Supplementary Material. Population modeling methods

Patch-based integral projection models

Our analysis of *Callitris intratropica* demography incorporated two covariates – (i) fire disturbance (no fire vs. low intensity fire vs. high intensity fire) and (ii) grove state (intact groves vs. degraded groves vs. singleton trees) – into size-dependent linear and generalized linear models of *C. intratropica* survival, growth and fecundity (see Methods). We used these vital rate functions to construct integral projection models (IPMs) of population dynamics (Easterling, Ellner, & Dixon, 2000; Ellner & Rees, 2006) and assess the population stability of each grove state under each fire disturbance type. We also constructed an environmental state transition matrix (Horvitz & Schemske, 1986) using a Markov chain of grove state transition probabilities per fire disturbance type. This enabled us to examine how the frequency of low-intensity and high intensity fires affects the long-term projected proportions of intact grove, degraded groves and singleton trees. We then integrated the IPM and environmental state transition matrix into a ‘megamatrix’ that modeled the patch- and size-based population dynamics of C. intratropica (Pascarella & Horvitz, 1998; Valverde & Silvertown, 1997) and thereby allowed us to examine how changes in the frequency of low and high intensity fires affects overall population stability of *C. intratropica* across all grove states.

The IPM combines continuous vital rate functions (see Methods) into a single function – the kernel - to derive probabilities of individuals among size stages remaining in that stage, transitioning to another stage, and/or producing new individuals the next year. Thus, they are effectively operationalized as very large population matrix models from which one can derive long-term population stability, lambda (λ) as the dominant eigenvalue of the resultant matrix. Values of λ>1 indicate a growing population whereas λ<1 indicates a population expected to decline, although lambda may best be interpreted as a measure of relative growth rate among populations, rather than a prediction of actual future population growth (Menges, 2000). The advantages of IPMs over matrix models are twofold. First, whereas matrix models have limited capacity to handle environmental covariates, the use of linear and generalized linear models of vital rate functions in IPMs allows the inclusion of covariates derived from data collected within a single population. Second, continuous vital rate functions enable IPMs to effectively estimate transition probabilities across many more size class divisions (i.e., 100s) than traditional matrix models (typically <10). These probabilities are therefore based on size transitions observable in the field and provide more accurate predictions of population behavior, especially for slow-growing, long-lived plants (Zuidema, Jongejans, Chien, During, & Schieving, 2010).

We constructed the IPM kernel using four sections of transition probabilities, derived from *C. intratropica* vital rates, according to Zuidema et al (2010). These sections included (i) seedlings remaining seedlings (kSS), (ii) seedlings transitioning to adults (kAS), (iii) adults remaining to adults (kAA), and (iv) adults contributing to seedlings (kSA). Each of these sections was then combined to create the complete kernel:

Thus, the left hand side of the kernel is determined by the product of seedling growth and survival, with kAS representing the growth of seedlings beyond >1300 mm in height (ie into the 'adult' size range). The lower right hand quadrant, kAA, represents adult growth and survival. The production of new seedlings by adults, kSA, was determined using a fertility function based on the product of (i) adult survival, (ii) the size-based probability of cone production, (iii) the number of seeds germinated per cone, and (iv) the probability of seedling establishment.

We used the midpoint rule according to Zuidema et al. (2010) to numerically integrate the demographic kernel and produce transition probabilities across C. intratropica size classes. Each statistical model was a function of adult or seedling size and incorporated fire disturbance and grove state as categorical covariates where possible and appropriate (see Table S1). The use of these covariates effectively resulted in nine separate IPMs, each accounting for a different combination of fire disturbance and grove state categories: (i) unburnt, intact groves, (ii) unburnt, degraded groves, (iii) unburnt singletons, (iv) low intensity burn, intact groves, (v) low intensity burn, degraded groves, (vi) low intensity burn, singletons, (vii) high intensity burn, intact groves, (viii) high intensity burn, degraded groves, and (ix) high intensity burn, singletons. We calculated the projected population growth rate (λ) for each IPM with the popbio package in R (Stubben & Milligan, 2007).

Environmental State Change Transition Matrix

We used the differential responses to low and high intensity fires among intact groves, degraded groves and singleton *C. intratropica* trees derived from field observations and experimental burns (Prior, McCaw, Grierson, Murphy, & Bowman, 2011; Trauernicht, Murphy, Portner, & Bowman, 2012; Trauernicht, Murphy, Tangalin, & Bowman, 2013) to develop fire-dependent transition probabilities among *C. intratropica* grove states (Fig 2). We used these probabilities to constructed three 3 × 3 Markov chain matrices for grove state transition probabilities from time *t* to time *t+1* under each fire disturbance type: (1) *G*U for unburnt groves, (ii) *G*E for early burnt groves, and *G*L for late burnt groves. Thus, for example, grove states remain mostly stable under no fires in *G*U, whereas proportions of intact and degraded groves switch to the degraded and singleton states, respectively, under late dry season (high intensity) burns in *G*L.

These grove state transitions do not include ‘empty patches’ (ie, dead groves/eucalypt savanna) because we are not modeling the abundance/proportion of C. intratropica patches relative to all patches in the landscape. Rather, we are only interested in linking fire disturbance to the proportion of the C. intratropica population occurring among these three grove states to understand how differences in population behavior among grove states contributes to overall population stability. ‘Grove mortality’ under high intensity fires, although not explicitly accounted for in the grove state transitions, is modeled using population-level mortality integrated via the megamatrix model that combines patch and population dynamics (see below). Singleton trees are a category both in the patch-dynamic model as well as the population dynamic model (the IPM). In the megamatrix, when an individual transitions into the singleton environmental state, that tree’s mortality (and thus the mortality of the ‘grove state’) is determined by the vital rate models for singleton trees under the given fire disturbance. In addition, although the formation of new groves via the recruitment of *C. intratropica* seedling/sapling cohorts occurs in the field, we do not include ‘new groves’ as a category. Instead, we model grove ‘recruitment’ by allowing for small contributions to intact groves from degraded groves and singleton trees under conditions of no fire (See Figure 2). In the field, seed production from adult trees in any grove state may result in abundant seedling establishment and therefore contribute to the formation of new groves. However, this process is ultimately dependent on seedling survival and thus the maintenance of unburnt habitat – a rare phenomenon in these savannas. Yet to account for the low frequencies at which grove establishment has been observed in the field, we allowed for very small rates of grove recruitment in our patch dynamic model.

We then derived the probability of fire disturbance from LANDSAT imagery of early and late dry season fire scars for each annual time-step between 1990 and 2011 across the entire 28,000 km2 region encompassing our field site and comprising the Western Arnhem Land Fire Abatement project (Edwards & Russell-Smith, 2009). We used these data to derive a fire disturbance matrix, *D*: a 3 × 3 Markov chain consisting of the probability of a given patch of landscape experiencing one of three disturbance states (unburnt, early burnt, or late burnt) at time *t+1* based on its disturbance state at time *t*:

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  |  |  | Time *t* |  |
|  |  | Unburnt | Early burnt | Late burnt |
|  | Unburnt | 0.586 | 0.605 | 0.709 |
| Time *t+1* | Early burnt | 0.173 | 0.201 | 0.093 |
|  | Late burnt | 0.241 | 0.194 | 0.198 |

The stable stage distributions (SSD) of fire disturbance types based on matrix *D* (Unburnt: 62%; Early burnt: 16%; Late burnt: 22%) were similar to the actual mean proportions of the landscape under each disturbance type derived from the LANDSAT data (Unburnt: 64%; Early burnt: 12%; Late Burnt: 24%).

We combined the Markov chains for fire disturbance and grove state transitions to construct an environmental state change matrix, *F* (Horvitz & Schemske, 1986; Pascarella & Horvitz, 1998; Valverde & Silvertown, 1997), by multiplying the elements of matrix *D* by the individual grove state matrices GU, GE, and GL as follows:

This yielded a 9 × 9 discrete state Markov chain of transition probabilities for all grove states across all fire disturbance states from time *t* to time *t+1* (Table S2). We used matrix *F* to project stable stage distributions (SSDs) of each of the nine possible 'fire-states', from which we derived the predicted proportions of grove states across the landscape under known or hypothetical fire disturbance probabilities. We also used these SSDs to examine the sensitivity of the patch dynamic model to changes in the grove state transition parameters (Figure S1).

The Megamatrix

Finally, we combined our environmental state change matrix, *F,* with the IPMs derived for each of the nine fire-states using a 'megamatrix’ to project population demography across different environmental patches (Pascarella & Horvitz, 1998; Valverde & Silvertown, 1997). By classifying individuals both by size stage and patch type, this approach produces probabilities of a plant of a given size within a given environmental state transitioning to another combination of size and state. Thus this model describes individuals moving from patch to patch as opposed to patches ‘carrying’ populations through successional states (Caswell, 2006). Our censuses occurred in June and July, after *C. intratropica* trees grow and recruit during the wet season (DecemberMay) and before the occurrence of the environmental state transitions that are driven by fire disturbance later in the dry season (June–October). Therefore, as with Pascarella and Horvitz (1998), our megamatrix first modeled the size stage transitions (using IPMs) followed by the environmental state transitions (matrix *F*).

IPMs were operationalized as 265 × 265 matrices of transition probabilities among *C. intratropica* size stages and integrated with the 9 × 9 environmental state change matrix *F* to construct megamatrix *M*, following Pascaralla and Horvitz (1998), as follows:

*M* = (*F* ⨂ *I*) × *A*1,9

Where *F* ⨂ *I* is the Kronecker product of *F*, the environmental state change matrix described above, and *I*, an identity matrix of the same dimensions as each IPM output. In the equation above, *A*1,9 is a sparse matrix constructed of each of the nine IPMs (*A*1,*A*2,…*A*9; corresponding to each combination of fire disturbance type and grove state) arranged diagonally as submatrices among equally sized submatrices (*Z*) composed of all zeros:

This produced a final, 2385 × 2385 matrix, megamatrix *M*, from which it was possible to project long-term stability (lambda) for the entire population across all environmental states. To our knowledge, this is the first application of this approach to patch-based environmental state changes using IPMs in place of traditional population matrix models.

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Table S1. Summary of statistical analyses used to model *Callitris* *intratropica* vital rates in the integral projection model. Fixed effects included In tree/seeding size in addition to two categorical explanatory variables: Fire (no fire, early dry season fire, late dry season fire) and Grove state (intact grove, degraded grove, singleton tree). The seedling growth model also included the density of adult trees within plots (basal area per ha) as a fixed effect. Model acronyms are as follows: GLM - general linearized model, GLMM - general linearized mixed model, LMM - linear mixed model.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Model | Form (R Package) | Response Variable | Fixed Effect in Global Model | Random effect | Interactions | Transformation |
| Adult Growth | LMM (nlme) | Adult size@*t+1* | Size@*t*, Fire, Grove state | Individual | Size:Grove state & Grove state:Fire | response0.7 |
| Adult Survival | Binomial GLM\* | Adult survival from time *t* to time *t+1*† | Size, Fire, Grove state | None | Size:Grove state & Grove state:Fire | None |
| Seedling Growth | LMM (nlme) | Seedling size@*t+1* | Size@*t*, Fire, Density | Individual | None | *log*(response) |
| Seedling Survival | Binomial GLMM (lme4) | Seedling survival from time *t* to time *t+1* | Size, Fire | Time step | None | None |
| Cone Production | Log-normal Poisson GLMM (lme4)‡ | Count of cones produced | Size, Grove state | Individual | None | None |
| Cone Probability | Binomial GLM | Probability of cones produced | Size, Grove state | Individual | None | None |

\*Model convergence issues prevented the use of a mixed-effects model

†Response variable was modeled as a quadratic term

‡Log-normal Poisson GLM used for overdispersed data (Elston, Moss, & Boulinier, 2001)



Figure S1. The sensitivities of the environmental state change Markov chain (matrix *F* described in the Methods) to changes in fire-dependent grove state transition probabilities, illustrated via stable stage projections of the proportions of *Callitris intratropica* grove states (right eigenvectors summed across fire disturbance types; solid lines) under the actual probabilities of regional fire occurrence in Arnhem Land. Panels illustrate sensitivities to changes in (a) the probability that intact groves remain intact under low intensity fires, (b) the probability that intact groves remain intact under high intensity fires, (c) the probability that degraded groves remain degraded under high intensity fires, and (d) the probability of grove recruitment under no fire. Dashed lines indicate the grove transition probabilities used in the final model parameterizations, estimated from field observations.