Author's Response

Title: Fire intensity impacts on post-fire temperate coniferous forest net primary productivity
Author(s): Aaron M. Sparks et al.
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Point-by-point response (in red text): pages 1-6
Marked-up manuscript version: pages 7-26

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Anonymous Referee #1
Received and published: 29 September 2017

Overall response: We would like to thank referee #1 for the supportive comments on the manuscript. We implemented their suggestions in our revised manuscript. Below we respond to each of the comments individually.

The manuscript by Sparks and colleagues examined how forest composition and fire intensity affected forest net primary productivity (NPP) following fire. The authors argue that higher fire intensity leads to progressively larger reduction in post-fire NPP among fire resistant and mixed-resistance communities, while fire intensity had little effect on the magnitude of NPP change in fire susceptible communities. The manuscript is well written and presents an analysis that provides novel insight into forest carbon dynamics following fire in a region where fire activity is likely to intensify over the coming century due to regional warming and drying. As detailed below, it seems there are several aspects of this analysis could be refined to further improve its rigor.

Primary comments

1. The manuscript states that, "Fire-affected pixels were grouped by FRP and FRE percentile classes (0-25, 25-50,: : :) for each fire" and then changes in post-fire NPP were evaluated among these percentile classes across all fires within a forest type. Why group pixels by fire-specific percentile class rather than by the absolute magnitude of fire intensity? Perhaps I am misunderstanding the approach, but let's say there are two fires of contrasting intensity, both of which occur in a fire-susceptible forest type. In this forest type, about 50% of pixels had FRE < 2000 MJ km-2 and about 50% of pixels had FRE between 2000 and 12000 MJ km-2 (figure 2). If the low-intensity fire only experienced FRE < 2000 MJ km-2 and the high intensity fire only experienced FRE > 2000 MJ km-2, then what happens when the pixels within each fire are grouped by the fire-specific percentile class and then these classes are subsequently grouped across fires? The 75-100th percentile class for the low severity fire might have FRE of, say, 1000-2000 MJ km-2, whereas this same percentile class for the high severity fire might encompass areas where the FRE was > 10,000 MJ km-2. You might expect a very different post-fire trajectory of NPP between these two fires for the same percentile class, but at present these would get grouped together, correct? This might somewhat explain why you don't see any difference between percentile classes in post-fire NPP trajectory for the fire-susceptible forest type.

R1: We thank the reviewer for this comment. These comments made us realize that we had worded the section poorly. As such, we have clarified this section in the revised version. To be clear, percentile classes were based on absolute magnitude of FRE (or FRP) by forest type, not for each individual fire.

2. The description of the statistical analysis is vague and the results do not present any statistics. Also, how do account for taking multiple pixels from the same fire and using them as independent samples, when in fact they are not independent?

R2: We thank the reviewer for their comment. We have included statistics relevant to the differences in NPP groups (see Figure 4). In terms of the comment regarding multiple pixels from the same fire, we believe that the text may have been unclear as we are using a census of fire-affected pixels and not a sample (i.e. all of the pixels within the fire perimeter are considered in the analysis, and not a sample of pixels within that perimeter).

Secondary comments

1. The researchers frequently note that there are dose-response relationships between fire intensity and post-fire changes in NPP. Given this focus, it would be worth including a figure that more explicitly shows this relationship. The figure could show the change in NPP one year after fire as a function of fire intensity for each of the three forest types.

R3: We think this is an excellent suggestion and have included a 1-year post-fire dose-response figure (Figure 3) in the revised manuscript.

2. Could it be that fire intensity is higher in fire-susceptible forests than mixed or fire-resistant forests not solely because of differences in trait characteristics, but rather because there is more biomass (fuel) in these forests? It could be worth normalizing fire intensity by forest biomass to see whether fire intensity per unit of fuel differs between these three broad forest types. The National Biomass and Carbon Data set 2000 (NBCD2000) could be a useful source of information for this endeavor (https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=1161)

R4: We thank the reviewer for this insight and suggestion. We downloaded this dataset and found that, on average, estimated biomass did not match trends in fire intensity (FRP, FRE). Average biomass per unit area (Mg $ha^{-1}$) decreased from mixed (157 Mg $ha^{-1}$) to fire-susceptible (129 Mg $ha^{-1}$) to fire resistant (110 Mg $ha^{-1}$), whereas fire intensity (FRP, FRE) decreased from fire-susceptible to mixed to fire resistant. We include this discussion point in an expanded results and discussion section (along with other potential drivers – e.g. climate, forest structural differences between the three types).

3. The manuscript includes figures showing the relative change in NPP following fire, but not the absolute change in NPP. It would be informative to show how the absolute magnitude of NPP changes after fire.

R5: We agree with this suggestion and have modified Figure 4 to show absolute change in NPP in addition to relative NPP.

4. Does including the FRP90th percentile add to the story? It seems somewhat redundant given the inclusion of FRPpeak and FRPmean.

R6: We agree with the reviewer and will remove 90$^{th}$ percentile FRP. Additionally, NPP response grouped by FRP and FRE were very similar, and to avoid redundancy, we have moved NPP response to peak FRP and mean NPP to supplemental files.

Line specific comments

1. Page 4, line 31: What does "Unburned pixels (nunburned = nFRP percentile group): : :" mean? Does this mean that you selected the same number of unburned pixels as there were pixels in the percentile group?

R7: That is correct – we have clarified this in the revised manuscript.

2. Page 5, lines 14-25: The researchers present the average and variation (presumably SD, but not defined) in fire intensity metrics for each forest type; however, Figure 2 shows that these metrics are very non-normally distributed. Consequently, mean and standard deviation are not appropriate summary statistics. The median and interquartile range would be more appropriate.

R8: We have corrected this in the revised manuscript.

3. Page 5, lines 29-30: the researchers state that, “in forests dominated by fire-resistant species, there was a stronger dose-response pattern for relative NPP grouped by FRE percentile class rather than FRP percentile class.” This pattern is not particularly evident looking at figure 3. I would suggest providing additional evidence, or removing the statement.
R9: We have removed this statement.

4. Page 6, line 4: “The dose-response relationship was much weaker in forests dominated by fire susceptible species. There were few differences between percentile classes with only the highest FRE percentile class displaying lower relative NPP compared with other percentile classes.” Is this based on a qualitative comparison, or statistical analysis?
R10: The revised text has clarified this in terms of the ANOVA analysis that was performed.

5. Page 6, line 14: The authors state that “generally, recovery trajectories [in NPP] were linear for all fire-resistant groups, except for a few fires were NPP begin decrease again around 2011.” Looking at the supplemental figures, it appears that many, if not most, of the fires show non-linear changes in NPP after fire.
R11: This is a valid point. We have corrected the text to say that some fires had linear recovery trajectories, while most did not.

6. Page 7, lines 19-21: The authors note that the number of MODIS FRP observation differed between “fires with a clear dose- response relationship” and those with a “weak relationship.” Does this suggest that there were differences in the number of MODIS FRP observations between forest types? Perhaps clarify what is meant by a clear relationship versus a weak relationship.
R12: The revised text clarifies this in terms of how dose-response studies are commonly analyzed and reported (e.g. Ruberg 1995). Specifically, the presence or absence of significant differences between fire intensity classes (and the unburned ‘control’ pixels) is emphasized in the revised text. Additionally, in response to reviewer #2 comment #1, we have added text in the discussion that addresses how the number of MODIS FRP observations affects FRP uncertainty and how it relates to the analyses that we performed.

7. Page 8, Conceptual framework: The following citations could bolster this section: i. Michaletz, S. T., E. Johnson, and M. Tyree. 2012. Moving beyond the cambium necrosis 1. Hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. New Phytologist 194:254-263. ii. van Mantgem, P. J., J. C. Nesmith, M. Keifer, E. E. Knapp, A. Flint, and L. Flint. 2013. 1. Climatic stress increases forest fire severity across the western United States. Ecology Letters 16:1151-1156.
R13: Thanks for the suggestions, these were added.

8. Page 8, line 22: Always hesitant to say things are “obvious” in a paper.
R14: This was re-worded in the revised manuscript.

9. Supplemental figures: The Saddle fire appears to be missing the vertical line denoting the year in which the fire occurred. Also, what do the plotting characters and error represent in these figures? Mean and standard deviation?
R15: This was corrected and clarified.

Response references:
Ruberg, S.J., 1995. Dose response studies II. Analysis and interpretation. Journal of biopharmaceutical statistics, 5(1), pp.15-42.

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Anonymous Referee #2
Received and published: 30 October 2017

Overall response: We would like to thank referee #2 for the supportive comments on the manuscript. We have implemented their suggestions in our revised manuscript. Below we respond to each of the comments individually.

This is an interesting paper detailing how NPP varies with fire severity across 15 large fires in the western U.S. MODIS satellite data at the 1-km pixel scale was used, giving a coarse view of fire severity effects on productivity. The paper addresses relevant scientific questions, presents novel results, and reaches substantial conclusions. However, some aspects of the paper, both major and minor, could be improved. General and specific comments follow.

General comments:
1. Freeborn et al. 2014 reported that differences in per-pixel FRP measured near simultaneously have a standard deviation of 27%, and that clumping pixels helps a lot (50-pixel aggregation reduces uncertainty to 5%; citation at end of comments). This seems like a relevant issue for the current study, since it uses pixel-level data. Would including the uncertainty in the analysis change the results or the interpretation of the results?
R1: This is a great point. Spatiotemporal aggregations of observations have been shown to reduce uncertainties in sums of FRP. Due to the pixel level variability in ages and species composition in the forests analyzed in this paper, only temporal FRP aggregations were employed (i.e. FRE, mean FRP). It seems clear that further aggregation through time, if data were available, would reduce the uncertainty in FRP aggregations and improve the strength of our reported relationship (which is in line with Freeborn et al. (2014) for temporal aggregation). Given that our method reports changes in pixel-level NPP that are varying as functions of structure, age and composition to a fire, we do not think that spatially aggregating the FRP observations would be appropriate. Freeborn et al (2014) advocate this methodology for abiotic relationships between FRP and emissions (fuel is fuel regardless of location), however, we are relating FRP to biotic responses of living organisms that are clearly related to the fire resistance/sensitivity of the species.

2. I don't find the conceptual framework (page 8 and Figure 4) to be very strong. The authors state that they are linking individual tree-level processes to fire intensity and forest growth and productivity. But they go on to say in the Limitations section that understory vegetation may recover rapidly and make it appear that the overstory recovers rapidly. It doesn't seem that the authors can actually say much about individual tree mortality, given the heterogeneity of fires on the ground, the large size of the pixels being used, and the lack of on-the-ground severity measurements. Couldn't it be that shrubs are what are responding post-fire rather than trees?
R2: Sparks et al. 2016 and Smith et al. 2017 observed mechanistic links between FRP and sapling mortality and productivity. These, and other studies (e.g. Sparks et al. 2017), also collectively demonstrated that the mechanism scaled from the saplings in a laboratory fire to mature trees in stand-scale fires. Prior studies (Ryan and Reinhardt 1988; Hood et al. 2007) had previously reported similar relationships between proxies of fire intensity and mature tree mortality. Although the current paper suggests that this may further scale from the watershed to the regional scale, we agree that this is not yet proven. As such, we have adjusted the text to be more circumspect and cautious of a regional scale relationship.

3. Finally, I agree with the first reviewer in questioning why the authors grouped the FRP and FRE into percentile classes, because then it's difficult to compare actual FRP and FRE in terms of their effect on NPP across fires- you've limited the analysis to within fire differences. Similarly, I also question why

relative NPP rather than absolute NPP is shown in the supplemental figures. Are there are interesting absolute differences among forest types?
R3: This section was poorly worded and was clarified in the revised text. Percentile classes were based on absolute FRP/FRE magnitude by forest type, not for each individual fire. Per reviewer #1 comment #3 we have included absolute NPP in Figure 4.

Specific comments:
4. Page 4, Line 1: MTBS only includes fires 1000 acres and bigger: are the authors able to verify through other data sources that these areas haven't burned since 1984? Does it matter?
R4: This is a great point. We mapped smaller burned areas within each MTBS polygon using the Normalized Burn Ratio Thermal Index (Holden et al. 2005) computed by Google Climate Engine (climateengine.org) annually from 1984 to the present. Google Climate Engine uses data from Landsat 4, 5, 7, and 8 depending on availability and cloud cover to produce 30 m spatial resolution datasets. Using these data we found that, on average, less than 1.5% of the MTBS polygon area burned between 1984 and the year that each fire burned. We have included this information for each fire in Table 1.

5. Page 4, MODIS datasets: Was FRP available for all pixels inside the MTBS perimeters?
R5: On average, FRP data was available for >88% of the area within MTBS perimeters. We have added this information for each fire into Table 1.

6. Page 5, section 3.1: All of the numbers in this paragraph could go into a table and it might be easier to read.
R6: Thanks for the suggestion. We have removed the numbers for easier reading, and refer readers to Figure 2.

7. Page 5, Line 7: It's mentioned here that other things besides fire may contribute to NPP variability, but I don't think it was mentioned again. It's worth noting in the discussion whether climate or other factors might play a role in post-fire recovery of NPP.
R7: This is a good point – we have added text in the discussion that addresses these factors.

Technical Corrections:
8. Page 3, Line 12: Some of the sites are not in the Northern Rocky Mountains.
R8: This was re-worded in the revised manuscript.

9. Page 3, Lines 19-24: Pick past or present tense to be consistent throughout.
R9: This was corrected in the revised manuscript.

10. Page 3, Line 26: "Canopy cover for each fire"- do you mean pre-fire canopy cover?
R10: This was clarified in the revised manuscript.

Citation: Freeborn, P.H. M.J. Wooster, D.P. Roy, and M.A. Cochrane. 2014. Quantification of MODIS fire radiative power (FRP) measurement uncertainty for use in satellite based active fire characterization and biomass burning estimation. Geophysical Research Letters 41(6):1988-1994.

Response references:
Hood SM, McHugh CW, Ryan KC, Reinhardt E, Smith SL (2007) Evaluation of a post-fire tree mortality model for western USA conifers. International Journal of Wildland Fire 16(6), 679–689. doi:10.1071/WF06122.

Holden, Z.A., Smith, A.M.S., Morgan, P., Rollins, M.G. and Gessler, P.E., 2005. Evaluation of novel thermally enhanced spectral indices for mapping fire perimeters and comparisons with fire atlas data. International Journal of Remote Sensing, 26(21), pp.4801-4808.

Ryan KC, Reinhardt ED (1988) Predicting post-fire mortality of seven western conifers. Canadian Journal of Forest Research 18, 1291–1297. doi:10.1139/X88-199.

Smith, A.M., Talhelm, A.F., Johnson, D.M., Sparks, A.M., Kolden, C.A., Yedinak, K.M., Apostol, K.G., Tinkham, W.T., Abatzoglou, J.T., Lutz, J.A. and Davis, A.S., 2017. Effects of fire radiative energy density dose on Pinus contorta and Larix occidentalis seedling physiology and mortality. International Journal of Wildland Fire, 26(1), pp.82-94.

Sparks, A.M., Kolden, C.A., Talhelm, A.F., Smith, A., Apostol, K.G., Johnson, D.M. and Boschetti, L., 2016. Spectral indices accurately quantify changes in seedling physiology following fire: towards mechanistic assessments of post-fire carbon cycling. Remote Sensing, 8(7), p.572.

Sparks, A.M., Smith, A.M., Talhelm, A.F., Kolden, C.A., Yedinak, K.M. and Johnson, D.M., 2017. Impacts of fire radiative flux on mature Pinus ponderosa growth and vulnerability to secondary mortality agents. International Journal of Wildland Fire, 26(1), pp.95-106.

# Fire intensity impacts on post-fire temperate coniferous forest net primary productivity

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**Abstract.** Fire is a dynamic ecological process in forests and impacts the carbon (C) cycle through direct combustion emissions, tree mortality, and by impairing the ability of surviving trees to sequester carbon. While studies on young trees have demonstrated that fire intensity is a determinant of post-fire net primary productivity, wildland fires at landscape to regional scales have largely been assumed to either cause tree mortality, or conversely, cause no physiological impact, ignoring the impacted but surviving trees. Our objective was to understand how fire intensity affects post-fire net primary productivity in conifer-dominated forested ecosystems at the spatial scale of large wildland fires. We examined the relationships between fire radiative power (FRP), its temporal integral (fire radiative energy - FRE), and net primary productivity (NPP) using 16 years of data from the MOderate Resolution Imaging Spectrometer (MODIS) for 15 large fires in western United States coniferous forests. The greatest NPP post-fire loss occurred ~~one~~ one-year post-fire and ranged from -67 to -312 g C $m^{-2}$ $yr^{-1}$ (-13 to -54%) across all fires. Forests dominated by fire-resistant species (species that typically survive low intensity fires) experienced the lowest relative NPP reductions compared to forests with less resistant species. Post-fire NPP in forests that were dominated by fire-susceptible species were not as sensitive to FRP or FRE, indicating that NPP in these forests may be reduced to similar levels regardless of fire intensity. Conversely, post-fire NPP in forests dominated by fire resistant and mixed species decreased with increasing FRP or FRE. In some cases, this dose-response relationship persisted for more than a decade post-fire, highlighting a legacy effect of fire intensity on post-fire C dynamics in these forests.

## 1 Introduction

Forested ecosystems cover ~30% of Earth's land surface and serve as one of the largest terrestrial carbon (C) sinks (Bonan 2008, IPCC 2013). Dynamic ecological processes such as wildfires impact this sink through direct C emissions from combustion, loss of C uptake through tree mortality, decomposition processes, and sequestration of black C within forest soils (Bowman et al., 2009; Brewer et al., 2013; Tinkham et al., 2016). Recent research has demonstrated that greater fire intensity impairs the ability of surviving saplings to photosynthesize (Smith et al., 2016, 2017). However, at landscape spatial scales, while many studies have examined and projected post-fire trends in forest productivity (Goetz et al., 2007; Hicke et al., 2003; Kashian et al., 2006; Romme et al., 2011), none have evaluated relationships between the fire intensity and those trends. Characterization of such relationships is essential given both lower fuel moisture (Gergel et al., 2017) and ~~higher~~ increased fire activity (frequency, intensity, and area burned) are predicted in North American forested ecosystems under anthropogenic climate change (Balshi et al., 2009; de Groot et al. 2013; IPCC 2013; Barbero et al., 2015; Abatzoglou and Williams, 2016; Bowman et al., 2017).

Recent studies have observed that increasing fire radiative energy (FRE: J) and peak fire radiative power (FRP: W) incident on trees results in reduced tree growth and increased mortality (Smith et al., 2017; Sparks et al., 2016, 2017). FRP is the instantaneous radiative flux, which is strongly related to common field-based fire intensity metrics (Kaufman et al., 1996; Kremens et al., 2012; Sparks et al., 2017), and its temporal integral is FRE. These are two of the most commonly used metrics to quantify fire intensity from satellite remote sensing products (Andela et al., 2015; Freeborn et al., 2016; Heward et al., 2013; Roberts et al., 2011; Smith and Wooster, 2005). Under controlled experiments on saplings, a toxicological "dose-response" relationship was observed, whereby increasing FRE resulted in decreasing net photosynthesis in surviving *Pinus contorta* and *Larix occidentalis* saplings (Smith et al., 2016, 2017) and increased mortality 1-year post-fire (Sparks et al., 2016). Furthermore, Sparks et al. (2017) observed decreasing radial growth in mature Pinus ponderosa 1.5 years post-fire with increasing peak FRP. These findings suggest that there is a strong link between measures of fire intensity and subsequent vegetation productivity and mortality.

Prior studies have been limited to the spatial scale of the individual plant and only up to ~1.5 years following fire treatments. They have also not evaluated how relative fire resistance, or the ability of a tree species to withstand and survive heat-induced damage from fire (Midgley et al., 2011; Starker, 1934; VanderWeide and Hartnett, 2011), may affect the observed dose-response relationship. Numerous studies have linked morphological traits to post-fire survival; thicker bark, deep rooting depth, and a high, open tree crown have all been identified as characteristics that increase relative fire resistance of a tree (Fischer and Bradley, 1987; Harrington, 2013; He et al., 2012; Keeley, 2012; Midgley et al., 2011; Ryan and Reinhardt, 1988; Starker, 1934; VanderWeide and Hartnett, 2011). However, many studies assume a binary response regarding fire impacts on vegetation: either mortality (immediate or delayed) or no physiological effect (Smith et al., 2017). Consequently, there is a need to investigate if dose-response relationships can be quantified at larger spatial and temporal scales and across forest stands dominated with species of varying levels of fire resistance.

Active and post-fire observations from MODIS provide an avenue to expand previous dose-response studies to a landscape spatial scale and across decadal temporal scales. Terra and Aqua satellites can observe active fires up to four times daily at 1 km resolution at nadir (Justice et al., 2002), enabling the coarse integration of FRP over the duration of a fire, described as fire radiative energy (Boschetti and Roy, 2009; Kumar et al., 2011). However, the relatively low temporal resolution results in significant underestimations of FRE when compared with higher temporal resolution sensors (Vermote et al., 2009). MODIS observations have also enabled global estimations of Gross Primary Production (GPP), the total amount of C fixed by vegetation, and Net Primary Production (NPP), GPP minus C losses to respiration, when used in tandem with local meteorological data (Running et al., 2004; Zhao and Running, 2010). These estimates have been critical to understanding C fluxes and forest disturbances over large spatial extents (Bright et al., 2013; Zhao and Running, 2010). Given the lack of landscape scale studies that quantify fire intensity and species composition impacts on post-fire C dynamics, the objective here was to understand how fire intensity affects post-fire productivity in conifer-dominated forested ecosystems. Our results provide further insight into post-fire C dynamics and a framework for spatiotemporal assessments of fire effects.

In this study, we sought to answer the following questions:

1. What are the relationships between fire intensity (i.e., FRP and FRE) and post-fire forest NPP at spatial scales of large wildland fires?
2. How do these relationships vary over time?
3. How do these relationships vary with species composition?

## 2 Methodology

### 2.1 Wildland fire selection

Fifteen wildland fires in the ~~Northern~~ NorthwesternRocky Mountains, U.S.~~,~~ were selected for this study (~~Figure~~ Fig. 1). Fires were chosen to represent coniferous forest stands ranging from those dominated by fire-resistant species to those dominated by fire-susceptible species. Forests dominated by fire-resistant species typically were composed of *Pseudotsuga menziesii*, *Pinus ponderosa*, *Larix occidentalis*, and lesser quantities of *Abies grandis*. Forests dominated by fire-susceptible species typically were composed of *Picea engelmannii*, *Abies lasiocarpa*, *Pinus contorta*, and lesser quantities of *Pinus albicaulis*. To assess the pre-fire dominant forest cover for each fire, we used the LANDFIRE Existing Vegetation Type (EVT) 30 m product (LANDFIRE 2013). Fire selection was based on the following criteria:

(i) Located in ~~northwestern~~ Northwestern United States temperate forests to minimize latitudinal climatological gradients;

(ii) Located completely within a designated wilderness or other protected area to minimize confounding factors such as land management disturbance;

(iii) Must have ~~O~~occurred in a closed canopy (mean canopy cover > 60%), conifer-dominated forest to minimize mixed pixels;

(iv) Located in forests where the majority of fire-affected area has not been observed to have burned in the last ~30 years; and

(v) Each fire must have at least 3 years of pre- and post-fire MODIS NPP estimates.

Pre-fire ~~C~~canopy cover ~~for each fire~~ was determined by aggregating the 30 m National Land Cover Database (NLCD) Percent Tree Canopy product (Homer et al., 2007) to the 1 km spatial resolution of the MODIS products. We used the Landsat-derived Monitoring Trends in Burn Severity (MTBS) fire polygons to estimate whether a forest had burned since 1984 (Eidenshink et al., 2007). MTBS does not typically map fires smaller than ~404 ha, so smaller burned areas within each selected fire perimeter were mapped using the Normalized Burn Ratio Thermal Index (Holden et al., 2005) computed by Google Climate Engine (climateengine.org) annually from 1984 to the present. Google Climate Engine uses data from Landsat 4, 5, 7, and 8, depending on availability and cloud cover, to produce 30 m spatial resolution datasets. Summary information for each fire is given in Table 1.

**2.2 MODIS datasets**

For each fire, we assessed post-fire NPP trajectories as a function of co-located FRP using MODIS NPP and FRP products. We used the MOD17A3 version 055 1 km NPP product (kg C $m^{-2}$ $yr^{-1}$) to characterize changes in productivity within and between our study fires. The NPP product is detailed in Running et al., (2004) and Hasenauer et al., (2012). MODIS land cover, FPAR (fraction of photosynthetically active radiation), and LAI (leaf area index) products are used in tandem with meteorological data (incoming PAR, stress scalars for high vapor pressure deficit and temperature) and physiological parameters for different vegetation types to calculate daily GPP. NPP is calculated as the sum of GPP over a year minus maintenance and growth respiration. We acquired the NPP product from the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana. NPP data for years 2000-2015 were downloaded from the NTSG FTP site and analyzed in the native Sinusoidal equal area projection.

To calculate FRP metrics co-located with each NPP pixel we used the Collection 6 MODIS 1 km Level 2 active fire product that identifies and quantifies active fire detections from NASA Terra (MOD14) and Aqua (MYD14) satellites (Giglio et al., 2016). MODIS FRP is derived from the linear relationship between mid-infrared (4 µm) spectral radiance and FRP (Wooster et al., 2003) and is affected by several factors, including fire background characterization and atmospheric water vapor (Wooster et al., 2005). The 1 km spatial resolution MOD14 and MYD14 products provide an active fire mask showing which pixels contain active fire as well as the date, time, FRP, and other ancillary data (Giglio 2010). Following Boschetti and Roy, (2009), MOD14 and MYD14 data were projected to the 1 km MODIS sinusoidal projection using nearest neighbor resampling. Importantly, this methodology accounts for increasing MODIS pixel size at large scan angles (Wolfe et al., 1998) so that the location of fire detections and total FRP is preserved post-reprojection. The resulting range of FRP for all fires was comparable to FRP observed in other closed-canopy temperate forests (Giglio et al., 2006; Heward et al., 2013). We used MTBS fire perimeters and metadata to screen any fire detections that were not co-located with recorded fire events spatially and temporally. Fire detections outside the MTBS perimeter were included in the subsequent analysis if they were closer than 1000 m from the MTBS fire boundary (as fires can occur anywhere in the 1 km FRP product). On average, FRP observations were available for >88% of the area within the MTBS fire polygons (Table 1).

**2.3 Data analysis**

We calculated FRP distributional statistics (peak, $90^{th}$ percentile, mean) and FRE for each fire-affected pixel. FRE was calculated following Boschetti and Roy, (2009), where FRP values are integrated over time assuming that FRP varies linearly between observations. FRP and FRE metrics were chosen as they have been demonstrated to have a dose-response relationship with conifer growth and mortality (Smith et al., 2016, 2017; Sparks et al., 2017). Fire-affected pixels were grouped by FRP and FRE percentile classes (0-25, 25-50, 50-75, 75-100) for each ~~fire~~forest type (fire-susceptible, fire-resistant, mixed). Unburned pixels ~~($n$unburned = $n$FRP percentile group)~~ were manually selected outside the MTBS fire perimeters to serve as 'control' pixels. Control pixels were selected if they: 1) were within a 5 km buffer of the MTBS perimeter, 2) were in the same forest type as the fire-affected pixels, and 3) had pre-fire mean NPP within ±50 g C $m^{-2}$ $y^{-1}$ of pre-fire mean NPP of fire-affected pixels. Pre- and post-fire NPP were used to calculate the percent deviation from mean pre-fire NPP, or relative NPP, for each pixel (*i*,*j*) and year (*t*), which was calculated following Eq. (1):

$$Relative\ NPP_t\ (\%) = \frac{(NPP_{i,j,t} - \overline{NPP}_{prefire\,(i,j)})}{\overline{NPP}_{prefire\,(i,j)}} \quad (1)$$

To account for interannual variability in NPP not caused by the fires we subtracted the unburned (control) pixel values from the burned pixel values (Bright et al., 2013; Goetz et al., 2006). After confirming normality and homogeneity of variances, differences between FRP percentile classes were assessed using ANOVA with a post hoc Tukey's honest significant difference test (α = 0.05). Recovery time for the fire affected pixels was also assessed and was defined as the time necessary for post-fire total mean NPP to equal or surpass mean pre-fire NPP at the same location.

## 3 Results

### 3.1 Fire intensity differences between forest types

Fires in forests dominated by fire-susceptible species were more intense, in terms of FRP metrics and FRE, than those dominated by a mix of species or fire-resistant species (Figure Fig. 2). This finding is consistent with other observations in these, and similar, forest types where lower biomass, open-canopy forests dominated by fire-resistant species tend to support lower intensity fires, and higher biomass, closed-canopy forests dominated by fire-susceptible species tend to support higher intensity fires (Shinneman and Baker 1997; Morgan et al., 2001; Schoennagel et al., 2004; Rogers et al., 2015). Average peak FRP values were 212.5 ± 292.3 MW $km^{-2}$ in forests dominated by fire-susceptible species, 150.8 ± 117.4 MW $km^{-2}$ in mixed forests and 100.2 ± 77.5 MW $km^{-2}$ in forests dominated by fire-resistant species (Figure 2a). Similarly, average 90$^{th}$ percentile FRP was 159.7 ± 90.8 MW $km^{-2}$ in forests dominated by fire-susceptible species, 109.4 ± 78.6 MW $km^{-2}$ in mixed forests and 75.7 ± 53.6 MW $km^{-2}$ in forests dominated by fire-resistant species (Figure 2a). Mean FRP values ranged from 83.5 ± 43.8 MW $km^{-2}$ in forests dominated by fire-susceptible species, 58.9 ± 45.9 MW $km^{-2}$ in mixed forests and 43.5 ± 29.7 MW $km^{-2}$ in forests dominated by fire-resistant species (Figure 2a). Average FRE followed the same trend as FRP (Figure 2b). FRE was greater in forests dominated by fire-susceptible species (4,158.3 ± 2,630.4 MJ $km^{-2}$) than those dominated by a mix (2,685.2 ± 1,660.5 MJ $km^{-2}$) or fire-resistant species (2,095.2 ± 1,389.5 MJ $km^{-2}$).

### 3.2 Higher fire intensity results in lower post-fire NPP

FFor fires that occurred in forests dominated by a mix of species or fire-resistant species, higher FRP or FRE magnitude led toresulted in lower post-fire NPP (Figure 3, columns 1-2). This dose-response relationship was most apparent strongest (more significant differences between the relative NPP across FRP and FRE percentile classes) one one-year post-fire, where mean relative NPP decreased with increasing FRE FRP(Figure 3, row 1) and FRP FRE (Figure Fig. 3, rows 2-4). In forests dominated by fire-resistant species, there was a stronger dose-response pattern for relative NPP grouped by FRE percentile class rather than FRP percentile class (Figure 3, column 1). For forests dominated by fire-resistant species and mixed forests, the dose-response pattern was the samevery similar regardless of whether relative NPP was grouped by FRE or FRP percentile classes (Fig. 4, S1). The observed dose-response relationship for these forest types persisted for up to >8 years post-fire, especially in forests dominated by mixed species (Figure Fig. 34a,b, column 2). The dose-response relationship was much weaker in In forests dominated by fire-susceptible species (Figure Fig. 34a,b, column 3). T there were few differences between percentile classes with only the highest FRE percentile class displaying lower relative NPP compared with the other percentile classes (Fig. 4b).

Maximum relative NPP loss occurred at one--year post-fire for all fires and differed by species composition. Generally, mixed stands consisting of fire-susceptible and fire-resistant species had the largest relative post-fire NPP losses with an average loss of 40.7% (-216.7 g C $m^{-2}$ $yr^{-1}$), followed by stands that were dominated by fire-susceptible species with an average loss of 33.9% (-154.8 g C $m^{-2}$ $yr^{-1}$). Stands dominated by fire resistant species had the smallest average loss of 23.3% (-126.8 g C $m^{-2}$ $yr^{-1}$).

### 3.3 Recovery and trajectories of post-fire NPP

Post-fire observations ranged from 4-12 years post-fire (average 8.4 years) for the fifteen fires, however, only the lowest FRP class of one fire (2006 South Fork Fire) had recovered to pre-fire NPP levels at the end of the observational period (~9 years post-fire). Generally,While some fires displayed linear recovery trajectories were linear for all fire resistance groups, except for a few firesmost exhibited non-linear trajectories where NPP increased until ~2011 and then began decreasing again or levelling off around 2011 (Supplemental Figures Fig.S1 S2-S4).

## 4 Discussion

### 4.1 Higher fire intensity results in lower post-fire NPP

To date, research has largely analysed post-fire forest productivity with fire as a binary predictor variable (presence-absence). In the current study, we applied a dose-response methodology that has been demonstrated at the tree-scale (Smith et al., 2016, 2017, Sparks et al., 2016, 2017) to large fires using landscape remote sensing datasets. A dose-response relationship between FRP or FRE and NPP was shown in forests dominated by fire-resistant species and mixed species (Figures Fig. 3, and 4, columns 1-2). Forests that were dominated by fire-susceptible species were not as sensitive to FRP or FRE, indicating that NPP in these forests may be reduced to similar levels regardless of fire intensity (Figure Fig. 3 and 4, column 3). Additionally, forests dominated by fire resistant species had lower post-fire relative NPP losses compared to those dominated by fire-susceptible species or a mix (Figure Fig. 43). These data are congruent with evidence at the tree scale where trees that do not develop fire resistant traits, such as thick bark, have a higher probability of fire-induced damage and mortality (Midgley et al., 2011; Ryan and Reinhardt, 1988; VanderWeide and Hartnett, 2011). NPP loss at two years post-fire (~19-152 g C $m^{-2}$ $yr^{-1}$) in forests dominated by fire-resistant species is comparable to two-year post-fire aboveground NPP differences between unburned and burned temperate *Pinus ponderosa* forest stands (~83-148 g C $m^{-2}$ $yr^{-1}$), estimated using field measurements (Irvine et al., 2007).

There was considerable variability in the dose-response relationships within each fire resistance grouping, which could potentially be attributed to differences in stand structure and age as well as differing proportions of burned and unburned area within each NPP pixel (mixed pixels). Previous studies have indicated that smaller trees are more susceptible to fire-induced mortality than larger trees (Hood et al., 2007). Additionally, there is evidence that similar FRP doses can lead to widely different growth responses depending on tree age (Smith et al., 2017; Sparks et al., 2017). For example, 2.5-year-old *Pinus contorta* and *Larix occidentalis* saplings exposed to highly controlled laboratory surface fires (peak FRP ranged from 4.1-12.9 kW $m^{-2}$) had radial growth at 1-year post-fire that was -2.5% to -20% of unburned saplings (Smith et al., 2017). In contrast, a similar range of peak FRP (0.2-16.3 kW $m^{-2}$) was observed in prescribed fires in 34-year-old *Pinus ponderosa* stands, but resulted in tree radial growth that was -10% to -45% of unburned tree radial growth at 1.5 years post-fire (Sparks et al., 2017). The forests analysed in this study likely had highly heterogeneous stand structures and ages within each 1 km MODIS pixel, which could lead to highly heterogenous fire behaviour and vegetation response within a pixel. While previous studies mainly assessed surface fire impacts on trees, it is likely that areas within each of the fires in this study had complete overstory removal via crown fire. Variability in fire behaviour can also lead to unburned islands within each fire perimeter. Previous studies have quantified unburned proportions within MTBS perimeters ranging from ~10-25% of within perimeter area (Kolden et al., 2015; Meddens et al., 2016), which could lead to more mixed pixels (pixels containing burned and unburned forest). These sub-pixel differences could lead to widely different patterns of mortality and recovery and mask any pixel-scale dose-response relationship.

~~T~~he observed dose-response relationship was ~~also~~ likely affected by the number of MODIS FRP observations per pixel. ~~The mean number of FRP observations per pixel decreased from fires with a clear dose-response relationship (4.8 ± 0.6 obs. pixel$^{-1}$) to those with a weak relationship (2.9 ± 0.1 obs. pixel$^{-1}$).~~ Spatiotemporal aggregations of observations have been shown to substantially reduce uncertainties in sums of FRP (Freeborn et al., 2014). Due to the pixel level variability in ages and species composition in these forests, only temporal FRP aggregations were employed in this paper. There were many pixels with few (1-2) MODIS FRP observations and large NPP losses (Fig. 3). This pattern could be attributed to greater FRP uncertainty resulting from the long temporal intervals between consecutive satellite overpasses and consequently, a poorer overall characterization of the fire behavior for a particular pixel (Giglio, 2007; Freeborn et al., 2014). This factor could also account for the slight differences observed between FRP metrics and FRE, as the long intervals between consecutive satellite overpasses have a high probability of missing increased fire activity associated with peak ~~and 90$^{th}$ percentile~~ FRP (Giglio, 2007).

**4.2 Recovery and trajectories of post-fire NPP**

Despite an average post-fire observational period of 8.4 years across all fires, only the lowest FRP or FRE percentile class of one fire (2006 South Fork Fire) had recovered to pre-fire NPP levels ~9 years post-fire. Other studies that have used remote sensing observations reported recovery time ranging from 5 years (Goetz et al., 2006) to 9 years (Hicke et al., 2003) in boreal forests. Likewise, chronosequence studies in boreal forest have estimated recovery to be ~10 years (Amiro et al., 2010). The results from this study are consistent with observations showing large differences in productivity between burned and unburned forest stands at time periods greater than 10 years post-fire (Dore et al., 2008). The convergence of some of the NPP trajectories could be attributed to rapid recovery and colonization of fire affected areas by understory species (Goetz et al., 2006). The forests in the current study occur in areas where rapid post-fire colonization by shrub and herbaceous species is common (Jorgensen and Jenkins, 2011), which could make NPP appear to recover more rapidly in areas where the forest overstory has been removed (Bright et al., 2013). Additionally, it is clear that variability in climate can significantly alter vegetation establishment and growth post-fire. Drier post-fire conditions can significantly reduce tree regeneration (Stevens-Rumann et al., 2017) and potentially lead to conversion to non-forest (Millar and Stephenson 2015). Higher temperatures can also reduce tree growth and recovery, while increased precipitation can lead to greater growth (Bond-Lamberty et al., 2014). In this study, the incorporation of unburned pixels in the relative NPP calculation allowed for this methodology to control for climate variability and help isolate impacts resulting from the initial fire intensity.

**4.3 Conceptual framework for assessing spatiotemporal post-fire effects**

A growing number of studies have observed mechanistic links between fire intensity (or proxies of fire intensity such as crown scorch) and post-fire mortality and productivity in saplings (Sparks et al. 2016; Smith et al. 2017) and mature trees (Ryan and Reinhardt, 1988; Hood et al. 2007; Sparks et al. 2017). The results presented in this work, building upon tree-scale studies, provide a framework that linkssuggest that such linkages fire intensity to post-fire changes in individual tree and forest growth/productivityscale to the landscape scale. However, it is clear that more ground measurements will be needed to confirm this hypothetical framework (Figure Fig. 45). In this conceptual system, several post-fire recovery pathways exist for trees/forests depending on the initial fire intensity. We hypothesize that higher intensity fires cause trees to incur more damage, which can lead to rapid mortality if trees have insufficient resources to repair physiological function in the weeks and months following a fire. The highest fire intensities lead to the greatest losses in physiological function and net primary productivity in surviving trees (Smith et al., 2017; Sparks et al., 2017) as well as the highest probability of delayed mortality in the years after a fire (Sparks et al., 2016). Several studies have observed heat-induced cavitation in xylem conduits of cut plant segments (Michaletz et al., 2012; West et al., 2016), leading to the hypothesis that reduced xylem conductivity is a dominant mechanism behind fire-caused mortality (Kavanagh et al., 2010; van Mantgem et al., 2013). Moderate levels of fire intensity cause enough damage to decrease growth/productivity and alter a tree's vulnerability to secondary mortality agents (e.g. insects, disease and drought). Vulnerability may be lessened if permanent defensive structures, such as resin ducts in *Pinus* species used for expelling bark beetles, are induced by the fire (Hood et al., 2015; Sparks et al., 2017). On the contrary, fire may make trees more susceptible to secondary mortality agents if the photosynthetic machinery of trees is sufficiently impaired (Davis et al., 2012). Trees experiencing low intensity fires will likely have reduced growth, but a higher probability of surviving than trees subjected to higher fire intensities. For any post-fire pathway, trees in better physiological condition or those exposed to fewer environmental stressors will likely experience a lower impact to post-fire growth and a lower probability of mortality.

### 4.4 Limitations

The dose-response relationship we observed between FRP or FRE and post-fire NPP does not necessarily mean this methodology can now be directly applied to the characterization of landscape-scale C dynamics; several limitations ~~are obvious~~need to be considered. First, this study analysed fires that occurred in forests with little-to-no management disturbance. Applying this methodology to managed forests may produce significantly different results as land management disturbances (e.g. timber harvest, urban development) may alter the dose-response relationship between FRP and NPP. Second, in forests with canopy cover less than 100%, or where fire has completely removed the overstory, MODIS observes reflectance from overstory and understory forest vegetation. Understory vegetation that recovers rapidly could alter the magnitude of post-fire NPP reduction and make it appear that the overstory recovers more (or less) quickly. Finally, due to the fact that MODIS FRP observations per pixel were generally low ~~for fires in this region~~ (mean = 3.9 observations pixel$^{-1}$), caution should be used when interpreting results and comparing to other ground and remote sensing based measurements.

## 5 Conclusions

Through the use of remotely sensed fire radiative power and net primary productivity, we demonstrate that increasing ~~doses of~~ FRP and FRE ~~lead to~~results in decreasing post-fire net primary productivity in coniferous forests, especially those dominated by fire-resistant tree species. This dose-response relationship appears to have a legacy effect on C dynamics, in some cases lasting ~~for greater than~~beyond a decade post-fire. Species composition also influenced the magnitude of post-fire NPP loss, highlighting the importance of the relative fire resistance of forest species in accounting for post-fire C dynamics. While this dose-response relationship is promising, our results indicate that a low number of FRP observations diminish the detectability of this relationship. Despite post-fire observations ranging up to 12 years, most of the forests had not recovered to pre-fire productivity levels, which agrees with field observations showing large differences in productivity between burned and unburned temperate forests up to a decade post-fire (Dore et al., 2008). ~~Ultimately, t~~This study extends prior tree-scale dose-response studies and presents a conceptual framework for using fire radiative metrics to quantify~~ing~~ long-term post-fire effects, such as reduction and recovery of NPP, at the landscape spatial scale. Ultimately, this study could serve as a basis for new questions surrounding variability in post-fire recovery within forested ecosystems at large spatial scales.


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**Table 1.** Summary of the fifteen fires analysed in this study.

| Fire Name | Size (ha) | Dominant Conifer Species[a] | Ignition Date | Proportion of MTBS polygon burned (1984 - ignition date) (%) | Proportion of MTBS polygon with MODIS FRP observations (%) |
|---|---|---|---|---|---|
| Ahorn | 18,778 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO, Larix occidentalisLAOC, Picea engelmanniiPIEN, Abies lasiocarpaABLA, Pinus albicaulisPIAL* | June 28, 2007 | 0 | 86.2 |
| Arnica | 4,556 | *Pinus contortaPICO* | September 23, 2009 | 0 | 76.9 |
| Bridge | 15,116 | *Picea engelmanniiPIEN, Abies lasiocarpaABLA* | July 18, 2007 | 8.9 | 91.0 |
| Columbine | 7,115 | *Picea engelmanniiPIEN, Abies lasiocarpaABLA, Pinus albicaulisPIAL* | August 9, 2007 | 1.6 | 91.2 |
| East | 7,145 | *Picea engelmanniiPIEN, Abies lasiocarpaABLA, Pinus albicaulisPIAL, Pinus contortaPICO* | August 8, 2003 | 0.6 | 93.6 |
| Fawn Peak | 31,870 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO, Larix occidentalisLAOC, Picea engelmanniiPIEN, Abies lasiocarpaABLA, Pinus albicaulisPIAL* | June 30, 2003 | 0.3 | 91.8 |
| Fool Creek | 22,186 | *Picea engelmanniiPIEN, Abies lasiocarpaABLA, Pinus albicaulisPIAL* | June 28, 2007 | 2.0 | 89.9 |
| Little Salmon | 13,598 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO, Larix occidentalisLAOC, Picea engelmanniiPIEN, Abies lasiocarpaABLA* | July 18, 2003 | 0.1 | 78.2 |
| Meriwether | 7,762 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO, Larix occidentalisLAOC* | July 21, 2007 | 0.2 | 98.1 |
| North Fork | 6,774 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO* | August 1, 2009 | 1.1 | 92.1 |
| Saddle | 12,706 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO, Larix occidentalisLAOC, Picea engelmanniiPIEN, Abies lasiocarpaABLA* | August 18, 2011 | 0.2 | 80.1 |
| Sawmill | 6,015 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO, Larix occidentalisLAOC* | July 13, 2007 | 3.0 | 95.5 |
| Shower Bath | 19,911 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO* | July 17, 2007 | 1.1 | 78.0 |
| South Fork | 11,494 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO* | August 7, 2006 | 1.2 | 82.3 |
| Tatoosh | 20,185 | *Pseudotsuga menziesiiPSME, Pinus ponderosaPIPO, Larix occidentalisLAOC, Picea engelmanniiPIEN, Abies lasiocarpaABLA, Pinus albicaulisPIAL* | August 22, 2006 | 2.3 | 92.4 |

[a]Conifer species codes: ABLA – *Abies lasiocarpa*, LAOC – *Larix occidentalis*, PIAL – *Pinus albicaulis*, PICO – *Pinus contorta*, PIEN – *Picea engelmannii*, PIPO – *Pinus ponderosa*, PSME – *Pseudotsuga menziesii*.

**Figure 2.** Location of study fires overlaid on current distribution of U.S. forest types classified using relative fire resistance information in the literature and the LANDFIRE Existing Vegetation Type (EVT) 30-m product.

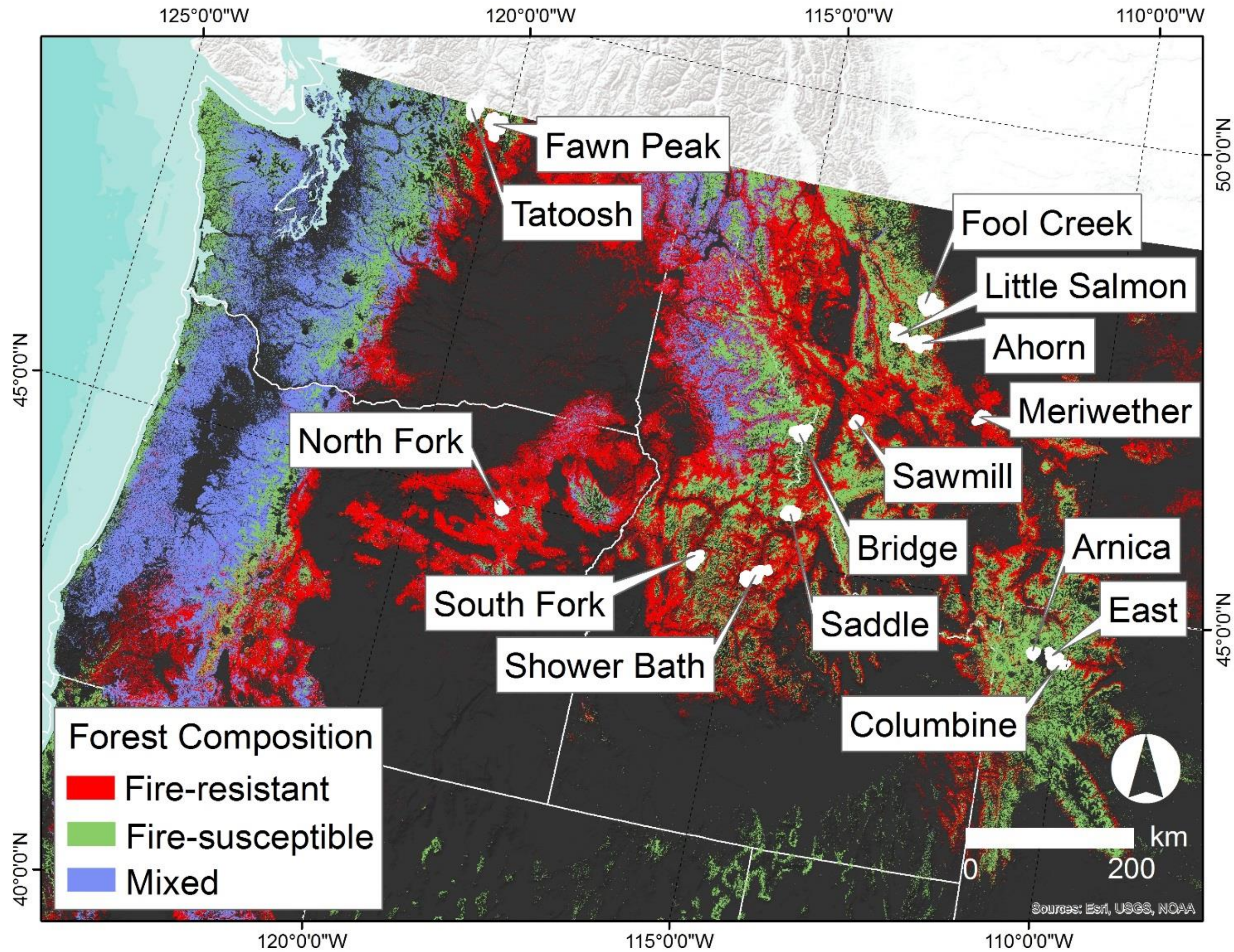

**Figure 2.** Fire radiative power (a) and fire radiative energy (b) distributional statistics grouped by dominant forest composition (fire-resistant to fire-susceptible). Black arrows indicate mean values.

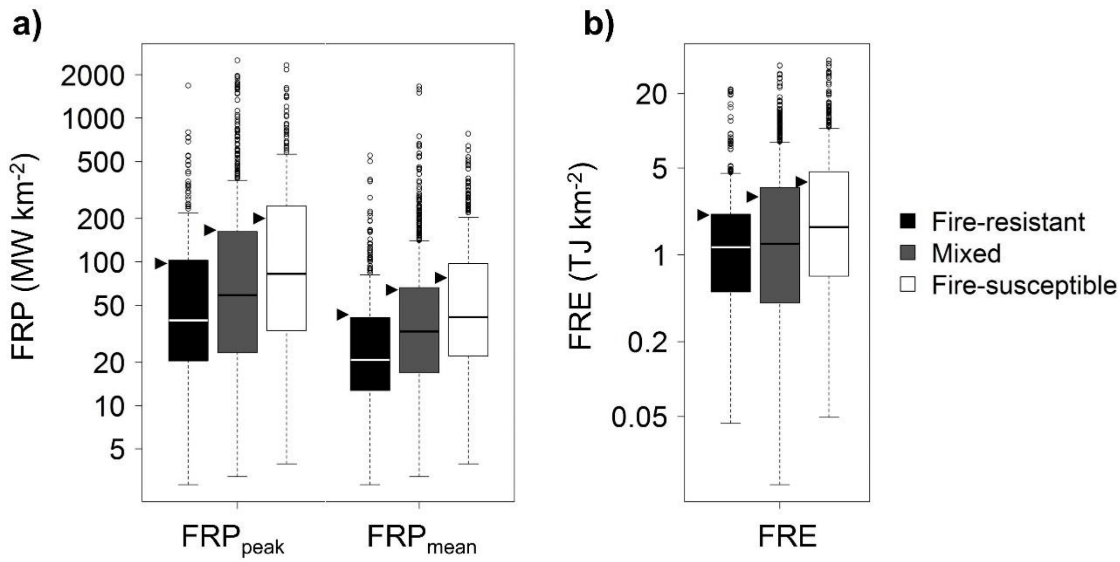

**Figure 3.** Fire intensity impacts on one-year post-fire NPP observed in forests dominated by species varying from fire-resistant to fire susceptible (first column – third column). Distributional statistics are shown for NPP grouped by: a) peak FRP percentile class and b) FRE percentile class.

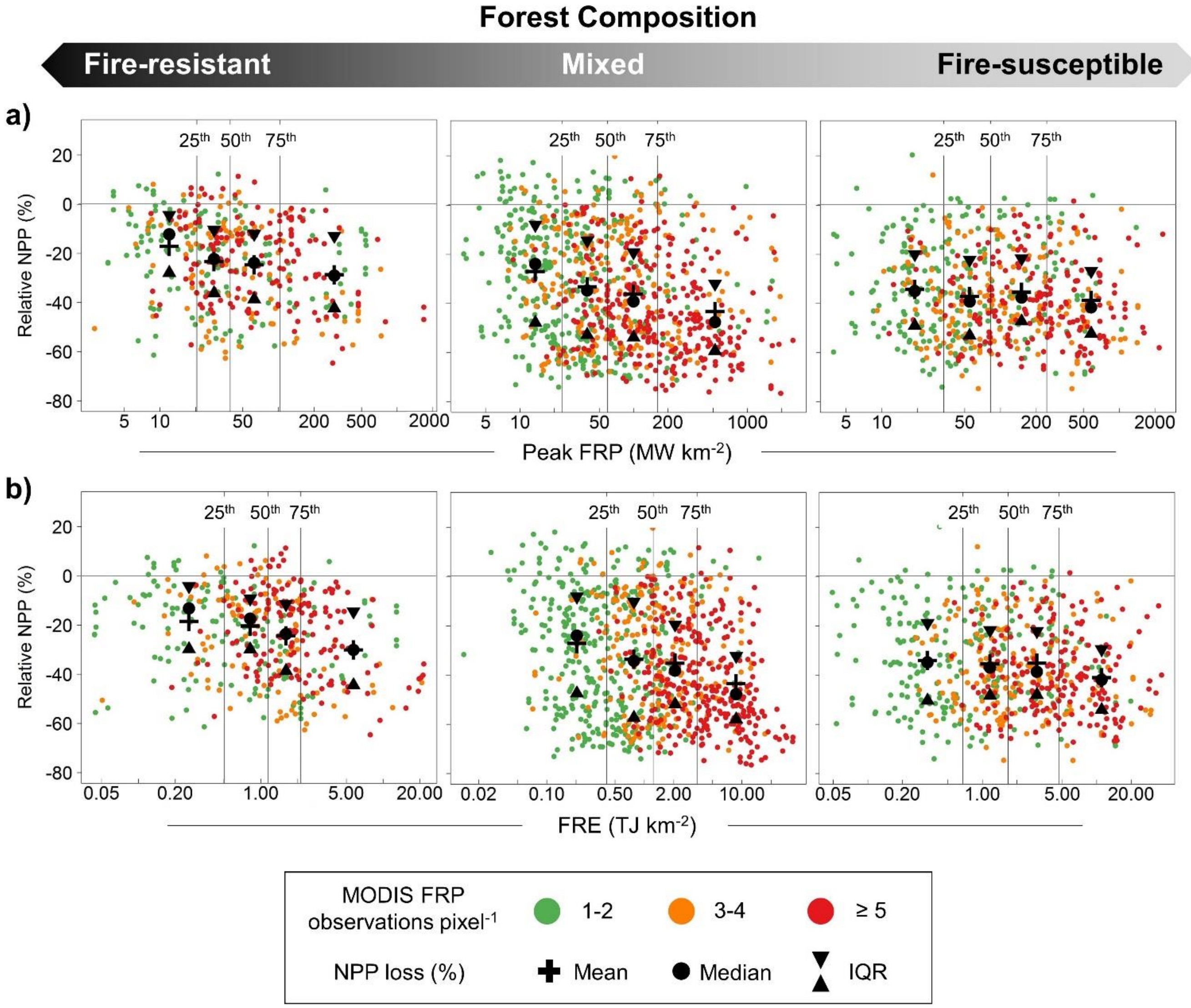

**Figure 4.** Fire intensity impacts on net primary productivity. ~~FRP and~~ a) FRE dose impacts on absolute NPP (g C $m^{-2}$ $yr^{-1}$) and relative NPP (%) ~~response~~ observed in forests dominated by species varying from fire-resistant to fire-susceptible (first column – third column). ~~Mean relative~~ NPP is grouped by ~~FRP and~~ FRE percentile classes and shading represents 95% confidence intervals in all panes. Grey dotted line marks fire year. b) Results from ANOVA with a post hoc Tukey's honest significant difference test (α = 0.05). Black bars indicate years where relative NPP groups differed.

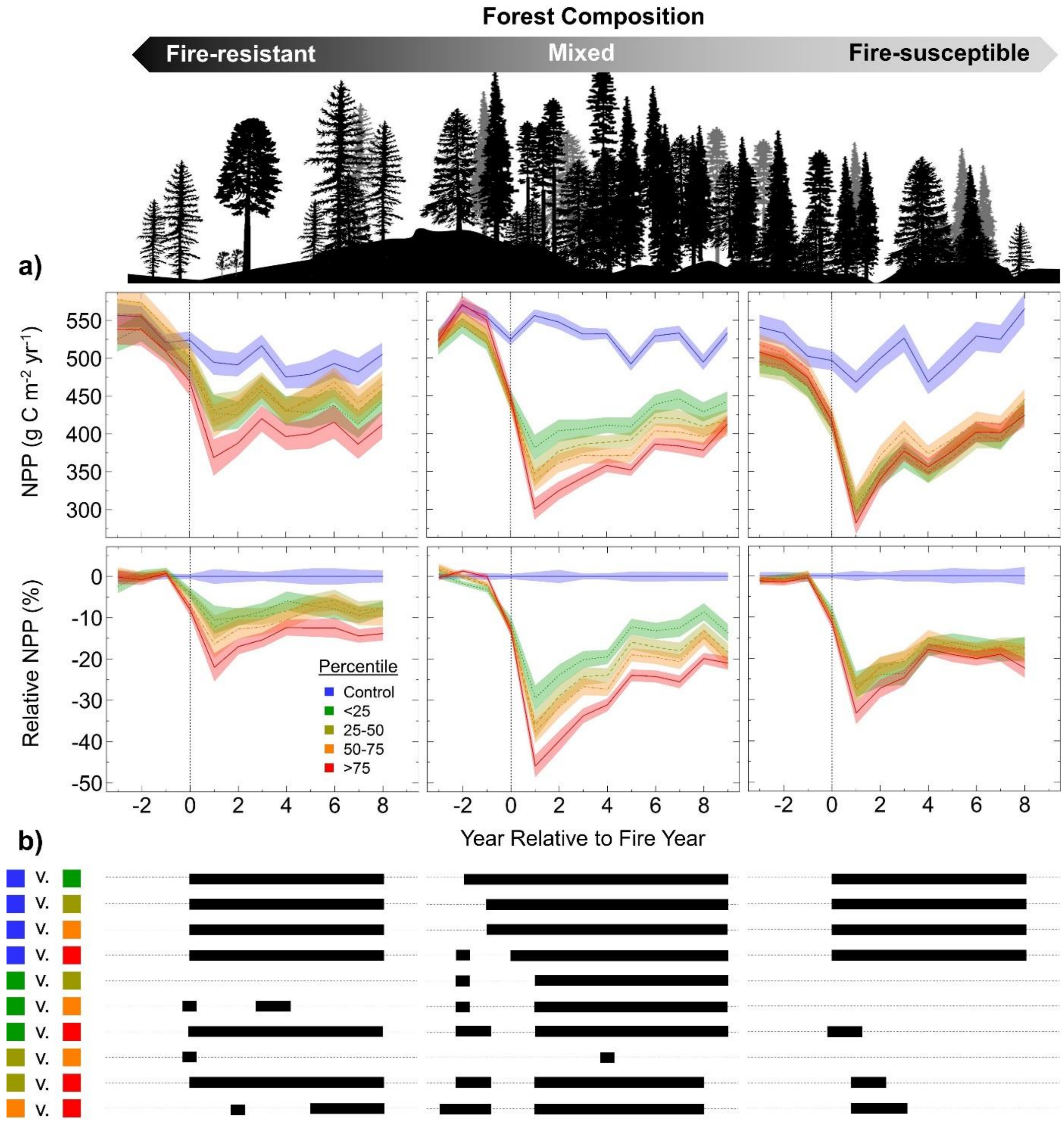

**Figure 5.** Conceptual framework for quantifying impacts of fire intensity on physiology, growth, and vulnerability of coniferous forests.