

Despite these 'subtle' population mean resprout curves, we can discern different curve shapes corresponding to our proposed forms and equilibrium heights at which individuals are more likely to persist or escape (Figures 3 and 4).

The escape curve is apparent in the three eucalypts; *Corymbia nesophila* (EDS: Figure 3A and LDS: Figure 3B), *Eucalyptus miniata* (EDS: Figure 3C) and *Eucalyptus tetrodonta* (LDS: Figure 3F); as well as in *Erythrophleum chlorostachys* (EDS: Figure 4A, and LDS: Figure 4B). In each of these cases, except *E. miniata* EDS, escape height was more than three meters greater than persistence height, indicating the large range of height classes that are caught within the fire trap. This is contrary to the suggestion that eucalypt persistence sizes are very close to their escape size (Grady and Hoffmann 2012). *Planchonia careya* (EDS: Figure 4C and LDS: Figure 4D) and *Terminalia ferdinandiana* (LDS: Figure 4F) exhibit the persistence curve. In the Williams et al. (1999) dataset, all individuals within a defined transect were marked and measured. Accordingly, the restriction of *P. careya* LDS to a discrete cluster of individuals below 1 m is evidence that the population had already converged on the persistence equilibrium at the outset of the study. In fact, the high density of datapoints below 2 m height, evident across all species, illustrates the highly left-skewed resprout/sapling population distributions that result from individuals converging on the persistence equilibrium. *Eucalyptus miniata* (LDS: Figure 3D), *Eucalyptus tetrodonta* (EDS: Figure 3E) and *Terminalia ferdinandiana* (EDS: Figure 4E) show (weak) curves of constant growth. Given the proximity of these constant growth curves to the 1:1 line, a conservative interpretation is that individuals are, on average, able to at least recover their pre-fire height across this range of resprout/sapling sizes. This was unexpected, given substantial evidence of the sensitivity of saplings to fire. It is possible that the greater patchiness of EDS fire (both spatially and in intensity) is responsible for a relatively high proportion of saplings avoiding deleterious effects of burning and thus retaining their pre-fire height (Table 2).

The persistence curve was only evident in the LDS fire treatment of pantropical non-eucalypts, which conformed to our expectations. Only for *T. ferdinandiana* and *P. careya* does fire regime shift the response curve from complete recovery across all size classes under EDS fire to a persistence curve under LDS. Our case study confirms the previously recognised negative impacts of intense LDS fire on these non-eucalypts. Similarly, the escape potential of eucalypts under both EDS and LDS fires is substantiated (Bond et al. 2012), as is that of the non-eucalypt *E. chlorostachys* (Russell-Smith et al. 2003). There is no conclusive evidence that escape height is taller in LDS than in EDS, which we expected to see due to on average greater scorch heights resulting from higher fire intensity (Williams et al. 2003). There is also no evidence of any population embarking on a ‘death spiral’ (as per **Error! Reference source not found.**D), which was expected, given the strong persistence potential of these fire-prone savanna species.

Allocation patterns to above and below-ground biomass may be the critical determinant of whether a species is likely to conform to the persistence model (Tomlinson et al. 2012, Tomlinson et al. 2013), as in long-leaf pine savanna (Grady and Hoffmann 2012, Schafer and Just 2014), Brazilian cerrado (Hoffmann and Solbrig 2003) and here, with the example of the non-eucalypts *T. ferdinandiana* and *P. careya* under LDS. Escape sizes for these populations lie somewhere between the upper limit of the prediction interval around the stable persistence equilibrium and maximum potential height of the species (Table 1). Preferential allocation of carbon to the below-ground bud bank implies a strategy based on achieving long-term persistence in the shrub layer (Bond and Midgley 2001, Clarke et al. 2013). To some extent, all resprouting individuals in savanna do this, however the difference between a persistence population and an escape-curve population is that once an individual, whose life-strategy relies on escape, has accumulated enough resources, it will use these stores to bolt through a window of opportunity (Wigley et al. 2009, Werner 2012). Such an escape strategy is particularly exemplified by the eucalypts in this case study.

The dynamics around zero height cannot be clearly characterised using these datasets, which include only established resprouts (not seedlings) and use height as a size measure. There is no evidence in these data of a height below which mortality is more likely. The concept of a mortality threshold in this case study can therefore not be evaluated. Further, the minimum size that a seedling must attain to exceed the mortality equilibrium and become an established resprout is part of a separate process that cannot be resolved here. Size of the lignotuber or starch reserve, rather than any measure of above-ground biomass, may be a more consistent predictor of the unstable equilibrium between persistence and mortality (Fensham and Bowman 1992, Iwasa and Kubo 1997, Canadell and López-Soria 1998)

High individual variation in height recovery suggests localised environmental conditions and factors beyond only fire season significantly influence growth responses (Clark 2010, Clark et al. 2012). Using data or modelling techniques such as quantile regression that represent only exceptional individuals (Wakeling et al. 2011), or including model covariates that describe site-specific or fine-scale patch conditions, may lead to greater precision in estimates of fire trap limits for specific scenarios. Estimated escape and persistence heights in our case study reflect the full range of variation that a population may experience under EDS and LDS fire season regimes. This approach is of interest because it takes into account the mechanisms that lead to escape (i.e. windows of opportunity) without explicitly having to define them. If we only modelled topkilled or exceptional individuals, or a single site, our estimations of persistence and escape would reflect a more homogeneous population and could not be assumed to apply to an "average" population of that species.

Our flexible approach to modelling the resprout curve provides improved capacity to determine the limits of, and uncertainty around, the fire trap compared to Grady and Hoffmann (2012). LOESS regression has proven a useful method for exploring responses of resprout tree populations to fire without the restriction of a particular functional form. A problem with LOESS, however, is that although it may be used for prediction, it cannot inform, for example, the growth kernel of an Integral Projection Model (Easterling et al. 2000). If a parametric function is required, we suggest a linear modelling framework with polynomial terms would approximate response curves best and have the benefit of generality.

Conclusions – Defining the Fire Trap

Estimating persistence and escape sizes is fundamental to predicting the impact of fire on savanna composition and structure. As we have presented here, visualising tree growth responses in the context of persistence and escape provides an opportunity to conceptualise tree population dynamics in highly fire-prone landscapes.

Our case study confirmed that a variety of resprout curves are possible beyond the persistence model proposed by Grady and Hoffmann (2012). Although simple, such a graphical analysis is a flexible tool for defining the fire trap for different species under different fire regimes. The approach could be strengthened by incorporating other fire, competition and environmental covariates for extension to predictive studies of population dynamics.

Acknowledgements

We thank Dick Williams, Patricia Werner and Lynda Prior for use of their data. We thanks Pattricua Werner and William Hoffmen for critical comments that both sharpened our understanding and improved the manuscript, even if we did not agree with all. Tiwi data were collected with invaluable field assistance provided by Jon Schatz, Willy Rioli, Willy Roberts, Colin Kerinauia, Vivian Kerinauia, José Puruntatameri and Kim Brooks. In particular, we acknowledge the support provided by the Tiwi Land Council and CSIRO TERC in Darwin and funding provided through the Australian Government Department of Environment. BPM was supported by a grant from the Australian Research Council (DE130100434). PAV was supported by The Australian Research Council Centre of Excellence for Environmental Decisions.

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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: Summary of the data used in our case study, including descriptions and methods of collection of the three datasets.

Appendix S2: Resprout curves for each species, fire treatment and dataset modelled separately

Species	**Family**	**Maximum height (m)**	**Habit**
Corymbia nesophila (Blakely) Hill & Johnson	Myrtaceae	25	Evergreen
Eucalyptus miniata Cunn. Ex Schauer	Myrtaceae	20	Evergreen
Eucalyptus tetrodonta F. Muell.	Myrtaceae	30	Evergreen
Erythrophleum chlorostachys (F.Muell.) Baillon	Fabaceae	18	Semi-deciduous
Planchonia careya (F. Muell.) Knuth	Lecythidaceae	10	Deciduous
Terminalia ferdinandiana Exell	Combretaceae	10	Deciduous

Table 1: Species included in the case study. Maximum heights are from Brock and Dunlop (2007)

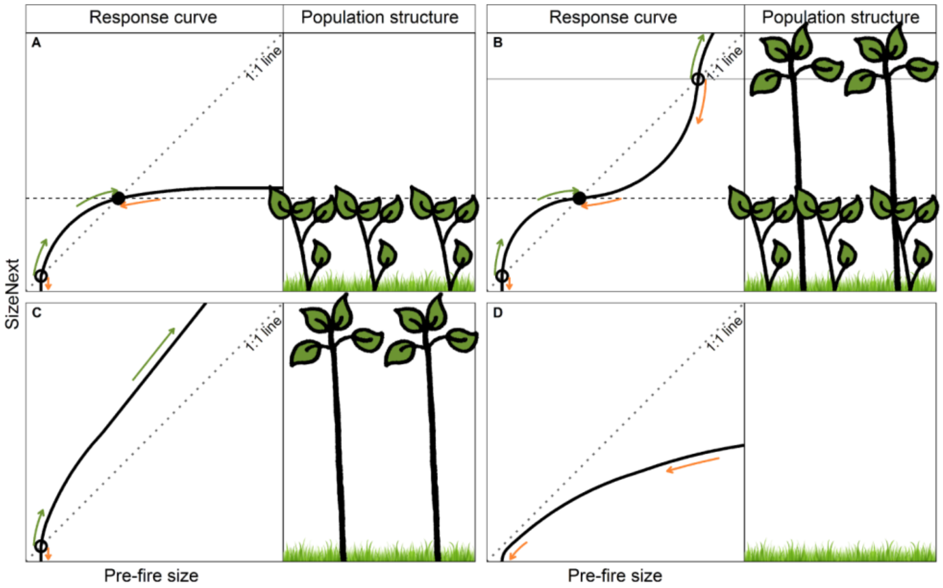

Figure 1: Conceptual models: possible forms of the resprout curve and resultant population structure under recurrent fire: **A**: the Grady and Hoffmann (2012) persistence equilibrium curve; **B**: the escape curve; **C**: the curve of constant growth; **D**: the death spiral. ● : stable equilibrium; ○ : unstable equilibrium. When the curve is above the one-to-one line, there is positive growth, i.e. the individual is able to recover and exceed its pre-fire size in the inter-fire period. If below the one-to-one line, the individual experiences negative growth i.e. it cannot recover its pre-fire size in the inter-fire period. Arrows indicate direction of size growth through subsequent inter-fire periods. The depicted population structures represent a single cohort of resprouts and/or canopy trees, however we acknowledge multiple cohorts might occur, particularly in scenario C.

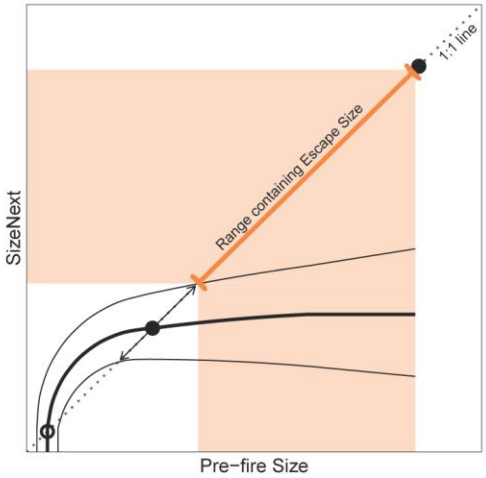

Figure 2: Size range containing ‘escape size’ (shaded region) for a population where only the persistence equilibrium curve (▬) is detected. The maximum entropy distribution of escape size is between the upper bound of the prediction interval (—) around ‘persistence size’ and the ‘maximum size’ (for example canopy height) of the species. Escape size defines the upper limit of the fire trap. ● : stable equilibrium (here, lowest is persistence size, uppermost is maximum size); ○ : unstable equilibrium (here, mortality threshold).

	Height Class	Topkilled	Not Topkilled	Topkilled %
Early Dry Season Fire Treatment				
Tiwi Dataset	<0.5 m	554	179	75.58
	0.5 - 1.5 m	127	17	88.19
	>1.5 m & <5 cm DBH	228	239	48.82
Werner dataset	<0.5 m	138	40	77.53
	0.5 - 1.5 m	121	52	69.94
	>1.5 m & <5 cm DBH	7	29	19.44
Late Dry Season Fire Treatment				
Werner dataset	<0.5 m	129	0	100.00
	0.5 - 1.5 m	192	0	100.00
	>1.5 m & <5 cm DBH	14	3	82.35

Table 2: Counts and percentage of individuals by size class that were topkilled compared to not topkilled in two of the case study datasets. The “Williams” dataset did not contain topkill information and so is not included here. The lower number of individuals topkilled in the Early Dry Season regime reflects lower fire intensity and greater patchiness of this fire treatment compared to the Late Dry Season

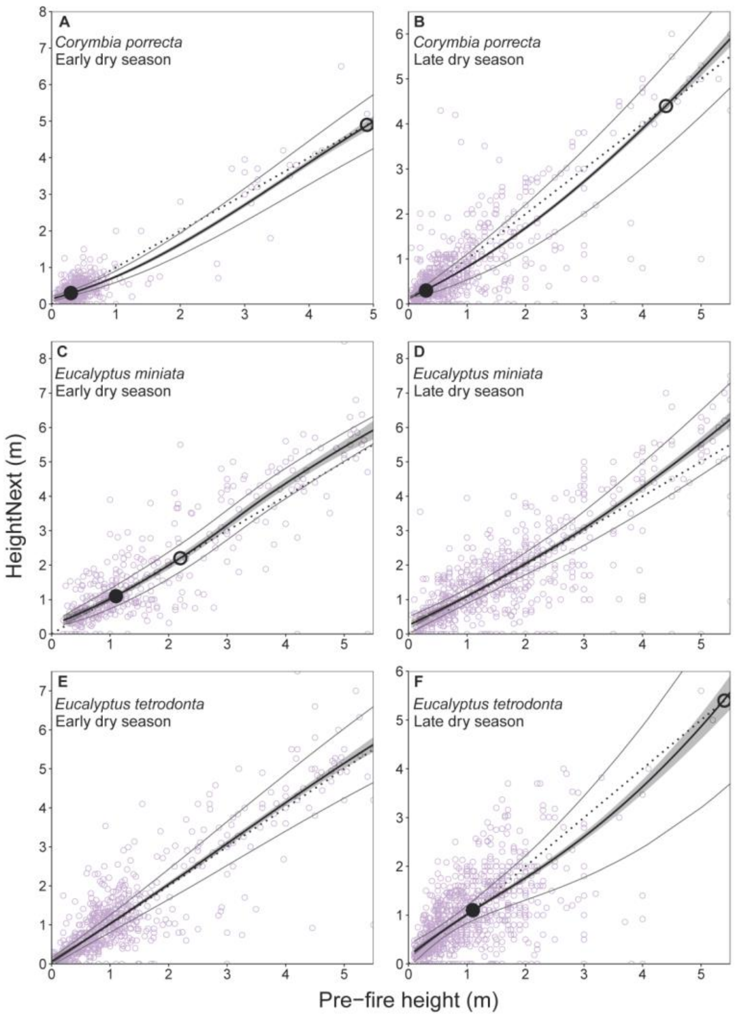

Figure 3: Eucalypt resprout curves of the relationship between pre-fire height and height before the next fire (HeightNext). Fire treatments were early dry season burning and late dry season burning with each census spanning 1 year. ● : stable (persistence) equilibrium; ○ : unstable (escape size) equilibrium. Data are combined from 3 separate datasets. Each data point (○) represents height growth response of one individual within one year, with fire occurring soon after the pre-fire height measurement. Curves are robust LOESS smooths with 95% confidence intervals (shaded) and 50% prediction intervals (thin lines). Figures A, B, C, and F conform show the escape resprout curve. Figures D and E are curves of constant growth (although close, the fitted curves do not actually cross the 1:1 line). These results indicate the strong ability of eucalypts to persist in and escape from the fire trap under both early and late dry season fire.

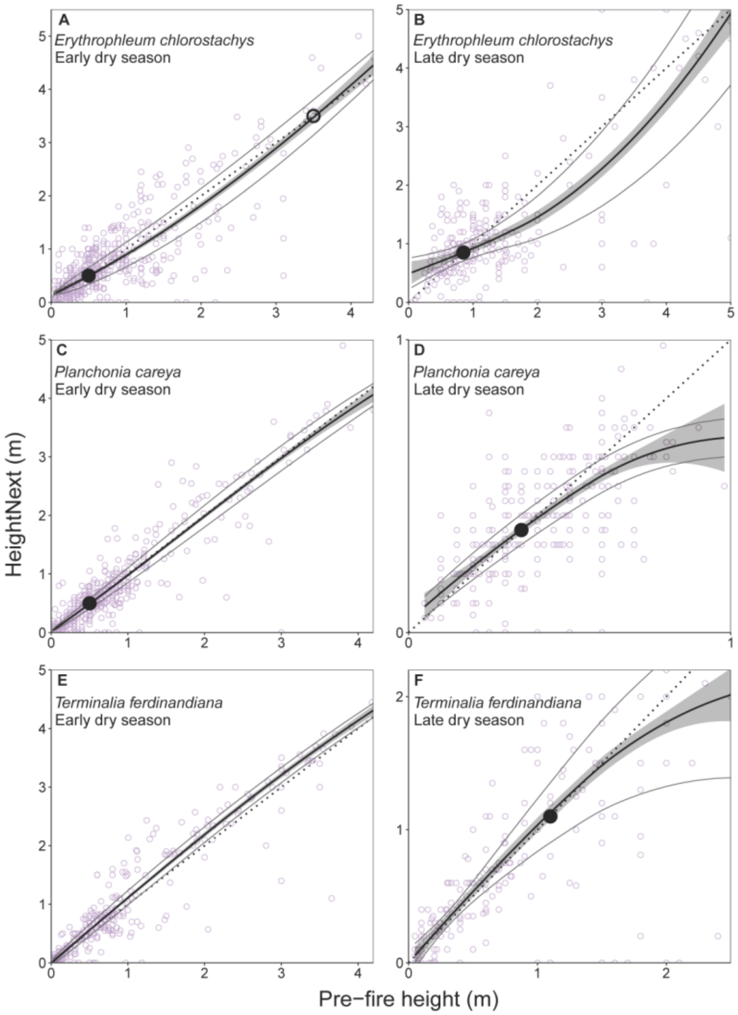

Figure 4: Non-eucalypt resprout curves of the relationship between pre-fire height and height before the next fire (HeightNext). Fire treatments were early dry season burning and late dry season burning with each census spanning 1 year. ● : stable (persistence) equilibrium; ○ : unstable (escape size) equilibrium. Data are combined from 3 separate datasets. Each data point (○) represents the height growth response of one individual within one year, with fire occurring soon after the pre-fire height measurement. . Curves are robust loess smooths with 95% confidence intervals (shaded) and 50% prediction intervals (thin lines). Figures A and B conform to the escape resprout curve (B escape height is just outside the limits of the data). Figures C, D and F conform to the persistence resprout curve. Figure E is a curve of constant growth. *Erythrophleum chlorostachys* performs similarly to eucalypts under these fire regimes. Late dry season fires, on average, indefinitely trap *Planchonia careya* and *Terminalia ferdinandiana* resprouts at their persistence equilibrium size.