Received: 1 September 2017 | Accepted: 31 January 2018

DOI: 10.1111/1365-2745.12950

RESEARCH ARTICLE

Journal of Ecology
BRITISH ECOLOGICAL SOCIETY

Influences of fire–vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes

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Funding information
National Science Foundation, Grant/Award Number: BCS-0956552, DEB-0823380, DEB-1353301, DGE-0333257, EAR-1738104 and OISE-0966472; Ministry for Business Innovation and Employment, Grant/Award Number: Project 3.1, New Zealand's National Heritage

Handling Editor: Emily Lines

Abstract

1. In the context of ongoing climatic warming, forest landscapes face increasing risk of conversion to non-forest vegetation through alteration of their fire regimes and their post-fire recovery dynamics. However, this pressure could be amplified or dampened, depending on how fire-driven changes to vegetation feed back to alter the extent or behaviour of subsequent fires.
2. Here we develop a mathematical model to formalize understanding of how fire–vegetation feedbacks and the time to forest recovery following high-severity (i.e. stand-replacing) fire affect the extent and stability of forest cover across landscapes facing altered fire regimes. We evaluate responses to increasing burn rates while varying the direction (negative vs. positive) of fire–vegetation feedbacks under a continuum of values for feedback strength and post-fire recovery time. In doing so, we determine how interactions among these variables produce thresholds and tipping points in landscape responses to changing fire regimes.
3. Where the early-seral vegetation was less fire-prone than older forests, negative feedbacks limited the reductions in forest cover in response to higher fire frequency or slower forest recovery. By contrast, positive feedbacks (more flammable early-seral vegetation) produced a tipping point beyond which increases in burn rates or a slowing of forest recovery drove extensive forest loss.
4. With negative feedbacks, the rates of forest loss and expansion in response to variation in fire frequency were similar. However, where feedbacks were positive, the conversion from predominantly forested to non-forested conditions in response to increasing fire frequency was faster than the re-expansion of forest cover following a return to the initial burn rate. Strengthening the positive feedbacks increased this asymmetry.
5. *Synthesis*. Our analyses elucidate how fire–vegetation feedbacks and post-fire recovery rates interact to affect the trajectories and rates of landscape response to altered fire regimes. We illustrate the vulnerability of ecosystems with positive fire–vegetation feedbacks to climate change-driven increases in fire activity, especially

where post-fire recovery is slow. Although negative feedbacks initially provide resistance to forest loss with increasing burn rates, this resistance is eventually overwhelmed with sufficient increases to burn rates relative to recovery times.

KEYWORDS
alternative stable state, fire regime, fire–vegetation feedback, flammability, forest recovery, hazard rate, non-stationary, tipping point

1 | INTRODUCTION

As the climate warms, there is a growing concern that forest landscapes risk transformation to non-forest systems through alteration of their fire regimes (Gonzalez, Neilson, Lenihan, & Drapek, 2010; Westerling, Turner, Smithwick, Romme, & Ryan, 2011). Despite the intuitive relationship between warmer, drier conditions and larger, more severe fires (Barbero, Abatzoglou, Larkin, Kolden, & Stocks, 2015; van Mantgem et al., 2013), the degree to which climatic warming and other global change pressures transform landscapes may depend on more complex interactions and feedbacks between fire and vegetation (McKenzie & Littell, 2017). Fire modifies vegetation composition and structure, including effects on fuel amount and type, fuel connectivity, and canopy-mediated influences on microclimate and fuel moisture (MacDermott, Fensham, Hua, & Bowman, 2017; Ray, Nepstad, & Moutinho, 2005). Those effects may then shape the spread and severity of subsequent fires (Coppoletta, Merriam, & Collins, 2016; Harvey, Donato, & Turner, 2016b; Hoffmann, Jaconis, et al., 2012). As key fire regime drivers (e.g. climate, human ignitions) shift and become increasingly conducive to fire, it is imperative that the fire ecology research and management communities learn to recognize how fire-mediated changes to vegetation and fuel feed back to alter the ability of those changing drivers to transform landscapes.

Fire–vegetation feedbacks could either amplify or dampen the effects of climate changes conducive to extensive fire. In ecosystems where closed-canopy forests have cool, moist sub-canopy microclimates (e.g. Nothofagaceae-dominated southern temperate forests), severe fire can convert forest to a shrub-dominated system with denser, more continuous surface fuels that dry readily in the open conditions (Figure 1a,b). The post-fire vegetation is then more easily burned by subsequent fires, driving a positive feedback whereby non-forest vegetation can be perpetuated or expanded by repeated fires (Paritsis, Veblen, & Holz, 2015; Tepley, Veblen, Perry, Stewart, & Naficy, 2016). In other regions, the vegetation that develops after severe fire is less fire-prone than older forests—for instance, severe fire can convert subalpine or boreal conifer forests to early-seral vegetation dominated by less flammable deciduous species (Figure 1c)—and a negative feedback could therefore reduce the potential for climatic warming to drive more extensive fire (Héon, Arseneault, & Parisien, 2014; Kelly et al., 2013).

The strength of fire–vegetation feedbacks (i.e. the degree to which fire-driven changes to vegetation, fuels and microclimate affect the spread and behaviour of subsequent fires) is influenced by numerous global change pressures. For example, where closed-canopy forests have high fuel moisture that impedes the spread of fire from adjacent shrublands except when the fuels have dried during severe or sustained drought, increases in the frequency or duration of dry periods when fire can spread into the forests could weaken the positive feedbacks by reducing differences in flammability among age classes (Mermoz, Kitzberger, & Veblen, 2005; Uhl, Kauffman, & Cummings, 1988). Also, when flammable non-native plants invade post-fire environments, they could either enhance existing positive feedbacks or produce a switch from negative to positive feedbacks (Brooks et al., 2004; Gaertner et al., 2014; Taylor et al., 2017). Introduced livestock can also alter feedback direction and strength by modifying fine fuel amount and continuity (Blackhall et al., 2017; Raffaele, Veblen, Blackhall, & Tercero-Bucardo, 2011).

The time to forest recovery after high-severity fire (i.e. fire that causes near complete above-ground mortality of the existing vegetation) also has important implications for how landscapes respond to altered fire-regime drivers. Climatic warming could delay forest recovery by either hindering tree seedling establishment and growth (Rother, Veblen, & Furman, 2015; Tercero-Bucardo, Kitzberger, Veblen, & Raffaele, 2007), or through the loss of seed sources if patches of high-severity fire become larger (Harvey, Donato, & Turner, 2016a; Tautenhahn et al., 2016; Tepley, Thompson, Epstein, & Anderson-Teixeira, 2017). Prolonged forest recovery could then increase the likelihood that the flammable early-seral vegetation of systems with positive feedbacks is reburned and so maintained in the landscape (Thompson, Spies, & Ganio, 2007), or it could counteract the fire-favouring effects of climate change in systems where low flammability of the early-seral vegetation provides a negative feedback (Héon et al., 2014).

Given the many interacting variables that influence how ecosystems respond to disturbance, mechanistically rich models calibrated to a specific study area are highly valuable in evaluating how that ecosystem responds to alterations of its disturbance regime. However, when generalizing across systems to understand why different ecosystem types vary in their responses to a common suite of global change pressures, it may be more useful to focus on a few key processes and relationships. These variables are commonly synthesized in qualitative conceptual models (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015; Johnstone et al., 2016), which help refine and prioritize questions for further empirical work, and in turn, inform additional evaluations with both simple and complex models. Though less common, the implementation of these conceptual

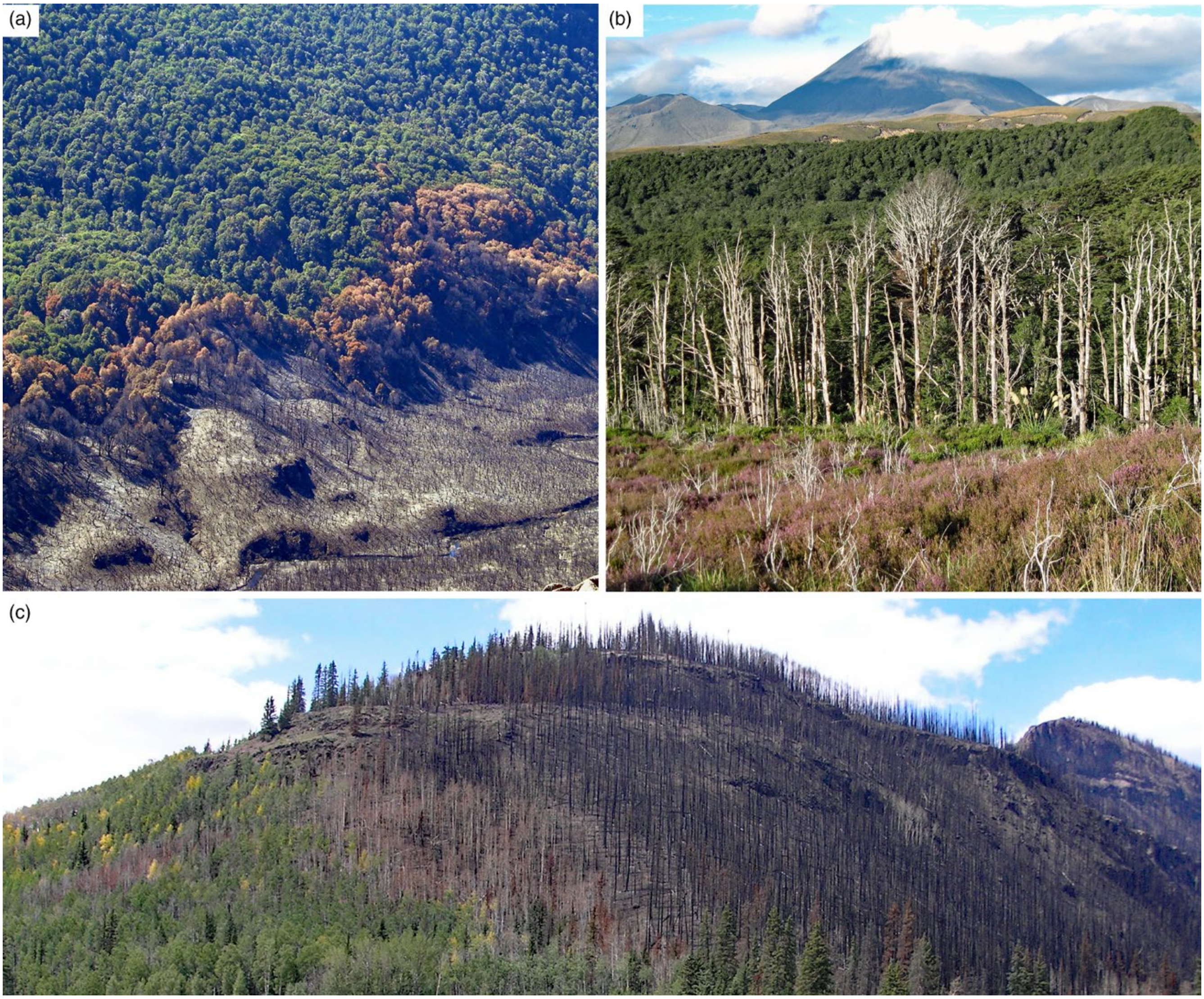


FIGURE 1 Examples of fire–vegetation feedbacks affecting fire spread. Positive feedbacks are evident in southern beech (Nothofagaceae) forests of (a) southern Argentina (photo: Thomas Kitzberger) and (b) New Zealand (photo: Alan Tepley). Both photos were taken soon after fires had spread readily through the more recently burned, shrub-dominated vegetation in the foreground and stopped abruptly at the edge of the older forests, where more severe fire weather is needed to sustain fire spread beneath the cool sub-canopy microclimate. When beech forests do burn, the post-fire vegetation may be burned repeatedly until the fire-free interval is long enough to re-establish a beech canopy. The positive feedbacks in (b) may have been strengthened by the invasive European heather, *Calluna vulgaris* (pink flowers), which is highly flammable and can increase in dominance over successive fires due to its greater resprouting potential than most indigenous species. Negative feedbacks are evident in subalpine forests of the southern Rocky Mountains (c), where a recent fire severely burned a mature forest of spruce (*Picea*) and fir (*Abies*) but went out along the edge of an adjacent aspen (*Populus*) forest (photo: Thomas Veblen). A narrow band of light-coloured aspen snags marks the abrupt change in fire behaviour at the boundary between charred conifer snags and unburned aspen. Aspen sometimes dominates the early-seral vegetation following severe fire in this landscape, where its low flammability provides a negative feedback against subsequent fire

models in a quantitative form (e.g. Turner, Romme, Gardner, O'Neill, & Kratz, 1993) advances this iterative process by providing a more explicit understanding of how alternative formulations of key ecosystem properties influence the response to altered drivers and generating testable predictions for future work.

Here we construct an analytical model aimed at providing a formal understanding of how fire–vegetation feedbacks and post-fire recovery rates interact to affect the extent and stability of forest cover across landscapes facing altered fire regimes and post-fire environments. We apply the model to address the following questions: (1) How do interactions among the direction (negative vs. positive) and strength of fire–vegetation feedbacks and the time to forest recovery after severe fire affect the equilibrial extent of forest cover across landscapes where the rate of burning at high severity (and by implication, top-down fire-regime drivers) is fixed? (2) How do feedback direction, feedback strength and post-fire recovery time interact to affect the stability of forest cover across landscapes facing increasing rates of high-severity fire? (3) How do interactions among feedback direction and strength and post-fire recovery time affect the rates of forest loss and expansion across landscapes in response to changes in the frequency of high-severity fire? We evaluate the utility of the model by applying it to empirical examples of past and potential future responses to altered fire regimes in selected temperate forests of the northern and southern hemisphere. Then we compile a list of suggested mechanisms of change to the model parameters and discuss pathways for expanding on our analyses to assess how these changes might play out under the complexities of real landscapes.

2 | MATERIALS AND METHODS

2.1 | Modelling feedbacks and recovery time

We developed an analytical model representing how the direction and strength of fire–vegetation feedbacks and the time to forest recovery after severe fire affect the extent and stability of forest cover across landscapes facing altered fire regimes. Our approach expands on previous applications of survival analysis to fire ecology by incorporating feedback direction and strength and post-fire forest recovery time into a function describing how the probability of burning varies with time since the previous fire (Appendix S1). Rather than calibrating the model to a specific vegetation type or geographic setting, we evaluate the extent of forest cover and its stability in the face of changing burn rates across a continuum of values for the direction and strength of fire–vegetation feedbacks and post-fire recovery time. Then we assess how interactions among these variables produce thresholds and tipping points in landscape response to altered fire-regime drivers.

In our model, the hazard rate (i.e. the rate of burning in the next year conditioned on the time since the previous fire; see Appendix S1 for further explanation) is a piecewise constant function, where the annual probability of burning differs between forests and the early-seral vegetation that develops after severe fire (Figure 2a). The rate of burning at high severity in stands old enough to have re-established forest cover since the last high-severity fire (hereafter, forest burn rates) reflects top-down drivers of fire regimes (e.g. climate or ignitions). The direction and strength of fire–vegetation feedbacks represent the bottom-up mechanisms by which local vegetation moderates the response to changing drivers. Our analyses focus only on high-severity (i.e. stand-replacing) fire, which we define as fire that causes complete or nearly complete above-ground mortality of the existing vegetation and initiates a new succession sequence, such that stand age, t, is equivalent to the time since the last high-severity fire.

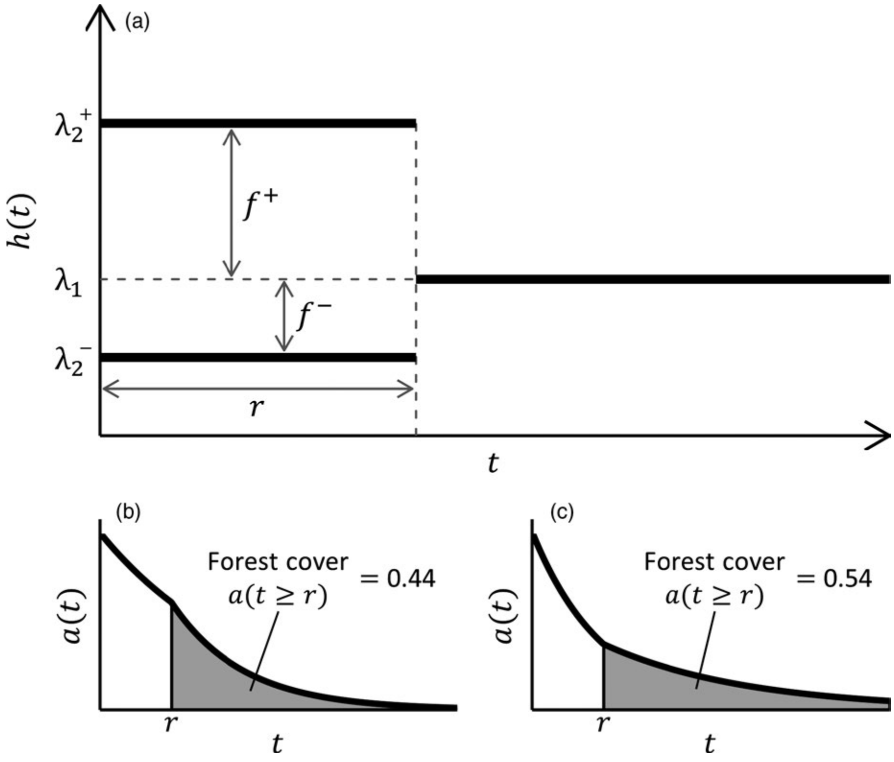


FIGURE 2 Piecewise constant hazard rate (a) representing influences of the direction and strength of fire–vegetation feedbacks (f^- and f^+) and the time to forest recovery after fire (r) on variation in the probability of fire occurrence with time since the previous high-severity fire. Superscripts (+ or −) are added to λ_2 to distinguish between positive and negative feedbacks when both are shown on the same graph. Double-headed arrows denote the variables (feedback strength and recovery time) that we vary for a given value of λ_1 to produce the response surfaces in Figures 3 and 4. Examples of the stand-age distribution ($a(t)$, black curves) and the extent of forest cover ($a(t \geq r)$, grey shading) are shown for systems with (b) negative feedbacks ($\lambda_1 = 0.01$, $\lambda_2 = 0.005$, $r = 100$, $f^- = 2$) and (c) positive feedbacks ($\lambda_1 = 0.005$, $\lambda_2 = 0.01$, $r = 100$, $f^+ = 2$)

To represent the time to forest recovery after severe fire, we set a threshold stand age (r) as the transition from early-seral to forest vegetation (Figure 2a). This transition may be viewed as a threshold in tree-level fire-resistance traits (e.g. bark thickness or crown base height) or stand-level species composition, fuel amount and connectivity, and canopy-mediated fuel moisture, beyond which the probability of burning at high-severity changes abruptly (Hoffmann, Geiger, et al., 2012). Therefore, the hazard rate for forests ($h(t) = \lambda_1$) differs from that of the early-seral vegetation that develops after high-severity fire ($h(t) = \lambda_2$), depending on whether stand age (t) has reached the recovery time (r):

$$h(t) = \begin{cases} \lambda_2 & t < r \\ \lambda_1 & t \geq r \end{cases}$$

Negative feedbacks are represented by $\lambda_2 < \lambda_1$, and positive feedbacks by $\lambda_2 > \lambda_1$ (Figure 2a).

The difference between λ_2 and λ_1 defines feedback strength (Figure 2a). Feedbacks are absent where $\lambda_2 = \lambda_1$ (i.e. the probability of burning at high severity is independent of the time since the previous fire). Otherwise, the greater the difference between λ_2 and λ_1, the more strongly the differences in flammability between early-seral and forest vegetation affect the probability of high-severity burning. For systems with negative feedbacks, feedback strength is calculated as $f^- = \lambda_1/\lambda_2$, which represents how many times more likely forest vegetation (where the time since fire, t, exceeds the recovery time, r) is to burn severely in any year than is early-seral vegetation. The strength of positive feedbacks is $f^+ = \lambda_2/\lambda_1$, representing the number of times more likely that early-seral vegetation is to burn severely in any year than is older forest (Figure 2a).

2.2 | Response surfaces

To understand how fire–vegetation feedbacks and the time to forest recovery after severe fire influence the extent of forest cover across landscapes, we use the piecewise constant hazard rate to calculate the probability density function for stand age ($a(t)$; Appendix S1) under various combinations of feedback strength and recovery time (Figure 2b,c). First, we set the rate of burning at high severity (λ_1) in stands old enough to have returned to forest cover since the previous fire ($t \geq r$). Then we generate a sequence of values of λ_2 to produce feedback strengths (f^- and f^+) ranging from 1 to 100 in increments of 1, and we vary the recovery time from 0 to 150 years in 1-year increments. For any parameter combination, the equilibrium proportion of a landscape supporting forest cover (Figure 2b,c) is determined by integrating $a(t)$ over the ages where the time since the last high-severity fire (t) is at least as long as the recovery time (r):

$$a(t \geq r) = \int_r^\infty a(t)dt = \frac{\int_r^\infty \exp\left[-\int_0^t h(u)du\right] dt}{\int_0^\infty \exp\left[-\int_0^t h(u)du\right] dt} \tag{1}$$

Here, $h(u)$ is the hazard rate (Figure 2), but we replace t with the dummy variable, u, to clarify that $a(t)$ is a function of the upper limit of integration, t. To address our first question (how do feedback direction and strength interact with post-fire recovery time to affect the extent of forest cover across a landscape with the high-severity burn rate fixed?), we apply Equation 1 sequentially to produce a response surface representing the proportion of a landscape supporting forest cover under each combination of λ_2 and r for a given value of λ_1 (see Appendix S1 for additional explanation of the relationship between the hazard rate and the stand-age distribution).

We address our second question—how do interactions among feedback direction, feedback strength, and post-fire recovery time affect the stability of forest cover as high-severity burn rates increase (e.g. due to climate becoming more conducive to widespread fire)—by constructing multiple response surfaces at progressively higher values of λ_1. In each iteration, we vary feedback strength from 1 to 100 and recovery time from 0 to 150 years, as described above. For each combination of feedback strength and recovery time, we calculate the difference in forest cover relative to that under the initial, lower value of λ_1. Thus, for any increase in the forest burn rate, we evaluate the vulnerability to forest loss along gradients of feedback strength and recovery time, and we compare that vulnerability between systems with negative and positive feedbacks.

2.3 | Trajectories of change in forest cover

The analysis for question 2 compared the equilibrium forest extent towards which a landscape would eventually converge following an increase in forest burn rates, provided no further changes to the fire regime. However, the response surfaces do not indicate how quickly the landscape converges to this new state. Thus, we now remove the assumption of stationarity (Assumption 3 of Appendix S1) and develop an approach to track trajectories of change in the proportion of a landscape supporting forest cover after an abrupt change to the forest burn rate (λ_1).

Predicting changes in the distribution of stand ages over time is particularly challenging in systems with both top-down alteration of fire-regime drivers and bottom-up feedbacks to those changes. This complexity requires us to expand on the methods presented in Appendix S1 by representing the hazard rate as a function of both stand age, t, and continuous time, τ, where τ is analogous to calendar year (see Appendix S2 for further explanation of this approach). If we denote the year at which the fire regime changes as τ_0, the hazard rate for high-severity fire becomes,

$$h(t, \tau) = \begin{cases} h_1(t) & \tau \leq \tau_0 \\ h_2(t) & \tau > \tau_0 \end{cases}$$

In the present analysis, $h_1(t)$ and $h_2(t)$ are both piecewise constant functions of stand age with different values for λ_1.

Incorporating continuous time, τ, into the hazard rate enables us to calculate a density function for stand age that varies over time, $a(t, \tau)$. In a stationary regime, we calculate the density function for stand age by multiplying the rate of stand initiation by the probability of surviving to age t without fire, where the proportion of the landscape burned per year varies around a fixed mean (Appendix S1). In a non-stationary regime, the proportion of the landscape that burns per year varies as a function of the distribution of stand ages and the age-specific hazard rate in the respective year. This variation makes it difficult, if not impossible, to directly calculate the proportion of the landscape that burns at any point in time. However, our assumption that new stands initiate only after another stand is killed by fire (Assumption 2 of Appendix S1) enables us to calculate changes in the distribution of stand ages year-by-year (at an interval of $\Delta\tau = 1$):

$$a(t,\tau+1) = \begin{cases} a(t-1,\tau) - [a(t-1,\tau)h(t-1,\tau)] & t > 1 \\ 1 - \int_2^\infty a(t,\tau+1)dt & t = 1 \end{cases} \qquad (2)$$

Following the upper part of Equation 2, the abundance of stands of age $t = 100$ in year $\tau + 1$ is equal to the abundance of stands that were 99 years old in year τ minus the proportion of those stands that were burned in year τ, as determined by their age-specific hazard rate in year τ. The lower part of Equation 2 illustrates that the proportion of the landscape supporting new stands that initiate in year $\tau + 1$ is equal to 1 minus the proportion of the landscape supporting stands that survived to year $\tau + 1$. Therefore, if the initial stand-age distribution is known (regardless of whether it represents an equilibrium condition), we can iteratively apply Equation 2 to track changes in the distribution of stand ages at a 1-year interval ($\Delta\tau = 1$) following a change to the fire regime. The upper part of Equation 2 ($t > 1$) is calculated before the lower part ($t = 1$), and the output for each iteration serves as the input for the next timestep (Appendix S2).

To address our third question (how do interactions among feedback direction, strength and post-fire recovery time affect the rate of change in forest cover in response to changes to the high-severity burn rate), we first increase the high-severity burn rate (λ_1) and apply Equation 2 to track the rate of convergence to the equilibrium forest cover of the new regime in systems with negative and positive feedbacks. Then we return λ_1 to its initial value to compare whether the rate of return to the initial equilibrium forest cover differs from the rate of decrease to the lower equilibrium value after we increased the forest burn rate. We repeat these steps across several levels of feedback strength (f^- and f^+) and stand-level recovery time (r) to assess the degree to which changes in these variables affect the rates of landscape-level forest loss and re-expansion in response to changes in λ_1. All calculations were conducted in R version 3.3.0 (R Core Team, 2016), using the midpoint rule to approximate integrals (Weideman, 2002). Sample code for producing the response surfaces is provided in Appendix S3.

3 | RESULTS

3.1 | Response surfaces

With high-severity burn rates fixed, the direction of fire–vegetation feedbacks strongly influenced how the equilibrium forest extent varied along gradients of feedback strength and the time to re-establish forest cover after severe fire (question 1; Figure 3). In systems with negative feedbacks, forest cover decreased incrementally with increases in recovery time (Figure 3a). Because forests (i.e.

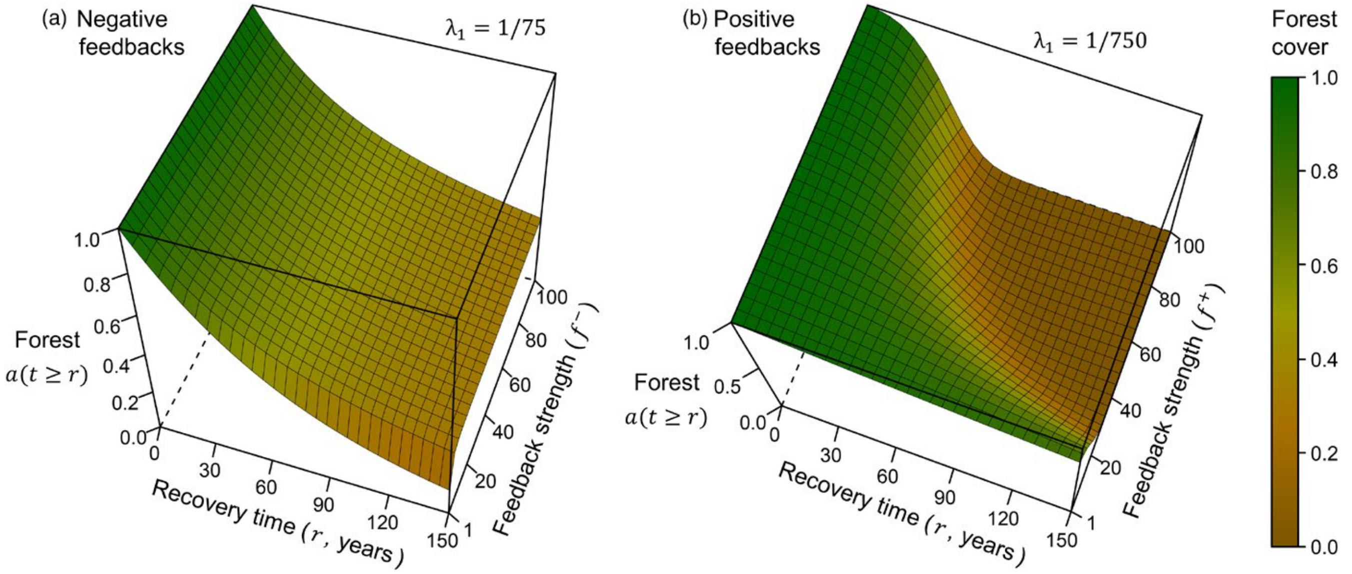


FIGURE 3 Response surfaces illustrating the equilibrium proportion of a landscape supporting forest cover ($a(t \geq r)$; Equation 1) along gradients of feedback strength (f^- and f^+) and recovery time (r) for a given rate of burning (λ_1) in forests (i.e. after stand age (t) has reached the recovery time). Values of λ_1 were selected to emphasize the differences in the shape of the response surface between systems with (a) negative and (b) positive fire–vegetation feedbacks (response surfaces for other values are shown in Figure 4). We denote λ_1 in the form $1/x$, where forests face a 1 in x chance of burning in each year after stand age has reached the recovery time

where stand age, t, exceeds the recovery time, r) of systems with negative feedbacks are more likely to burn in any year than early-seral vegetation ($t < r$), and increasing the strength of negative feedbacks increases the probability of reaching a forest state before the next fire, varying the hazard rate in early-seral vegetation (λ_2) to adjust the feedback strength had little effect on forest extent. Instead, the extent of forest cover was driven primarily by the time to forest recovery after severe fire (r) relative to the rate of burning in forest stands (λ_1; Figure 3a).

In systems with positive feedbacks, interactions between feedback strength and recovery time produced a bimodal response surface where landscapes supported either high or low forest cover, but few parameter combinations resulted in intermediate levels (Figure 3b). Unlike systems with negative feedbacks, where varying the recovery time produced proportional changes in forest extent regardless of the position on the response surface (Figure 3a), the position on the response surface in systems with positive feedbacks strongly influences whether forest cover varies minimally or shows extensive change in response to variation in feedback strength or recovery time (Figure 3b). Where positive feedbacks are weak and recovery times short, landscapes could absorb variation in feedback strength or recovery time with little effect on forest extent. However, near the response surface boundary between predominantly forested and non-forested states, small increases in feedback strength or recovery time drive extensive forest loss (Figure 3b).

Fire–vegetation feedback direction affected how systems respond to an increase in forest burn rates (question 2; Figure 4), where increasing λ_1 could represent altered climate or ignition patterns that make forest vegetation more conducive to severe fire. In systems with negative feedbacks, the magnitude of forest loss for a given increase in λ_1 depended on the relationship between the recovery time (r) and the reciprocal of λ_1 (where $1/\lambda_1$ represents the average number of years to the next fire after stands have reached the recovery time; Figure 4a). Landscapes remained predominantly forested with only small reductions in forest cover for a given increase in λ_1 so long as the recovery time remained less than $1/\lambda_1$. However, as recovery time increased beyond $1/\lambda_1$, the reduction in forest cover for a given increase in λ_1 grew substantially (Figure 4a).

Increasing the high-severity burn rate (λ_1) in systems with positive feedbacks shifted the boundary between predominantly forested and non-forested landscapes on the response surface towards weaker feedbacks and shorter recovery times (Figure 4b). For a given increase in λ_1, systems with weak positive feedbacks and short recovery times persisted as stable, forested landscapes, whereas non-forested conditions remained stable in systems with strong feedbacks and long recovery times (as shown in blue in the lower left and upper right portions, respectively, of the forest loss surfaces in Figure 4b). The stable forested and non-forested conditions were separated by a tipping point where a given increase in λ_1 resulted in a large reduction in forest cover (ridges on the forest loss surfaces of Figure 4b). An interaction between feedback strength and recovery time determined the position of the tipping point—the stronger the positive feedback, the shorter the recovery times that were vulnerable to being pushed beyond the tipping point for a given increase in the high-severity burn rate, λ_1.

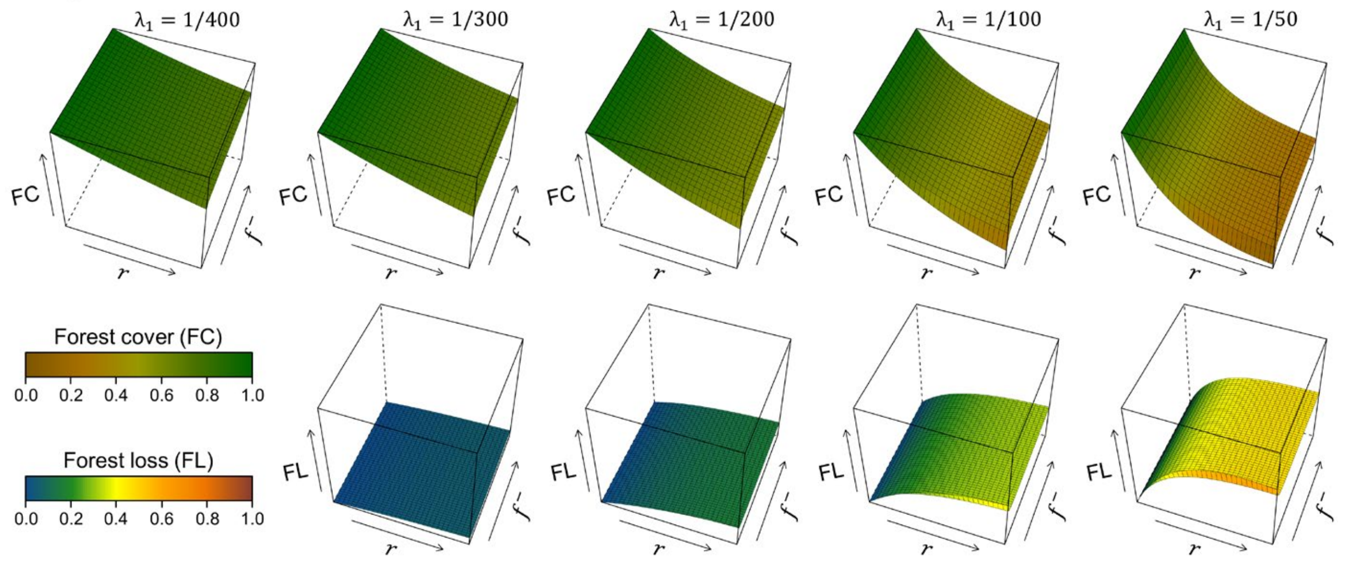
3.2 | Trajectories of change in forest cover

Fire–vegetation feedback direction affected not only the magnitude of change in forest cover after a change in fire frequency but also the time to transition to the new equilibrium forest extent and whether rates of forest loss and expansion differed (question 3; Figure 5). In systems with negative feedbacks, an increase in forest burn rates (λ_1) led to a relatively rapid reduction to a lower forest extent (Figure 5a). When λ_1 was returned to its initial value, forest cover returned to its initial extent at a rate similar to the rate of forest loss, regardless of feedback strength (f^-) or the time required for individual stands to return to forest cover after severe fire (r). Only at long stand-level recovery times did the return to the initial forest extent proceed more slowly than forest was lost, although the difference was small. For example, at a recovery time of 160 years, when we increased λ_1 from 1/500 to 1/100, it took 39 years for forest cover to decrease half the distance to the new equilibrium value. After reaching the lower equilibrium and returning λ_1 to its initial value, it took 68 years to regain half of the forest that was lost (Figure 5a).

Positive feedbacks produced asymmetry in the rate of response to changes in forest burn rates (λ_1); forest loss in response to an increase in λ_1 was typically much more rapid than the re-expansion of forest cover when λ_1 was returned to its initial value (Figure 5b). The difference between the rates of forest loss and forest expansion increased with both the strength of the positive feedbacks (f^+) and the time for stands to re-establish forest cover after severe fire (r). For instance, when λ_1 was increased from 1/500 to 1/100, essentially all the initial forest was lost, and half of that loss occurred in about 70 years regardless of feedback strength or recovery time. With a recovery time of 100 years, the time to regain half of the initial forest cover after returning λ_1 to its initial value varied from 108 years at $f^+ = 5$, to 466 years at $f^+ = 25$. After we increased λ_1 to its initial value with feedback strength fixed at 15, the time to regain half of the initial forest cover ranged from 102 years at $r = 60$ years, to 452 years at $r = 160$ years (Figure 5b).

4 | DISCUSSION

By focusing on a few key parameters, our model elucidates how alternative formulations of ecosystem properties (i.e. differences in the direction and strength of fire–vegetation feedbacks and their interactions with post-fire forest recovery time) produce different responses under similar pressures that alter fire regimes and post-fire environments. The model parameters represent key attributes of ecosystems and their disturbance regimes that are likely to be altered to varying degrees in different geographic settings under ongoing global change (Table 1). Our analyses provide a strengthened understanding and testable predictions regarding the types of behaviour different landscapes are likely to exhibit in response to these changes.


(a) Negative feedbacks

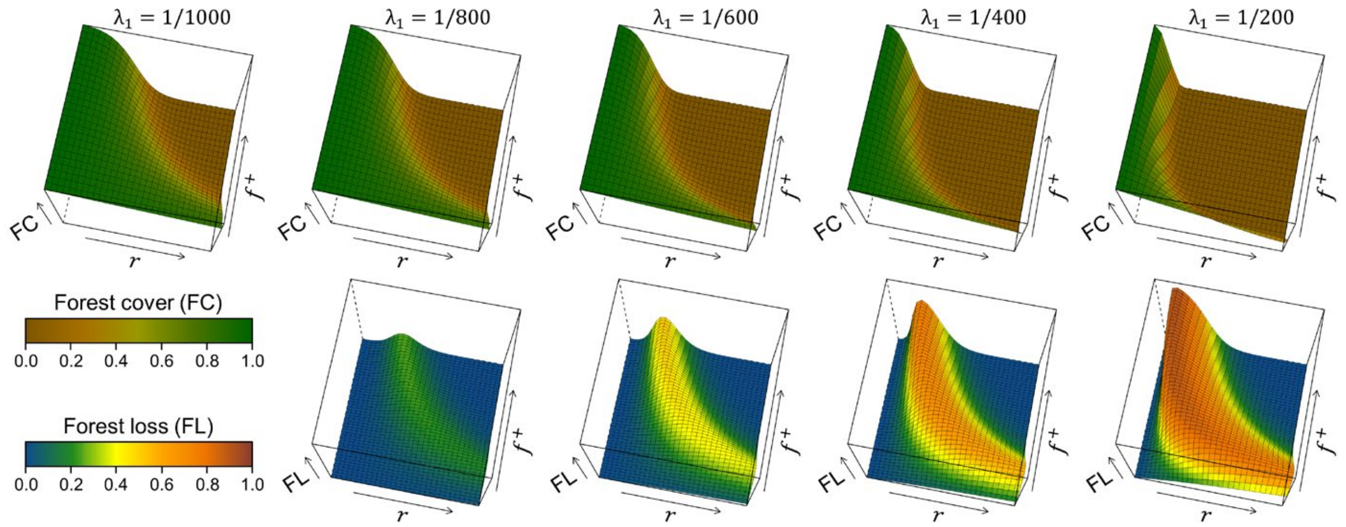

(b) Positive feedbacks

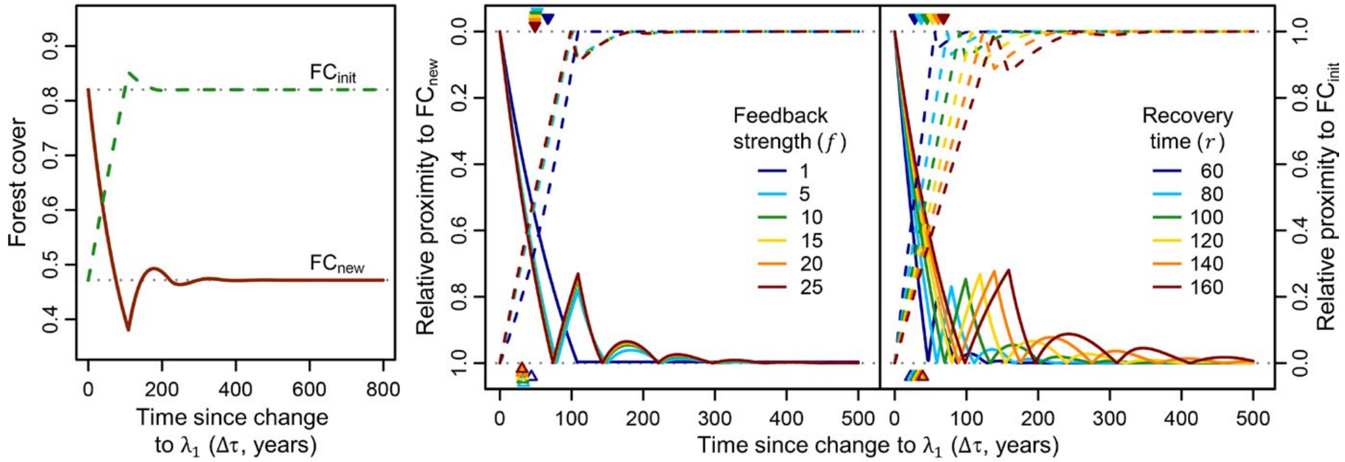
FIGURE 4 Illustration of how feedback strength (f^- and f^+) and post-fire forest recovery time (r) affect the vulnerability to forest loss in response to an increase in forest burn rates (λ_1) in systems with (a) negative and (b) positive fire–vegetation feedbacks. For each feedback direction, the upper row depicts variation in forest cover (FC = $a(t \geq r)$; Equation 1) along gradients of feedback strength and recovery time at progressively higher forest burn rates. The leftmost panel represents an initial condition with a relatively low burn rate. The forest loss (FL) below each response surface represents the difference in forest cover relative to the leftmost response surface for each combination of feedback strength and recovery time. In all panels, feedback strength (f^- and f^+) varies from 1 to 100 and recovery time (r) varies from 0 to 150 years, as in Figure 3

Systems with negative feedbacks showed the potential to maintain extensive forest cover in the face of top-down drivers (e.g. climate or ignitions) making forests increasingly conducive to high-severity fire, but this resistance was eventually overwhelmed with sufficient increases in forest burn rates relative to recovery times (Figure 4a). Positive feedbacks, by contrast, produced a tipping point beyond which small increases in feedback strength or recovery time transformed the system from predominantly forested to non-forested conditions (Figure 3b). Strengthening the positive feedbacks shifted the position of the tipping point on the response surface, making shorter recovery times increasingly vulnerable to being pushed beyond the tipping point. After transgressing the tipping point, the conversion from predominantly forested to non-forested conditions was typically much faster than the re-expansion of forest cover when parameters were returned to their initial values. This asymmetry became more pronounced with stronger positive feedbacks or longer post-fire recovery (Figure 5b).

4.1 | Application to empirical examples

Our finding that negative feedbacks provided resistance to top-down (i.e. climate-driven) increases in burn rates (λ_1; Table 1), but

(a) Negative feedbacks



(b) Positive feedbacks

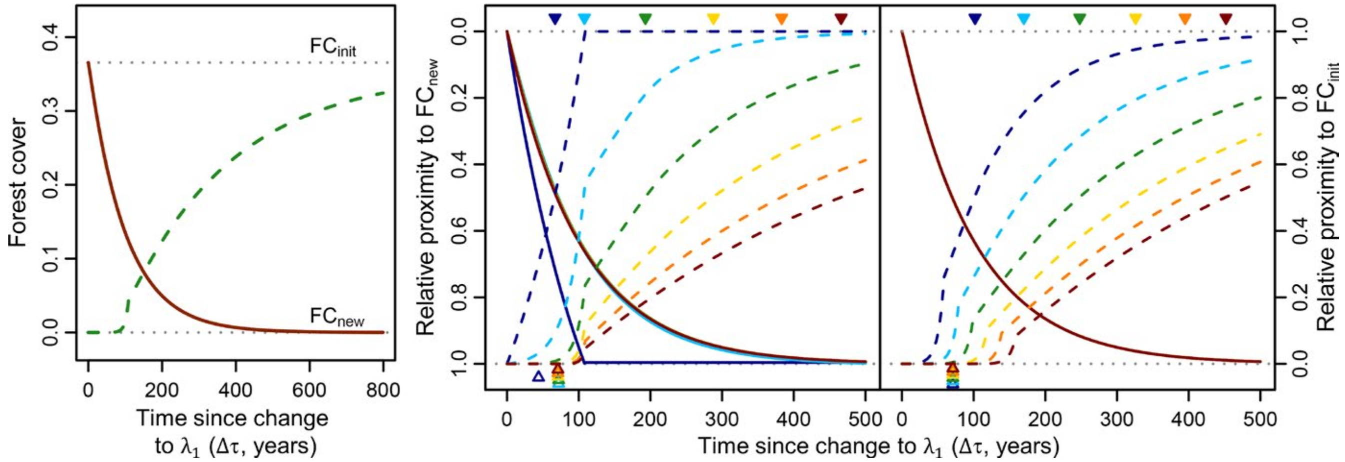


FIGURE 5 Comparison of trajectories of change in forest cover (Equation 2) in response to a change in the forest burn rate (λ_1) in systems with (a) negative and (b) positive fire–vegetation feedbacks. The left panels illustrate trajectories after λ_1 is increased from 1/500 to 1/100 and then returned to its initial value, with a feedback strength (f^- and f^+) of 15 and recovery time (r) of 110 years. The same parameter values are used in the other panels except feedback strength and recovery time vary in the centre and right panels, respectively. In all panels, solid curves represent the progressive loss in forest cover with increasing time ($\Delta\tau$) since the increase to λ_1, and dashed curves represent the re-expansion of forest cover after λ_1 is returned to its initial value. Dotted lines represent the equilibrium forest cover ($a(t \geq r)$; Equation 1) under the initial (FC_{init}) and new (FC_{new}) fire regimes. Because the equilibrium forest extent differs under the different levels of feedback strength and recovery time shown in the centre and right panels, we show the relative proximity to the initial and new equilibrium forest cover, where relative proximity represents the proportion of the difference between the two equilibrium values. Triangles represent the time at which half of the difference between the two equilibrium values has been reached on the trajectory of forest loss (open triangles) and the re-expansion to the initial forest extent (filled triangles)

only to a point beyond which further increases in fire activity overwhelm the feedbacks (Figure 4a), is consistent with interpretations of fire–vegetation dynamics in North American boreal forests. In northeastern Alberta, where fire-initiated aspen (*Populus tremuloides*) stands undergo succession to white spruce (*Picea glauca*) in the absence of fire, burn rates were lower in aspen stands ($\lambda_2 = 0.0005$) than white spruce ($\lambda_1 = 0.0017$; Cumming, 2001), providing $f^- = 3.4$. A large swath of boreal forest in northern Quebec also shows negative feedbacks, with lower burn rates in young deciduous stands than older conifer forests (Héon et al., 2014). Simulation models suggest that these feedbacks initially dampen the effect of climate becoming more conducive to fire, but continued warming eventually overrides the feedbacks (Johnstone, Rupp, Olson, & Verbyla, 2011; Krawchuk & Cumming, 2011; Mann, Scott Rupp, Olson, & Duffy, 2012). Comparison across modelling approaches could test the generality of our finding that the overwhelming of negative feedbacks tends to occur as the reciprocal of λ_1 approaches the recovery time (Figure 4a), or it could reveal how other factors (e.g. spatial patterns and connectivity of different age classes) cause a departure from this expectation.

The persistence of extensive forest cover across the Douglas-fir/western hemlock region of the US Pacific Northwest (western Washington and Oregon) despite widespread burning in two of the last five centuries (Weisberg & Swanson, 2003) is consistent with our

TABLE 1 Selected empirical examples of recent or projected future mechanisms of change to the model parameters

Variable	Mechanism of change	Reference
Change in the rate of high-severity fire in forests[a] – movement from left to right ($\uparrow \lambda_1$) or right to left ($\downarrow \lambda_1$) in Figure 4		
Effects of climate change		
$\uparrow \lambda_1$	Lengthening of the fire season due to reduced snowpack and earlier spring or warmer, drier conditions persisting later into fall; leads to larger annual area burned	Flannigan et al. (2013), Gergel, Nijssen, Abatzoglou, Lettenmaier, and Stumbaugh (2017), Westerling (2016)
$\uparrow \lambda_1$	Hotter summer temperatures and increased vapour pressure deficit lead to reduced soil and fuel moisture and larger or more severe fire	Abatzoglou and Williams (2016)
$\uparrow \lambda_1$	Drought stress prior to fire leads to greater tree mortality for a given fire intensity	van Mantgem et al. (2013)
Human-driven changes		
$\uparrow \lambda_1$	Increased ignitions or the targeting of ignitions in space and/or time to coincide with fuel flammability; increases annual area burned	Balch et al. (2017), McWethy et al. (2010, 2013)
$\uparrow \lambda_1$	Active suppression of formerly frequent surface fires in certain dry, conifer forests enables increases in fuel amount and connectivity conducive to high-severity fire	Agee and Skinner (2005), Brown (1983)
$\downarrow \lambda_1$	Active fire suppression in certain broadleaf forests leads to increased tree density and a cooler, moister sub-canopy microclimate, which reduces potential for high-severity fire (mesophication)	Lorimer (1984), Nowacki and Abrams (2008)
Changes to fire–vegetation feedback direction or strength[b] (**f^+ or f^-**) – movement along the *y*-axis in Figures 3 and 4		
Influences of climate change		
f^+ to f^-	Change from positive to negative feedbacks where warmer and drier conditions reduce vegetation cover and continuity, causing the primary constraint on fire to switch from fuel moisture (biomass is abundant but usually too moist to burn) to fuel amount and connectivity (biomass is sufficiently dry but discontinuous cover limits fire spread)	Batllori, Parisien, Krawchuk, and Moritz (2013), Krawchuk and Moritz (2011), McKenzie and Littell (2017), Pausas and Bradstock (2007)
$\downarrow f^+$ due to $\uparrow \lambda_1$	Increasing the frequency, severity or duration of drought reduces the microclimatic buffering capacity of closed-canopy forests, reducing flammability differences between forests and early-seral vegetation in systems with positive feedbacks	Ray et al. (2005), Uhl et al. (1988)
$\uparrow f^-$ due to $\downarrow \lambda_2$	Increases in boreal fire intensity with climatic warming may consume more soil organic matter favouring establishment of less flammable deciduous species (e.g. aspen) over conifers	Johnstone, Hollingsworth, Chapin, and Mack (2010)
Invasive plants		
$\uparrow \lambda_2$	Post-fire colonization by invasive plants that are more flammable than the native species strengthens existing positive feedbacks or produces a switch from negative to positive feedbacks	D’Antonio and Vitousek (1992), Pauchard et al. (2008), Taylor et al. (2017)
$\uparrow f^+$ due to $\downarrow \lambda_1$	Invasion by species that are less flammable than the native species (especially where invasion is facilitated by the suppression of formerly frequent fire) reduces flammability as the invasive plant increases in abundance with time since fire	Mandle, Bufford, Schmidt, and Daehler (2011), Stevens and Beckage (2009)
Disturbance interactions		
$\downarrow f^+$ due to $\uparrow \lambda_1$	Partial canopy-opening disturbances (e.g. by wind, biotic agents, non-stand-replacing fire or selective logging) reduce microclimatic buffering capacity of the forest canopy in systems with positive feedbacks, reducing flammability differences between forest and early-seral vegetation	Cochrane et al. (1999), Ray et al. (2005)

(Continues)

TABLE 1 (Continued)

Variable	Mechanism of change	Reference
↑ f^- due to ↓ λ_2	Disturbances by wind, biotic agents or logging prior to fire alters pre-fire stand composition and the post-fire environment, tending to favour regeneration by less flammable deciduous species (e.g. aspen that regenerates by resprouting and long-distance seed dispersal) over conifers in subalpine forests	Buma and Wessman (2012), Kulakowski, Matthews, Jarvis, and Veblen (2013)
Livestock grazing		
↑ λ_2	By altering post-fire species composition (browsing the most palatable species) and fine fuel properties (amount, bulk density, proportion of dead fuels, or vertical continuity), livestock grazing may increase the flammability of post-fire vegetation	Blackhall, Veblen, and Raffaele (2015)
↓ λ_2	By disrupting horizontal or vertical continuity of fine fuels, livestock grazing may reduce the potential for subsequent fire in recently burned vegetation	Belsky and Blumenthal (1997)
Active fire suppression		
↓ f^+ or ↓ f^-	Effective fire suppression under moderate fire weather coupled with an inability to suppress all fires under severe weather increases the proportion of the landscape that burns under severe fire weather, when differences in flammability across age classes have less influence on fire spread or severity	Turner and Romme (1994)
Alteration of post-fire recovery time (r) – movement along the x-axis in Figures 3 and 4		
Direct effects of climatic warming		
↑ r	Warmer, drier conditions lead to reductions in seedling establishment, growth, and survival; increases in recovery time may be particularly pronounced if the effects are more severe on trees than other growth forms	Rother et al. (2015), Tercero-Bucardo et al. (2007)
Indirect effects of climatic warming		
↑ r	Reduction of seed-source availability (in space) due to increasing patch sizes for high-severity fire	Harvey et al. (2016a), Tautenhahn et al. (2016)
↑ r	Reduction of seed-source availability (in time) due to high-severity fire at intervals too short for dominant species to reach reproductive maturity (demographic shift)	Enright et al. (2015)
Interactions between climatic warming and seed-source availability		
↑ r	As climatic aridity increases, greater seed-source availability may be required to support regenerating tree seedlings at a density sufficient for forest recovery	Tepley et al. (2017)
Livestock grazing		
↑ r	Exposure of mineral soil and reduction in cover by livestock grazing may initially favour tree seedling establishment, but grazing tends to limit the longer term survival and recruitment of tree seedlings to the sapling layer, slowing forest recovery after severe fire	Blackhall et al. (2017), Raffaele et al. (2011), Tercero-Bucardo et al. (2007)

[a] Mechanisms that alter the high-severity burn rate modify the value of λ_1, while λ_2 changes accordingly to maintain the same feedback strength.

[b] Mechanisms that alter feedback strength change the value of either λ_1 or λ_2 while the other parameter remains unchanged. Mechanisms specific to systems with either positive or negative feedbacks are indicated as altering f^+ or f^-, respectively. For mechanisms that alter the flammability of early-seral vegetation (λ_2), the effect on feedback strength depends on the initial direction and strength of the feedbacks.

finding that systems with weak positive feedbacks and short recovery times are relatively resilient to variation in fire frequency. Fuel succession following high-severity fire supports a positive feedback whereby early-seral vegetation has more abundant surface fuel capable of supporting higher fire intensity than mature forests (Agee & Huff, 1987). However, the rarity of large fires except under extreme fire weather probably weakens this feedback (Gedalof, Peterson, & Mantua, 2005). Post-fire recovery has consistently been rapid since the late 12th century, with fire-initiated pulses of Douglas-fir (*Pseudotsuga menziesii*) recruitment continuing for *c.* 40 years until the canopy grows dense enough to preclude further recruitment (Tepley, Swanson, & Spies, 2014). The weak positive feedbacks and short recovery times relative to typical fire intervals place this system far from the tipping point on our response surfaces.

To the south of the Douglas-fir/western hemlock region, portions of the drier, more fire-prone Klamath Mountains (SW Oregon and NW California) face greater risk of crossing their tipping point. Following severe fire, broadleaf trees and shrubs usually dominate for at least three decades, and their dense cover limits the initial pulse of conifer recruitment to a window of a few years (Tepley et al., 2017). Conifers eventually overtop the competing vegetation, but fires that occur before the development of larger, more fire-resistant conifers tend to be severe and reset the sequence (Lauvaux, Skinner, & Taylor, 2016; Thompson et al., 2007). By either promoting larger patches of high-severity fire that deplete conifer seed sources or creating a harsher competitive environment for regenerating conifers during the critical first few years following fire, climatic warming could delay forest recovery (i.e. increase *r*; Table 1), providing more time for repeated burns to perpetuate broadleaf tree and shrub-dominated vegetation (Tepley et al., 2017). Thus, climate change-driven increases in high-severity burn rates could shift the tipping point towards shorter recovery times, while a lengthening of recovery times could push portions of the region beyond the tipping point (Figure 4b).

Strong positive feedbacks and long recovery times make southern beech (Nothofagaceae) forests of the southern hemisphere vulnerable to increasing burn rates. The beech forests of New Zealand and southern South America support high fuel moisture in the cool, moist microclimate beneath the canopy, making them difficult to burn except under severe fire weather (Kitzberger et al., 2016; Mermoz et al., 2005). When they do burn, however, smaller trees and shrubs dominate the post-fire vegetation, providing denser, more continuous fuels that dry readily in the absence of a taller forest canopy (Paritsis et al., 2015; Tepley et al., 2016). The strength of the positive feedback is evident in the abrupt boundaries between forest and non-forest vegetation that persist in the absence of physical firebreaks (Figure 1a,b). Fires spread readily through the younger, shrub-dominated vegetation, but only under severe fire weather can they continue into the older forest (Mermoz et al., 2005). The short seed dispersal distance of beech trees limits forest recovery to a narrow strip (tens of metres) along the forest edge, with the interiors of larger burned patches potentially taking well over a century to recover (Kitzberger et al., 2016; Tepley et al., 2016).

High vulnerability to increasing burn rates in systems with strong positive feedbacks and slow forest recovery helps explain the rapid loss of nearly half of the initial forest cover of New Zealand within about two centuries following human colonization in the late 13th century (McWethy et al., 2010). Previously, fire had been exceptionally rare, and the landscape was primarily (*c.* 85%) forested (Perry, Wilmshurst, & McGlone, 2014). With the advent of human-ignited fire (i.e. an abrupt increase to λ_1; Table 1), large areas of forest were rapidly lost, given the inability of most indigenous tree species to survive even low-intensity fire. Once forests were burned, slow forest recovery combined with high flammability of the post-fire vegetation would have enabled the perpetuation and expansion of non-forest cover by repeated burning, as long as human ignitions continued (Perry, Wilmshurst, McGlone, McWethy, & Whitlock, 2012). By the mid-20th century, fire suppression had become highly successful (Anderson, Doherty, & Pearce, 2008), but consistent with our findings for systems with strong positive feedbacks and slow recovery, it may take several centuries to regain even half of the forest that was lost (Figure 5b). Additional factors (e.g. elimination of seed sources, loss of soil organic matter and mycorrhizae, or introduced plants and animals) could further delay or even preclude forest recovery in portions of the landscape (Perry, Ogden, Enright, & Davy, 2010; Perry, Wilmshurst, Ogden, & Enright, 2015; Richardson, Holdaway, & Carswell, 2014).

4.2 | Pathways to further evaluation

Our analyses support recent theoretical advances on how changes to fire frequency and post-fire recovery rates place certain forest landscapes at risk of transformation, and we expand on these advances by demonstrating how the direction and strength of fire–vegetation feedbacks modify that risk. There are several ways that climate change could both increase fire activity and slow post-fire forest recovery (Table 1), producing an “interval squeeze” that narrows or eventually eliminates the fire-interval window in which forests persist (Enright et al., 2015). We depict the narrowing of this window due to increases in fire frequency (movement from left to right panels of Figure 4) and a slowing of post-fire recovery time (movement from left to right along the *x*-axis in each panel of Figure 4). We further demonstrate that where feedbacks are negative, closure of this window is likely to be incremental with the potential to be reopened almost as quickly as it was closed. However, positive feedbacks lead to a more abrupt closure that may take several centuries to re-open. Factors that strengthen positive feedbacks (Table 1) reduce the capacity to absorb alterations of burn rates and recovery times, increasing vulnerability to forest loss. These findings highlight the value of determining the direction and strength of fire–vegetation feedbacks for different forest types as a first step in comparing their relative vulnerability to forest loss as fire regimes and post-fire environments change.

Our model isolates feedback direction and strength and post-fire recovery time from numerous other factors that potentially mediate landscape responses to altered fire regimes. We did this to understand why similar pressures may elicit varying responses among ecosystems, but we do not intend to downplay the influences of other factors. To the contrary, our approach provides baseline behaviours against which to evaluate whether the complexities of real landscapes could reinforce or buffer against the trends we identify. For instance, our model does not represent spatially contagious fire spread, but expanding the model to a spatial form could produce scenarios where the juxtaposition of different age classes more strongly influences the probability that a stand burns in the next timestep than the time since fire at the stand itself. Such an analysis could test whether factors that alter the strength of negative feedbacks (Table 1) could play a stronger role in facilitating or buffering against landscape transformation than suggested by our analyses in a non-spatial context. Similar comparisons could be made by adding non-fire disturbances or incorporating variable fire severity, where the results would depend on how these disturbances affect the probability of subsequent high-severity fire in a particular geographic setting.

Another direction for further evaluation is the need for a more explicit characterization of the conditions that violate our representation of a single equilibrium forest extent for each combination of input parameters. When we increased burn rates and then returned them to their initial value, we showed that under positive feedbacks it may take several centuries to return to the initial forest extent. However, our model does not preclude an eventual return to the initial conditions provided no further changes to system parameters. Alternatively, the additional complexities of real landscapes may produce a fold in the response surface (Zeeman, 1976), where a single parameterization can produce two stable equilibria (Beckage & Ellingwood, 2008; Staver & Levin, 2012).

That systems can return to the initial forest extent in our model, albeit slowly, might reflect the simplicity of our approach. For instance, by setting a fixed recovery time, we may discount the importance of the loss of ecological memory (Johnstone et al., 2016), which may be central to understanding how the progressive loss of New Zealand's beech forest and associated seed sources shifted a growing portion of the landscape to a slower, potentially indefinite forest recovery pathway (Tepley et al., 2016). However, our finding that even a simple model can produce transitions that proceed for centuries suggests that such slow transitions might be common, but difficult to recognize at the time-scales commonly addressed in empirical research (Fukami & Nakajima, 2011; Hughes, Linares, Dakos, van de Leemput, & van Nes, 2013; van Geest, Coops, Scheffer, & van Nes, 2007). This interpretation highlights the need to assess the degree to which present conditions represent gradual responses to past changes in climate or disturbance regimes (Perry, 2002; Turner et al., 1993), and understand how the disconnect between present conditions and the theoretical equilibrium state towards which the landscape would eventually converge under prevailing disturbance parameters might affect the response to future changes.

By modelling the landscape response to alterations of a few key parameters, we strengthen the foundation upon which ecosystem scientists and managers may interpret and predict trajectories of landscape change under altered fire regimes and post-fire environments. The model parameters are among the most likely factors to change as human and climatic pressures continue to alter fire regimes and post-fire environments (Table 1). Qualitative conceptual models have helped to predict whether resilient behaviour or threshold responses are likely in the face of these changes (Enright et al., 2015; Johnstone et al., 2016). By integrating the direction and strength of fire–vegetation feedbacks and the time to forest recovery after severe fire in a quantitative model, we provide a more detailed depiction of how interactions among these variables determine the shape and position of thresholds in the landscape response, and we identify conditions (i.e. negative feedbacks) conducive to incremental rather than threshold behaviour. Understanding these behaviours is an important step in enabling comparisons of the relative proximity of different physiographic settings to tipping points where extensive transformation is inevitable, and identifying the types of changes that could push landscapes beyond their tipping points (Table 1). This understanding helps to both prioritize areas for proactive management and refine questions for further empirical and modelling work to better understand forest landscape vulnerability and resilience to these transformations.

ACKNOWLEDGEMENTS

We thank three anonymous reviewers for their comments on an earlier draft. Research was supported by a U.S. National Science Foundation (NSF) Partnerships for International Research and Education (PIRE) grant (OISE-0966472) and two additional NSF grants: DEB-1353301 and BCS-0956552. Additional support for A.J.T. and E.T. was provided by an NSF–Integrative Graduate Education and Research Traineeship fellowship (DGE-0333257), and for A.J.T. under the Andrews Forest Long-Term Ecological Research program (DEB-0823380). A.H. was additionally supported by NSF award EAR-1738104. G.L.W.P. was supported by Project 3.1 of the National Science Challenge "New Zealand's Biological Heritage," funded by MBIE, NZ.

AUTHORS' CONTRIBUTIONS

A.J.T. developed the initial modelling approach; E.T. assisted with the mathematical formulations; T.T.V., G.L.W.P., A.H., J.P., T.K. and K.J.A.-T. provided feedback in the development and revision of modelling analyses; A.J.T. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY

All results were generated by subjecting a range of parameter values to our analytical modelling framework. Mathematical equations are provided in the text and also archived on the Dryad Digital Repository along with sample R code: https://doi.org/10.5061/dryad.6d29p1h (Tepley et al., 2018). No original raw data were collected for this study.

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How to cite this article: Tepley AJ, Thomann E, Veblen TT, et al. Influences of fire–vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. *J Ecol*. 2018;106:1925–1940. https://doi.org/10.1111/1365-2745.12950