EFFECTS OF COMPLEX SPATIAL PATTERNS ON BARK BEETLE-CAUSED TREE MORTALITY IN NORTHERN ARIZONA

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ABSTRACT

EFFECTS OF COMPLEX SPATIAL PATTERNS ON BARK BEETLE-CAUSED TREE MORTALITY IN NORTHERN ARIZONA

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Bark beetles are native forest insects that cause low levels of tree mortality at endemic population levels and have the potential to cause widespread mortality when populations increase. High stand densities increase competition between trees, increasing tree stress and susceptibility to mortality from bark beetles. Recent silvicultural treatments in northern Arizona create complex spatial patterns, leading to variable individual tree competition within treated stands. However, the effect of variable individual tree competition on mortality from bark beetles is understudied. We examined the effects of tree competition on bark beetle-caused tree mortality in paired treated and untreated stands using randomly located stand-scale plots and paired individual tree-scale plots. Biotic and abiotic data were collected. We asked the following questions: 1. Is there less inter-tree competition around a bark beetle-killed tree compared with a similarly sized live tree? 2. Is there less competition around a bark beetle-killed tree compared with the overall stand-scale competition? 3. Is tree size influencing bark beetle-caused tree mortality? 4. Is site productivity an influencing factor in tree competition and overall bark beetle-caused tree mortality? We calculated differences between treated and untreated stands, individual tree-scale plots, and individual tree- and stand-scale means then analyzed the data using weighted t-tests, and paired and unpaired t-tests. Although few significant differences were found between the paired individual tree-scale plots, between individual tree-scale and stand-scale competition (inferred from stand density index, basal area, and trees per acre), or between treated and untreated stands, there was a notable amount of variation (assessed from the coefficient of variation) in the data and differences within individual stands, which may indicate that reducing stand density does not always reduce susceptibility to bark beetle-caused tree mortality in northern Arizona. Furthermore, they could influence the perception of the relationship between bark beetles and tree competition because our results deviate from historical trends (high densities = susceptibility to bark beetles). This study highlights the importance and need for monitoring, even of well-studied disturbances.

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PREFACE

This thesis is presented in the form of two independent, unsubmitted manuscripts.

Chapter Two (General Manuscript)

Chapter Three (Formatted Manuscript for iForest – Biogeosciences and Forestry)

There may be redundancies featured amongst the chapters, due to the closely related nature of the studies included in this thesis. The term “we” is used frequently among chapters. Tables and figures are embedded within or at the end of each chapter. Citations are listed at the end of each chapter.

CHAPTER ONE

INTRODUCTION

Bark beetles (*Dendroctonus*, *Dryocoetes*, *Ips*, and *Scolytus*) are native insects that outbreak in forests and can cause low levels of tree mortality at endemic population levels with the potential for widespread mortality during outbreaks (Bentz et al. 2009). They live, feed, and reproduce in a tree's inner tissue, the phloem (Christiansen et al. 1987, Bentz et al. 2009). The phloem transports water, nutrients, and sugars throughout the tree allows water and when bark beetles impede on this layer of the tree, the result can be fatal (Bentz et al. 2009). Bark beetle outbreaks have been recorded for decades and are a natural driver of change in ecosystems; they help thin stands, redistribute nutrients and growing space, and release trees from competition (Romme et al. 1986, Christiansen et al. 1987, Bentz et al. 2009, Vega & Hofstetter 2015). Recent outbreaks are larger and more severe than ever recorded (Christiansen et al. 1987, Bentz et al. 2009). This increased severity is likely due to current forest conditions, climate change, drought, and/or the interactions between these factors (Bentz et al. 2009).

Current forest conditions over much of the Western US are a result of Euro-American settlement (Churchill 2020). They are overstocked and dense and have altered disturbance regimes (Churchill 2020). High densities increase stand susceptibility to bark beetle-caused tree mortality because tree defenses are weakened while competing for water and nutrients with other trees (Fettig et al. 2007, Negrón et al. 2009, Kolb et al. 2019). Warming temperatures from climate change allow bark beetle populations to thrive because their reproduction, metabolism, and survival are temperature dependent (Bentz et al. 2009, Vega & Hofstetter 2015). Cold winter temperatures (i.e. below 5°F) are a primary cause of bark beetle mortality but, when temperatures increase, so do their reproduction and metabolism rates (Bentz et al. 2009; Vega &

Hofstetter 2015). Therefore, when high densities of susceptible host type are coupled with climate change and drought, it creates a compounding stress effect that decreases the likelihood of tree survival and increases stand susceptibility to bark beetles (Franklin et al. 1987, Bentz et al. 2009, Vega & Hofstetter 2015, Kolb et al. 2019).

To reduce susceptibility, silvicultural treatments are implemented that often have goals of increasing resilience and resistance (DeRose & Long 2014, Long et al. 2018). Ecological resilience has been defined as an ecosystem's ability to endure change or disturbance and maintain their structure and function (Holling 1973). Ecological resistance is a separate but related concept and has been defined as an ecosystem's ability to remain unchanged when disturbances occur (DeRose & Long 2014), or as short-term resilience (Bryant et al. 2009). Resilience and resistance are suggested to be used together and can be assessed and contextualized for ecosystem disturbances (Bryant et al. 2009). Silvicultural treatments with objectives of enhancing resilience and resistance are being implemented throughout the western US to combat disturbances and create more resilient landscapes in the face of climate change. An example of this is in northern Arizona where treatments in the last decade have been implemented to emulate pre-Euro-American settlement forest conditions (Reynolds et al. 2013). The treatments result in a complex spatial arrangement where there are varying levels of tree sizes and densities (Reynolds et al. 2013). Previous research in Northern Arizona has examined bark beetles and drought, stand-level density, and tree vigor, but there is a lack of research in how bark beetles interact with these complex spatial patterns (but see Zausen et al. 2005, Kane & Kolb 2010, 2014, Ferrenberg et al. 2022, Hood et al. 2022). It is crucial to understand this relationship given the impacts of climate change on bark beetles and stand density on tree susceptibility.

The purpose of this thesis is to analyze how bark beetles interact with complex spatial patterns and factors leading to bark beetle-caused tree mortality at the individual tree and stand scales. The second chapter is a literature review of relevant information pertaining to the overarching research topic. Chapter three describes a research study undertaken to address the questions: 1. Is there less inter-tree competition around a bark beetle-killed tree compared with a similarly sized live tree? 2. Is there less competition around a bark beetle-killed tree compared with the overall stand-scale competition? 3. Is tree size influencing bark beetle-caused tree mortality? 4. Is site productivity an influencing factor in tree competition and overall bark beetle-caused tree mortality? The fourth chapter discusses the management implications from our results.

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CHAPTER 2

BARK BEETLES & SILVICULTURE IN THE SOUTHWESTERN UNITED STATES: A REVIEW

INTRODUCTION

Current forest conditions over much of the Western US are the result of fire exclusion and suppression, grazing, and logging following Euro-American settlement (Churchill 2020). Forests are overstocked and dense, and have altered disturbance regimes, which impacts forest health, resilience, and resistance (Churchill 2020). Fire, native insects, and drought are disturbances that pose a large threat to forests (Bryant et al. 2019). They have been historically recorded and at many levels of severity are part of natural succession processes, but in the last several decades they have increased in frequency, size, and severity (Bentz et al. 2010, Overpeck et al. 2012, Reynolds et al. 2013, Churchill 2020). The US Southwest experiences all of these disturbances but the most impactful biotic disturbance agents are bark beetles (*Dendroctonus*, *Dryocoetes*, *Ips*, and *Scolytus*) (Bentz et al. 2009). There are hundreds of bark beetle species in North America but less than one percent are aggressive, meaning they can kill the tree they attack (Gaylord 2014). In dense, overstocked forests that experience drought and uncharacteristic fire, bark beetle damage and mortality can cause detrimental stand- to landscape-scale impacts (Bentz et al. 2009, Vega & Hofstetter 2015). Management and silvicultural treatments often reduce mortality and restrict damage by lowering tree density and increasing tree vigor, therefore promoting stand resilience and resistance (defined below) (Fettig et al. 2007, Bryant et al. 2019). Understanding how bark beetles interact with silvicultural treatments is critical at multiple scales because of the threat they pose in conjunction with climate change (Bentz et al. 2009). This review will encompass an overview of the concepts of forest resilience and resistance, impacts by bark beetles, and forest conditions and silviculture in US southwestern ponderosa pine (*Pinus ponderosa* var. *scopulorum*) forests.

FOREST RESISTANCE AND RESILIENCE

In recent decades, resilience and resistance are concepts that have been adopted into forest management (Long et al. 2018), and each has several definitions. Holling (1973) defined ecological resilience as a system's ability to endure long-term disturbance and still maintain the same structure and function as before. Millar et al. (2007) defined resistance as the ability to forestall impacts and protect highly valued resources, and resilience as the ability for an ecosystem to return to desired conditions after disturbance. Peterson et al. (2011) defines resistance and resilience in terms of strategies. Resistance strategy encompasses actions that enhance the ability of species, ecosystems, or environments to resist forces of climate change and maintain values and ecosystem services in their present or desired conditions. Resilience strategy enhances the capacity of ecosystems to absorb changes without irreversible effects in processes and functionality. DeRose & Long (2014) break resistance and resilience into stand- and landscape-scales; stand-level resistance and resilience include one event and how structure and composition are impacted based on disturbance severity. The landscape definitions examine multiple disturbance events, how they spread, and the subsequent impacts on forest structure and composition (DeRose & Long 2014). Although there are minor differences between these definitions, generally speaking, resilience describes an ecosystem's ability to withstand disturbance and maintain relatively unchanged structure and function, while resistance is shorter-term and looks at stand characteristics that limit the severity of a disturbance (Bryant et al. 2019).

The two terms work together, but in practice should be separated (Holling 1973, DeRose & Long 2014).

In the US Southwest, fire, insects, and drought are the primary forest disturbances (Bryant et al. 2019). Historically, these disturbances have resulted in self-regulation that allowed for nutrient cycling, productivity, and regeneration (Cooper 1960, Covington & Moore 1994a), but due to fire exclusion and suppression, grazing, and logging, fire regimes and stand structure have been altered (Fulé 1997, Reynolds et al. 2013) and resilience has decreased (Bryant et al. 2019). To increase resilience, managers apply silvicultural treatments; stands that have not experienced treatments or disturbance tend to be less resilient compared with those that have (Bryant et al. 2019).

Forest stands are less resilient and more susceptible to bark beetle-caused mortality when tree densities are high, species diversity is low, and trees are of a specific size (Fettig et al. 2007, Negrón et al. 2009, DeRose & Long 2014, Bryant et al. 2019). Negrón et al. (2009) showed that stands with lower basal area were more resilient to bark beetles, smaller trees (under 10cm in diameter) were less likely to be attacked, and larger trees (greater than 25cm) had an increased likelihood of survival, likely because they have stronger defense systems and increased vigor. Furthermore, DeRose & Long (2014) suggest reducing suitable bark beetle habitat by promoting stands with a high proportion of nonhost species and a low relative density to decrease susceptibility and increase tree vigor. Similarly, Fettig et al. (2007) states that high stand density is correlated with bark beetle outbreaks and calls for a reduction in tree competition and density, and increased stand heterogeneity to increase tree vigor and stand resilience and resistance. To promote stands and landscapes that are both resistant and resilient and reduce susceptibility to damage and disturbance, Long et al. (2018) call for appropriate management to take place before a disturbance occurs. Effective management will increase resilience not only to bark beetles and other disturbances, but also to climate change (DeRose & Long 2014, Nagel et al. 2017).

PONDEROSA PINE FOREST ECOSYSTESM OF THE US SOUTHWEST

Prior to the settlement of Euro-Americans, the forests in the western US were variable in structure, density, spatial arrangement, and ecological function (Table 2.1) (Churchill 2020). Numerous studies have reconstructed southwestern ponderosa pine forest conditions and found they were less dense, had natural openings filled with grasses, and experienced frequent, low-intensity fires (Table 1) (Cooper 1960, Covington & Moore 1994a, Covington & Moore 1994b Swetnam & Baisan 1996, Fulé 1997, Reynolds et al. 2013). As described by Woolsey (1911), the forests were "pure park-like stand(s) made up of scattered groups, 2-20 trees, usually connected by scattering individuals." The forests have lost their historical structure because of heavy livestock grazing, logging, and fire exclusion and suppression (Cooper 1960, Covington & Moore 1994a, Covington & Moore 1994b Covington et al. 1997, Churchill 2020). Fire exclusion and suppression have played a particularly significant role because they led to increased stand density, which in-turn affects fire hazards, disturbance regimes, and ecosystem structure and function (Covington & Moore 1994a, Covington & Moore 1994b Fulé 1997).

Table 2.1. Historical fire frequency ranges and spatial patterns in the US Southwest. PIPO: ponderosa pine; the reference condition year is the year that the data were recorded prior to significant industrial human disturbance N/A: variable not included in study. Adapted from Reynolds et al. (2013).

Citation	Forest Type	Reference conditions year	Mean stand trees per acre	Fire frequency (years)	Trees per group	Group size (acres)	Group density (groups/acre)
Abella & Denton (2009)	PIPO	1880	23.7	N/A	2-25	N/A	1-33
Covington et al. (1997)	PIPO	1867	22.8	N/A	N/A	N/A	N/A
Reynolds et al. (2013)	N/A	N/A	N/A	2-26	N/A	N/A	N/A
Sánchez Meador et al. (2011)	PIPO	1874	79.5	N/A	3-24	0.03-0.37	5-11
White (1985)	PIPO	1875	15.0	N/A	3-44	0.05-0.72	N/A

Ecology of Ponderosa Pine

Ponderosa pine (*Pinus ponderosa*) is a major, widely distributed forest type in western North America (Long et al. 1995, Moir et al. 1997). The tree species is a long-lived (4-500 years), overstory species that inhabits elevations from sea level to 10,000 feet (Oliver & Ryker 1990), occurring as the only or primary species at lower elevations or within a mixed conifer forest at higher elevations (Moir et al. 1997). The forest type is found in dry climates where there tends to be a seasonal water-free period, which has adapted them to drought (Moir et al. 1997). Evidence shows they are fire-frequent (Table 2.1) (Swetnam & Baisan 1996, Fulé 1997), regulating composition, succession, and forest structure (Covington et al. 1997, Moir et al 1997). Because of this, they have thick, corky bark that insulates the cambium from killing temperatures (Moir et al. 1997).

Successful ponderosa pine regeneration is typically associated with moist springs and summers and fire-free periods that allow for germination (Pearson 1923, Moir et al 1997). Other factors influencing regeneration in these forests are elevation, vegetative cover, soil parent material and soil type (Puhlick et al. 2012, Reynolds et al. 2013). In areas where the soil parent material is not basalt, regeneration is more abundant and less condition-dependent (Puhlick et al. 2012). In areas where soil parent material is basalt, regeneration requires rare, specific conditions of precipitation and temperature (Maguire 1956, White 1985, Puhlick et al. 2012), and therefore it tends to be episodic (Savage et al. 1996). Regeneration is most successful when there are above-average monthly temperatures in April and May; this results in ponderosa pine trees flowering in abundance, which is followed by a large cone crop the next year (Maguire 1956, Moir et al. 1997). In the subsequent two years, frequent and regular rainfall increases germination rates, which can be as high as 30 to 40 seedlings per square foot (Maguire 1956). These conditions tend be a "climatic accident" rather than a normal weather pattern (Maguire 1956). An example of this type of regeneration event is the cohort from 1919 in areas surrounding Flagstaff, Arizona (White 1985). In 1918, there was a large seed crop, followed by favorable moisture conditions in 1919, and increased germination during July and August (Pearson 1923). In addition to the favorable weather conditions, heavy grazing and lack of fire resulted in reduced competition from grasses, which further allowed seedlings to establish (Madany & West 1983). The current untreated second growth ponderosa pine forests are a result of the 1919 cohort; there are dense thickets of pole-sized trees (White 1985) and the "park-like" structure (Woolsey 1911) no longer exists (Covington & Moore 1994a, Covington & Moore 1994b). These forests conditions are susceptible to high-severity fire (Swetnam & Baisan 1996, Fulé 1997) and insect outbreaks because of the high densities and fuel continuity (Covington & Moore 1994b, Reynolds et al. 2013).

BARK BEETLES

Bark beetles (*Dendroctonus*, *Dryocoetes*, *Ips*, and *Scolytus*) are native insects that have been associated with forests since at least the Holocene era (Bentz et al. 2009). There are thousands of bark beetle species, but less than one percent of species are aggressive, meaning they can kill an attacked tree (Stark 1982, Gaylord 2014). Aggressive bark beetle species are typically in the genera *Dendroctonus*, *Dryocoetes*, *Ips*, and *Scolytus*. Aggressive bark beetles have symbiont relationships with mites, nematodes, fungi, and bacteria (Mercado et al. 2014). The most studied are three fungi, blue stain fungi (filamentous Ascomycete), yeasts (unicellular Ascomycetes), and filamentous Basidiomycetes (Mercado et al. 2014). They are transported on the mycangial structure of a beetle and have negative health impacts on the host tree, contributing to their death (Mercado et al. 2014). Bark beetles are natural change agents in forests that help thin, redistribute nutrients and growing space, and release trees from competition (Romme et al. 1986, Bentz et al. 2009, Vega & Hofstetter 2015). They live, feed on, and lay their eggs in the phloem layer of a tree (Bentz et al. 2009). They attack both healthy and stressed trees and build galleries while releasing pheromones to attract other conspecific bark beetles resulting in a 'mass attack,' decreasing the likelihood of tree survival (Raffa et al. 2008, Bentz et al. 2009). Population sizes can be epidemic or endemic. Epidemic population levels span across a landscape, are large in size, can cause catastrophic levels of tree mortality, and successfully attack both healthy and stressed trees (Stark 1982, Coulson & Witter 1984, Christiansen et al. 1987, Howe et al. 2022). Endemic populations are smaller in size, localized in area, can cause low levels of tree mortality, and successfully attack previously stressed trees (Stark 1982, Coulson & Witter 1984, Christiansen et al. 1987, Howe et al. 2022). Typically, populations are endemic (Bentz et al. 2009). The shift from endemic to epidemic population levels depends on host and resource availability, host defenses, bark beetle behavior and development, presence of predators, symbionts, and other microorganisms, and stand structure and landscape features (Ryan et al. 2015). Outbreaks tend be linked to abundance of suitable and susceptible hosts, drought, and warm winters (Bentz et al. 2009), however they can begin or continue in the absence of these conditions (Ryan et al. 2015).

How bark beetles select host trees varies by species, but all use some combination of visual, olfactory, tactile, and gustatory signals, and external cues (Borg & Norris 1969, Wood 1972, Raffa & Berryman 1982, Pureswaran et al. 2006). Host tree selection is mostly dictated by visual and chemical cues (Saint-Germain et al. 2007). Chemical cues, such as monoterpenes, depend on the type of bark beetle. Secondary bark beetles (bark beetles that do not initially attack trees, instead attracted by pheromones) pick up on compounds that indicate stress, such as ethanol or acetaldehyde (Deal 2010, Raffa et al. 2015). Primary bark beetles (adult bark beetles that locate and initially attack host trees) rely less on monoterpenes and more on visual cues (Deal 2010, Wood 1972). After landing, they use their tactile senses, as well as continued use of olfactory senses for monoterpenes (Wallin & Raffa 2000). Specific monoterpenes elicit tunneling behavior or deter bark beetles from entering (Wallin & Raffa 2000). When populations shift from endemic to epidemic, bark beetles tend to select larger, healthier trees because as population densities increase, the ability to overcome tree defenses increases (Ryan et al. 2015). This is because of improved food quality and quantity (thicker phloem) in larger trees (Ryan et al. 2015).

Because phloem is essential to tree survival, after the bark beetle enters, the host tree begins to defend itself using constitutive and induced resin defenses (Raffa & Berryman 1983). Resin is released from ducts and glands to create a physical barrier and has the potential to completely engulf a bark beetle (Raffa et al. 2008). Tree vigor is the capacity to endure and resist stress and can be measured by quantifying leaf area, growth rates, basal area, and surrounding tree density (Waring & Pitman 1980, Larson et al. 1983, Kolb et al. 1998). Trees with high vigor have faster growth rates, low surrounding competition, and ample resources (Larson et al. 1983, Kolb et al. 1998). Trees with low vigor typically have slower growth rates, and are in high competition for a limited resource or enduring other stresses (Larson et al 1983, Kolb et al. 1998). A vigorous, healthy tree can successfully use its defenses to force bark beetles out and survive an attack (Raffa & Berryman 1983). In contrast, when tree vigor is low and/or bark beetle populations are epidemic, bark beetles can overcome the defenses and kill the tree (Raffa et al. 2015). To facilitate this, they release aggregation pheromones that signal to other bark beetles (of the same species) to attack the tree (Raffa et al. 2008). Pheromones produced by bark beetles are made up of chemicals from the tree (Raffa et al. 2015). Once bark beetles have reached intraspecific competition within the tree and/or depleted resources from the host, they release anti-aggregation pheromones to deter other bark beetles from attacking because of the reduced availability of resources (Raffa et al. 2015). At this time, tree mortality is likely to occur (Raffa et al. 2015).

Although its effect can vary among species, temperature impacts bark beetles by affecting development and reproduction rates, and susceptibility to cold-induced mortality (Stark 1982, Raffa et al. 2008, Vega & Hofstetter 2015). In general, because cold temperatures can negatively impact the bark beetle life cycle, warming temperatures are likely to contribute to the increased severity of outbreaks because they foster higher survival of overwintering (Bentz et al. 2009, Waring et al. 2009, Vega & Hofstetter 2015), and literature supports that bark beetles and climate are strongly correlated (Pyne et al. 1996, Bentz & Mullins 1999, Shaw et al. 2005, Raffa et al. 2008, Bentz et al. 2010, Hicke et al. 2016). Longer and more damaging outbreaks are occurring regionally, and some species have extended their range and are infesting new tree species (Raffa et al. 2008, Bentz et al. 2009). Furthermore, bark beetles are interacting with the landscape in new ways (Hood et al. 2022). The latter study monitored the long-term effects of radial thinning treatments, and found that despite the removal of vegetation around the focal tree, bark beetles were responsible for 79% of tree death. This varies from what is commonly shown; historically, higher densities are correlated with bark beetle-caused tree mortality (Negrón & Popp 2004, Fettig et al. 2007, Negrón et al. 2008a, Negrón et al. 2009, Hicke et al. 2016).

Over the last ten years in the US Southwest, bark beetle-caused tree mortality has been variable, but bark beetle populations have persisted on the landscape and were the most prevalent aerially-mapped mortality agent in 2020 (USDA Forest Service 2021). The major bark beetle species in this region are in the *Dendroctonus* and *Ips* genera (Table 2.2) (Gaylord 2014).

Table 2.2. List of aggressive bark beetles most commonly found in ponderosa pine in Arizona from Gaylord 2014.

Genus species	Common name
Dendroctonus adjunctus	Roundheaded pine beetle
Dendroctonus approximatus	Larger Mexican pine beetle
Dendroctonus brevicomis	Western pine beetle
Dendroctonus frontalis	Southern pine beetle
Dendroctonus ponderosae	Mountain pine beetle
Dendroctonus valens	Red turpentine pine beetle
Ips calligraphus	Six spined ips
Ips knausi	N/A
Ips lecontei	Arizona five spined ips
Ips pini	Pine engraver

Species of *Dendroctonus* are primary bark beetles that attack healthy, vigorous trees (Gaylord 2014). Many species have a one-year life cycle; females lay eggs in August or September, and eggs hatch into larvae September through June. In the larval stage, they go through four instars (development stages) and then develop into pupae from June to July. From July to August, they form into brood adults, and a parent adult in early August (Figure 2.1) (Amman & Cole 1983). It is when they become mature adults they emerge from the original host tree and fly to a new one, typically chosen by females (Amman & Cole 1983). Pheromones are then generated (by bark beetles) to attract other conspecific bark beetles which can eventually result in a mass attack; once the tree is at carrying capacity, an anti-aggregation pheromone is then released to discourage further population increases (Amman & Cole 1983).

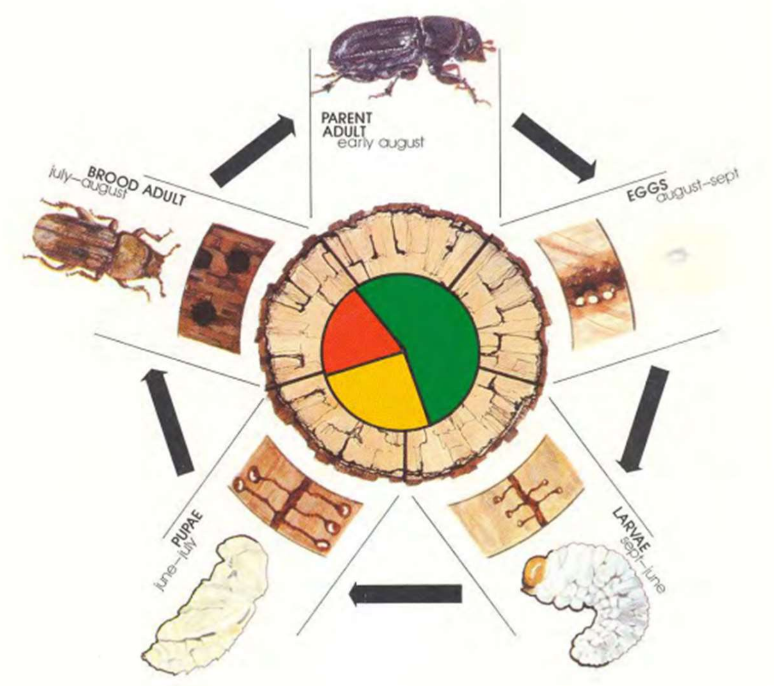

Figure 2.1. Typical life cycle of bark beetles in the Dendroctonus genera, specific example is mountain pine beetle (Dendroctonus ponderosae). There is typically one generation per year, however there can be more than one with increases in temperature. From Amman & Cole (1983).

Species in the *Ips* genus are typically secondary bark beetles which typically only attack weakened or stressed trees, but can attack healthy trees at epidemic population levels (Gaylord 2014, Stark 1982). Generally, *Ips* have two generations per year (Livingston 2004). They over winter in the adult stage within infested trees or duff in the forest floor, become active in late April or early May and infest fresh slash or weakened trees (Figure 2.2) (Livingston 2004). The male bark beetle initially enters the tree and constructs a "nuptial chamber" then begins releasing pheromones to attract females (Livingston 2004). After mating, the females begin tunneling, building a gallery that is mostly free of debris (unlike species within the *Dendroctonus* genera) and laying eggs. Brood adults develop in 40-55 days (Livingston 2004).

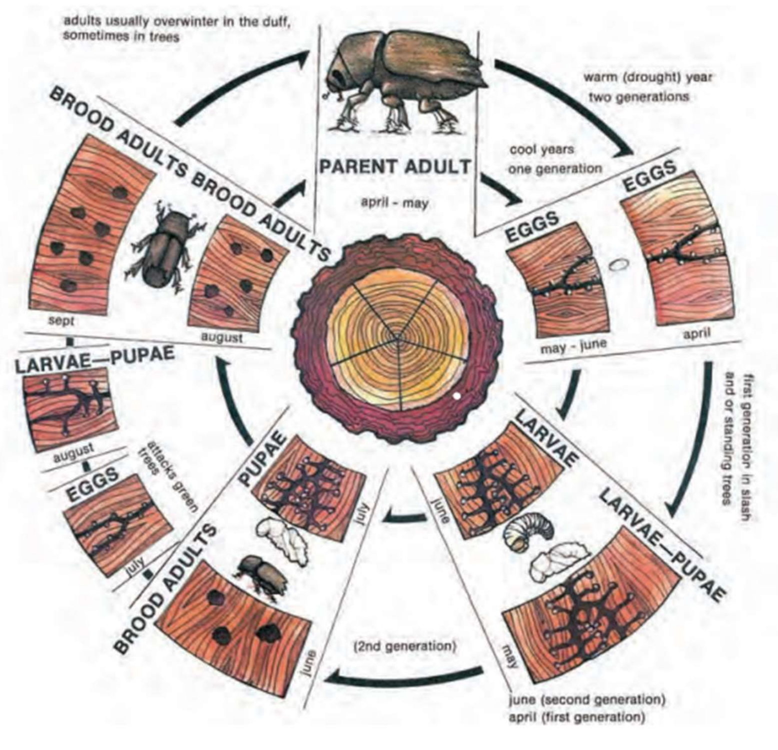

Figure 2.2. Typical life cycle of bark beetles in the Ips genera, specific example is pine engraver beetle (Ips pini). There are typically two generations per year, however there can be more than two with increases in temperature. From Livingston (2004).

For both species in the *Ips* and *Dendroctonus* genera, elevation also has an impact on reproduction and bark beetle-caused tree mortality. At lower elevations, temperatures are higher and at higher elevations, temperatures are lower; because bark beetles are temperature dependent, lower elevations have been associated with increased bark beetle-caused tree mortality (Amman et al. 1973, Hansen 1996, Fettig et al. 2005, Williams et al. 2008, Negrón et al. 2009). In the US Southwest, bark beetle outbreaks are commonly correlated with drought (Hicke et al. 2016, Kolb et al. 2019, USDA 2021), increased basal area, and high density and stocking levels, (Negrón & Popp 2004, Fettig et al. 2007, Negrón et al. 2008a, Negrón et al. 2009, Hicke et al. 2016). Drought predisposes trees to bark beetle-induced mortality because it limits the availability of resin defenses, resulting in lower tree vigor (Kolb et al. 2019).

Bark beetle outbreaks impact the ecosystem services forests provide, such as clean water, recreation, aesthetics, wildlife habitat, and economic value (Vega & Hofstetter 2015), and with increasing outbreaks, public awareness is high (Negrón et al. 2008b). When considering management interventions to mitigate the effects of bark beetle outbreaks, there is not one clear solution (Bentz et al. 2009), but because bark beetles are interacting with trees in new ways (Hood et al. 2022) and tree mortality is increasing with climate change (Raffa et al. 2008, Bentz et al. 2010, Vega & Hofstetter 2015, Hicke et al. 2016), management decisions should consider the probability of bark beetle outbreaks and be thoughtfully planned out (Long et al. 2018).

CURRENT FOREST MANAGEMENT IN US SOUTHWEST PONDEROSA PINE FOREST

Given the current forest conditions (see previous section) and the threat climate change poses, forest managers aim to restore southwestern ponderosa pine forests to pre-settlement conditions (Covington & Moore 1994b, Covington et al. 1997, Allen et al. 2002, Reynolds et al. 2013). Management objectives may also include increasing resilience and resistance, and reducing catastrophic disturbance and tree mortality (Allen et al. 2002, Larson & Churchill 2012, Reynolds et al. 2013). These objectives are achieved by considering fine-, mid-, and landscape-scales and using a combination of silvicultural techniques and prescribed fire (Figure 2.1) (Reynolds et al. 2013, DeRose & Long 2014). Fine-scale areas are under 10 acres, and consists of groups of trees, single trees, and grass-forb-shrub interspaces (Figure 2.1) (Reynolds et al. 2013). Mid-scale areas are aggregates of the fine-scale, and range from 10 – 1,000 acres; they are relatively homogenous in vegetation composition and structure (Figure 2.1) (Reynolds et al. 2013). Landscape-scale ranges from 1,000 – 10,000+ acres in size and are aggregates of mid-scale; they have variable elevations, slopes, aspects, soil types, plant associations, disturbance processes, and land use (Figure 2.1) (Reynolds et al. 2013).

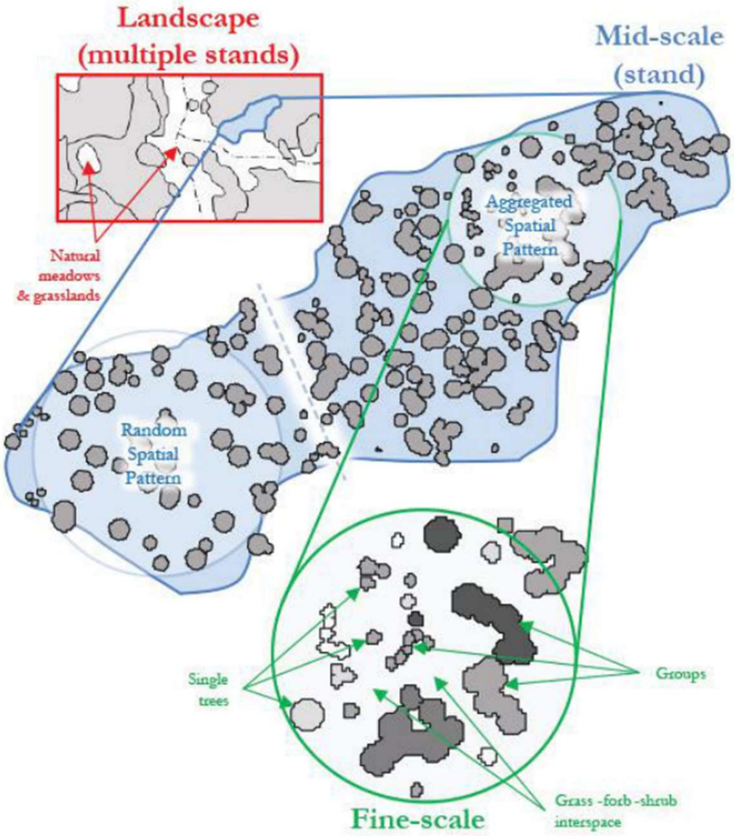

Figure 2.3. Vegetation patterns at three different spatial scales, fine, mid, and landscape from Reynolds et al. (2013).

To accomplish restoration and resilience and resistance objectives, silvicultural treatments are based on reference conditions (Table 2.1) (Kaufmann et al. 1994) and implemented using techniques such as density reduction, prescribed fire, or a combination of both (Covington et al. 1997, Allen et al. 2002, Reynolds et al. 2013). When implementation is successful, there is a decrease in tree density, a shift towards an uneven-aged stand structure, and a complex spatial arrangement (Cooper 1961, Covington et al. 1997, Reynolds et al. 2013). The complex spatial arrangement includes groupings, interspaces, and stand-alone, large, typically old growth trees (Figure 2.1) and the three elements are integrated throughout a stand (Covington & Moore 1994b, Reynolds et al. 2013). The groupings include varying levels of tree densities and the interspaces are openings with typically no trees (Figure 2.1) (Woolsey 1911, Covington

& Moore 1994b, Reynolds et al. 2013). The stand alone, old growth trees link together interspaces and groupings, but typically are not within groups (Figure 2.1) (Allen et al. 2002, Reynolds et al. 2013). Preserving the old growth trees is an especially important aspect to these treatments because they are rare, irreplaceable, contribute to the multi-aged stand structure and canopy cover, provide critical wildlife habitat, and impact understory vegetation (Allen et al. 2002). This heterogenous structure accomplishes the goals of restoration, increasing resilience and resistance, and reducing widespread disturbance and tree mortality because fuel continuity is reduced, tree vigor and growth rates increase, water and nutrients are less limiting, and there is less competition (Larson & Churchill 2012, Reynolds et al. 2013, DeRose & Long 2014, Erickson & Waring 2014).

Spatial Patterns, Competition, & Bark Beetles

The complex spatial arrangement resulting from the described silvicultural treatments results in varying levels of tree competition. Begon et al. (1986) defines competition as "the interaction between individuals brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survival, growth and/or reproduction of the individual concerned." Competition is a well-documented agent of tree mortality in forests (Franklin et al. 1987, Peet & Christensen 1987, Biging & Dobbertin 1992, Das et al. 2014, Knapp et al. 2021) and it can be quantified at the individual tree- or stand-scale. Stand-scale competition encompasses all the trees in a stand and is typically inferred from stand density (e.g. basal area, trees per acre, or relative density metric), whereas individual-tree competition only looks at a single tree and the immediate competing vegetation surrounding it (Franklin et al. 1987). Competition, in conjunction with tree size, micro-environment, genetics (Burkhart & Tome 2012), drought, and disturbance (Young et al. 2017), further impacts a tree's ability to grow and survive. For example, as previously stated, bark beetle outbreaks tend to cause higher levels of tree mortality in denser stands (Negrón & Popp 2004, Negrón et al. 2008a, Bentz et al. 2009, Das et al. 2014). Competition is correlated with density and therefore bark beetles and competition can act together to increase the likelihood of mortality because of increased stress to the tree (Franklin et al. 1987).

Reductions in stand density inherently impact bark beetle-caused tree mortality. Literature strongly supports this (Sartwell 1971, Feeney et al. 1998, Negrón & Popp 2004, Fettig et al. 2007, Gaylord et al. 2010, Hood et al. 2016, Negrón et al. 2017), since density reduction improves tree vigor, growth, and particularly in pines, the effectiveness of resin defenses (Larsson et al. 1983, Christiansen et al. 1987, Feeney et al. 1998, Kolb et al. 1998, Kane & Kolb 2010, Hood et al. 2016). Therefore, through these silvicultural treatments, resistance and resilience increases and trees are less likely to die from bark beetles (Bryant et al 2009, DeRose & Long 2014, Hood et al. 2016).

Climate Change in the US Southwest

The climate in the Southwestern US is actively changing due to anthropogenic climate change (Overpeck et al. 2012). Average temperatures are increasing, droughts are becoming unusually severe, snowmelt is arriving earlier, and average stream flows are decreasing (Overpeck et al. 2012). Future projections indicate with high confidence that observed changes will continue; surface temperatures will increase, summer heatwaves will become hotter and longer, droughts will be more intense, severe, and frequent, and late winter/spring snowpack will be reduced (Overpeck et al. 2012). These conditions will enhance the size, severity, and frequency of disturbances such as insect attacks, disease, and most notably wildfire (Fulé 2008, Bentz et al. 2009).

These projected changes underline the critical importance of effective management (Reynolds et al. 2013). Reynolds et al. (2013) states that if we do not restore the landscape and manage for resilience and resistance, there is risk of catastrophic loss. Nagel et al. (2017) similarly states the importance of managing for resilience and that when appropriate, adaptive silvicultural strategies where scientists and managers work together to find solutions should be used. Post-treatment monitoring should be done to continue to ensure objectives and goals are being met (Covington et al. 1997, Allen et al. 2002, Reynolds et al. 2013).

CONCLUSION

Bark beetle outbreaks will continue to be a threat to forests throughout the western United States, especially as the climate in the Southwest continues to get warmer and drier (Seager et al. 2007, Bentz et al. 2009, Bentz et al. 2010). Because of this, it is essential to have a clear understanding of the factors that lead to successful bark beetle outbreaks and bark beetle-caused tree mortality. To date, research has primarily focused on the effects of competition and density management at the stand-scale (Sartwell 1971, Feeney et al. 1998, Negrón & Popp 2004, Fettig et al. 2007, Gaylord et al. 2010, Hood et al. 2016, Negrón et al. 2017), but to our knowledge, individual tree competition is rarely addressed (but see Zausen et al. 2005, Kane & Kolb 2010, 2014, Ferrenberg et al. 2022 Hood et al. 2022). In the Southwestern US, understanding the effects of individual-tree competition on susceptibility to bark beetles is important because of the complex spatial patterns needed to replicate pre-settlement forest conditions. This literature review outlines the existing research and the study hereafter will address whether individual tree competition is a factor in predicting tree mortality from bark beetles, if competition varies between the individual tree- and stand-scales, and how these comparisons vary in treated and untreated forest stands. Beyond the assessment of tree competition, this study will further expand the existing literature on bark beetles, forest resilience, and effects of silvicultural treatments.

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CHAPTER THREE

EFFECTS OF COMPLEX SPATIAL PATTERNS ON BARK BEETLE-CAUSED TREE MORTALITY IN NORTHERN ARIZONA

INTRODUCTION

Bark beetles (*Dendroctonus*, *Dryocoetes*, *Ips*, and *Scolytus*) are native forest insects that cause low levels of tree mortality at endemic population levels with the potential for widespread mortality during outbreaks (Bentz et al. 2009). They live, feed, and reproduce in a tree's inner tissue, the phloem (Christiansen et al. 1987, Bentz et al. 2009). The phloem is the conducting tissue that transports water, sugar, and nutrients throughout the tree to. When bark beetles impede on this layer, in conjunction with symbiotic fungi, the results can be fatal (Bentz et al. 2009, Mercado et al. 2014). How bark beetles select host trees varies by species, but all use some combination of visual, olfactory, tactile, and gustatory signals, and external cues, and random landings (Borg & Norris 1969, Wood 1972, Raffa & Berryman 1982, Pureswaran et al. 2006). Host tree selection is primarily dictated by visual and olfactory (chemical) signals (Saint-Germain et al. 2007). When populations shift from endemic to epidemic, bark beetles tend to select larger, healthier trees because as population densities increase, the ability to overcome tree defenses increases (Ryan et al. 2015). Additionally, because larger trees have thicker phloem, bark beetles have more food which further allows for populations to increase (Ryan et al 2015). Bark beetle outbreaks have been recorded for centuries and are a natural driver of change in ecosystems, but recent outbreaks have been larger and more severe (i.e. increase in tree mortality) in both size and duration (Christiansen et al. 1987, Bentz et al. 2009). Increased severity is likely due to current forest conditions, climate change, drought, and/or the interactions between these factors (Shaw et al. 2005, Bentz et al. 2010).

Current forest conditions over much of the Western US are a result of forest management practices following Euro-American settlement, which have resulted in overstocked and dense forests with altered disturbance regimes (Churchill 2020). High densities increase stand susceptibility to bark beetle-caused tree mortality because tree defenses are weakened while competing for water and nutrients with other trees (Fettig et al. 2007, Negrón et al. 2009, Kolb et al. 2019). Warming temperatures from climate change allow bark beetle populations to thrive because their reproduction, metabolism, and survival are temperature dependent (Bentz et al. 2010, Vega & Hofstetter 2015). When high tree densities of susceptible host type are coupled with climate change and drought, there is a compounding stress effect that significantly decreases tree survival and increases stand susceptibility to bark beetles (Franklin et al. 1987, Bentz et al. 2010, Vega & Hofstetter 2015, Kolb et al. 2019).

Silvicultural treatments with objectives of increasing resilience and resistance are being implemented throughout the Western US to mitigate against the effects of undesirable catastrophic mortality levels and create a more resilient landscape in the face of climate change (DeRose & Long 2014); such treatments may reduce susceptibility to bark beetle-caused tree mortality (Bentz et al. 2009, Bentz et al. 2010, Vega & Hofstetter 2015). Ecological resilience has been defined as an ecosystem's ability to endure change or disturbance and maintain their structure and function (Holling 1973). Ecological resistance is a related but separate concept, and has been defined as an ecosystem's ability to remain unchanged when disturbances occur (DeRose & Long 2014), or as short-term resilience (Bryant et al. 2009). Resilience and resistance are suggested to be used together and can be assessed and contextualized for ecosystem disturbances (Bryant et al. 2009). In northern Arizona, beginning in the late 1990s, treatments have been implemented to emulate pre-Euro-American settlement forest conditions

(Kaufmann et al. 1994, Waltz et al. 2003, Roccaforte et al. 2009, Reynolds et al. 2013). When implementation is successful, there is a decrease in tree density, a shift towards an uneven-aged and sized stand structure, and a complex spatial arrangement of trees with groups, interspaces, and stand-alone, large trees (Cooper 1961, Covington et al. 1997, Reynolds et al. 2013). The groups include varying levels of tree densities and the interspaces are openings, typically with no trees (Woolsey 1911, Covington & Moore 1994, Reynolds et al. 2013). The stand-alone, old growth trees link together interspaces and groups, but usually are not within groups (Allen et al. 2002, Reynolds et al. 2013). Preserving the old growth trees is an especially important aspect to these treatments because they are rare, irreplaceable, contribute to the multi-age stand structure and canopy cover, and provide critical wildlife habitat (Allen et al. 2002, Kolb et al. 2007). This heterogenous structure accomplishes the objectives of restoration, resilience, and resistance (Stoddard et al. 2021). Furthermore, at the stand-scale, it reduces widespread disturbance and tree mortality because fuel continuity tree competition is reduced, which also leads to increased tree vigor and growth rates, and less limited water and nutrients (Larson & Churchill 2012, Reynolds et al. 2013, Erickson & Waring 2014, DeRose & Long 2014).

Although there is less competition in treated stands, the individual tree-scale competition varies due to the complex spatial patterns. Competition in the groups tends to be higher than the individual trees left in openings or interspaces. How bark beetles interact with individual trees within complex spatial patterns is understudied (but see Zausen et al. 2005, Kane & Kolb 2010, 2014, Ferrenberg et al. 2022, Hood et al. 2022). In this study, our objective was to examine individual tree- and stand-scale characteristics that may be favorable to bark beetle success. To do this, we paired individual trees, and treated and untreated stands, and asked the following questions: 1. Is there less inter-tree competition (stand density index, basal area, trees per acre) around a bark beetle-killed tree compared with a similarly-sized live tree? 2. Is there less competition around a bark beetle-killed tree compared with the overall stand-scale competition? 3. Is tree size influencing bark beetle-caused tree mortality? 4. Is site productivity an influencing factor in tree competition and overall bark beetle-caused tree mortality? The results from this study will allow a better understanding of how bark beetles affect individual trees and stands, and further inform managers on how treatments impact bark beetle-caused tree mortality.

MATERIALS & METHODS

Study area and stand selection

We sampled ponderosa pine stands in northern Arizona on the Coconino and Kaibab National Forests (NF) (Figure 3.1). Stand selection and sampling were completed during the summer of 2021. Criteria for stand selection are described below. Species composition was dominated by ponderosa pine (*Pinus ponderosa*) (>80%) with minor components of Gambel oak (*Quercus gambelii*), alligator juniper (*Juniperus deppeana*), one-seed juniper (*J. monosperma*), and Rocky Mountain juniper (*J. scopulorum*). Stand elevations ranged from 6,800 to 7,950 feet (Table 3.1) and slopes ranged from 1-5% (data not shown). No aspect was reported because mean slopes were less than 10% and therefore there were no dominant aspects (Perry et al. 2009). On the Coconino NF, the average annual precipitation is 19.8 inches and the average annual temperature is 47.1°F (NOAA 2022). On the Kaibab NF, the average annual precipitation is 21.2 inches and the average annual temperature is 52.9°F (NOAA 2022). Soils on the Coconino NF are primarily in the order of mollisols (USDA Forest Service 2018) and on the Kaibab NF, soils are primarily in the order alfisols (Brewer et al. 1991).

Stand selection

Ten paired stands, comprised of one treated and one untreated, were selected for sampling (Figure 3.1). Selection was completed by using maps showing recent (last 15 years) treatment areas and local USDA Forest Service expertise. Criteria included 1. No evidence of severe, stand-scale damage or mortality from fire, 2. 25-100 acres in size, and 3. Exposed to bark beetle populations in the last 10 years. Additionally, paired stands were within one mile of each other where possible (Figure 3.1). Treatment types varied, but all were intended to increase stand-scale heterogeneity (Table 3.1, A1). Untreated stands had no treatment listed in the previous 15 years. In each stand, we installed two different plot networks (Figure A1). Stand-scale plots were randomly located in each stand to measure stand structure, density, and abiotic characteristics (Figure A1). Individual tree-scale plots were implemented to measure individual tree competition by pairing a bark beetle-killed tree and a similarly sized live tree (Figure A2). Bark beetles were not identified at species level in either plot network because wood borers and termites quickly enter the tree after it dies which damages species-specific galleries. Additionally, northern Arizona hosts ten different bark beetle species, further making identification complex because attacks on the tree could be by one or more species (but at different times) (Gaylord 2014). Data collection for each plot network is described below.

Field data collection & lab processing

Stand-scale measurements

We randomly installed seven circular fixed-radius (r = 52.7ft) plots (Figure A1) in each stand (n = 20). At the plot center, slope, elevation, landform (valley bottom, ridge, side hill, flat) and GPS coordinates were recorded. We recorded the following data for every tree greater than one-inch diameter at breast height (DBH, measured 4.5 feet above ground) in each plot: species, DBH, and status (live, killed by bark beetles, strip attack, or dead from another cause). Other data, such as strata, crown class, regeneration and increment cores, were collected for use in a larger study and are not described here.

Site index trees were identified to estimate site productivity (Minor 1964) and an average of eight trees per stand were selected. Site index trees were dominant or codominant trees that were younger than 140 years old, straight, free of mechanical defects (including fire scars), insects and disease, and had experienced little suppression (Minor 1964). On each site index tree, we measured DBH (inches) and total height (feet), and collected two increment cores (90° apart) at breast height. After extraction, the cores were stored for later processing.

Individual tree-scale measurements

A paired plot network was established to measure individual tree-scale competition. Pairs were comprised of one tree recently killed by bark beetles and a live tree (Figure A2). 'Recently killed' was defined as being killed within the past one- to three-years and trees were identified by standing, fading coloration of needles attached to branches, presence of bark beetle emergence holes, and pitch tubes on the bole. The paired live tree was of similar size (within 10% of the diameter of the bark beetle-killed tree), located randomly, and more than 65 feet but less than 165 feet from the dead tree (to avoid overlap of competition-related measurements while ensuring they were growing under similar conditions for comparison) (Figure A2). There were up to five dead-live pairs in each stand and each selected tree was the plot center of a fixed-radius (r = 37.2ft) circular plot. On each plot center tree, we recorded DBH, species, and status (live or killed by bark beetles) and collected increment cores for use in the larger study. For every tree greater than one inch DBH in the plot, we recorded the following data: DBH, species, and status (live, killed by bark beetles, strip attack, or dead from another cause).

Data analyses

Stand-scale data

We calculated stand-scale means using the stand-scale plot data to infer competition and compare them with the individual tree-scale means. We calculated stand-scale means in treated and untreated stands for elevation, site index (described below), and three competition proxies: basal area per acre (BA) ($ft^2\ ac^{-1}$), trees per acre (TPA), and summation stand density index (∑SDI) (Tables 1 and 2). Basal area is the cross-sectional area of a tree at breast height and is closely related to tree volume. SDI is an index that expresses relative stand density in terms of the number of trees and average DBH (Reinke 1933). The maximum SDI value for ponderosa pine is 450 (Schubert 1974, Long and Shaw 2005). The index was created for even-aged stands with normal distributions of diameter classes and is inappropriate for other stands that don't follow a normal distribution. Our stands had variable size structures with diameter distributions that deviated from normal, and therefore, we calculated ∑SDI (Stage 1968, Long & Daniel 1990). The ∑SDI equation is:

$$= \sum\left(TPA_j * \left(\frac{D_j}{10}\right)^{1.6}\right)$$

where TPA_j is the number of trees represented by the *j*th tree and D_j is the diameter (inches) of the *j*th tree (Long & Daniel 1990). Higher SDI values indicate higher levels of stocking, and therefore competition (Reinke 1933). We used these calculations, ∑SDI, BA and TPA, as proxies for competition. We calculated differences between means for ∑SDI (Δ∑SDI), BA (ΔBA), and TPA (ΔTPA) because data were not normally distributed, even after being transformed (Shapiro-Wilks, $p < 0.05$). Differences were calculated by subtracting values in treated stands from those in untreated stands. We calculated the coefficient of variation (CV) for ∑SDI, BA, and TPA in treated and untreated stands to assess variation in the data (Table 3.4). We also calculated quadratic mean diameter (QMD, inches) for all stands, which is the DBH of the tree of average basal area and gives greater weight to large trees in a stand (Table 3.2) (Curtis & Marshall 2000).

Additionally, we used the site index trees to examine estimates of site productivity in each stand to assess the relationship between site productivity and competition proxies. Minor's (1964) criteria were used for site index tree selection. The number of site index trees ranged from 6 to 12; some stands had fewer site index trees because adequate site index trees were difficult to find in some stands. To calculate site index values, we processed the increment cores and followed Minor's (1964) equation for second-growth ponderosa pine in northern Arizona. To process the increment cores, they were dried for at least 24-hours, glued to wooden mounts, and sanded with sandpaper of increasingly fine grits (maximum 600 grit). After being processed, the two cores from each tree were visually cross-dated and the ring counts were averaged. We then calculated a mean site index value per stand (Table 3.1). Stands with higher site index values have greater site productivity (Minor 1964).

Individual tree-scale data

Similar to the stand-scale analyses, we calculated forest stand attributes from the individual tree-scale plots to determine if competition around bark beetle-killed trees varied from a similarly sized paired live tree, and from the stand-scale. We calculated means from the individual tree-scale plot data for the three competition proxies in the treated and untreated stands to assess differences in competition (Table 3.3). We calculated differences between means for ∑SDI (Δ∑SDI), BA (ΔBA), and TPA (ΔTPA) because data were not normally distributed (Shapiro-Wilks, $p < 0.05$). Differences were calculated by subtracting the bark beetle-killed tree mean values from the paired live tree mean values (Table 3.3). We calculated the CV for ∑SDI, BA and TPA for both the dead and live plot pairs in treated and untreated stands to assess variation in the data (Table 3.4). To examine the size of trees which bark beetles were attacking and ensure paired trees were similar in size, we calculated mean QMD per stand for the plot center trees only (Table 3.4).

Statistical analyses

We made comparisons using Δ∑SDI, ΔBA, and ΔTPA among the individual tree- and stand-scales (Figure A3). We also compared stand elevations and site index values, and paired individual tree-scale and stand-scale QMDs. Comparisons were done within individual stands, across forests, and across treated and untreated stands. Lastly, we used Spearman's ranked correlation tests to examine relationships among competition proxies and between competition proxies and site index. For all tests (described below), significance was determined with an $\alpha = 0.05$.

We used paired and one-way t-tests to compare stand-scale mean differences in treated and untreated stands. To test if treated stands had less competition than untreated stands, we used a one-way t-test for all competition proxies. Differences in stand elevations were tested with a paired t-test, determining whether there was a statistically significant difference in elevations between paired treated and untreated stands. Site index values and QMDs were also compared using a paired t-test, examining differences between paired treated and untreated stands. Additionally, we used Spearman's ranked correlation tests to examine relationships among BA and TPA, BA and ∑SDI, TPA and ∑SDI, and dead TPA and site index for stand-scale means in treated and untreated stands.

We used one-way t-tests and paired t-tests to test if competition (Δ∑SDI, ΔBA, ΔTPA) was lower around a bark-beetle killed tree compared with the paired live tree. To compare the difference among all stand means and within treatment types, a weighted t-test was used because of the varying number of individual tree-scale pairs; stands with a higher number of pairs were given more weight. We did this within treated and untreated stands, then used a paired t-test to see if there was a difference between treated and untreated stands. Additionally, we used a one-way t-test to test if competition was less around bark beetle-killed trees compared with paired live trees in individual stands. The same procedure was followed for each competition proxy (Δ∑SDI, ΔBA, and ΔTPA). We compared individual tree-scale QMDs using a paired t-test within stands and between treated and untreated stands. Lastly, we used Spearman's ranked correlation test to assess if there was a relationship between individual tree-scale, bark beetle mean values for ∑SDI, BA, and TPA and site index values in treated and untreated stands.

We used one-way t-tests and paired t-tests to assess if competition (Δ∑SDI, ΔBA, ΔTPA) was lower around bark beetle-killed trees compared with the stand-scale. To compare the difference among all stand means, we used one-way t-tests, and to compare the difference between treated and untreated stands, we used a paired t-test. We did not make within stand comparisons for bark beetle-killed trees and stand-scale competition. We also compared the bark beetle-killed mean QMD to the stand-scale QMD using a t-test.

RESULTS

Stand characteristics

Silvicultural prescriptions were obtained from local USDA Forest Service silviculturists and in all treated stands, prescriptions increased heterogeneity by selecting individual trees or groups for retention that created complex spatial patterns (Table A1). Stands were treated, on average, approximately 10 years prior to 2021 and untreated stands had not been treated in at least 15 years (Tables 3.1 and A1). Treated stands generally had lower density (∑SDI, BA, and TPA) compared with untreated stands (Table 3.2, Figure 3.2), and ∑SDI, BA, and TPA all showed strong, positive, and significant correlations ($p < 0.001$; ∑SDI and BA, $r = 0.989$; ∑SDI and TPA, $r = 0.873$; ΔBA and TPA, $r = 0.826$). The treated stands had higher CVs compared to the untreated stands for all competition proxies, however, the Coconino NF had larger differences in CVs between treated and untreated stands compared with the Kaibab NF (Table 4). On the Kaibab NF, the CV for TPA in the treated stands did not follow the same trend as all other means; it was lower in the untreated stands compared to that in the untreated stands (Table 3.4).

Site index ranged from 56.8 to 88.9 feet (base age 100) (Table 3.1). We found significant differences in site index values for 30% of the paired stands, all of which were on the Coconino

NF (Table 3.1). Stands were all classified as flat or on a hillside and elevations ranged from 6,850 to 7,925 feet (Table 3.1). We found significant differences (mean difference = 119.7ft) in elevation in 70% (40% Coconino NF, 30% Kaibab NF) of the paired stands; treated stands were at a lower elevation in 50% of the paired stands (Table 3.1). In the treated stands, the diameter distribution was not normally distributed with a right skew (uneven-sized, higher structural complexity), and the untreated stands approximated a normal distribution (even-sized distribution with one distinct size class, less structural complexity) (Figure 3.3) (Ashton and Kelty 2018). Although there were no significant differences ($p = 0.324$), QMDs were generally higher in treated stands (Table 3.2, Figure 3.4). There were two stands, Coco4 and Coco6, where the treated stand had a lower QMD compared with the untreated stand, but the difference was less than 1-inch (Table 3.2). Regardless of how QMD was calculated, the trends were the same for all competition proxies in treated and untreated stands (Figure 3.4).

We found significant differences (treated less than untreated) in $\Delta\sum$SDI, ΔBA, and ΔTPA in 60% of the paired treated and untreated stands; the other 40% were not statistically different, however less pronounced differences were observed (Table 3.2, Figure 3.5). For $\Delta\sum$SDI, and ΔBA, 50% of the differences were found in the Coconino NF stands and 10% in the Kaibab NF stands. For ΔTPA, 40% of the differences were found in the Coconino NF stands and 20% in the Kaibab NF stands (Figure 3.2). Significant differences were found in the same stands for $\Delta\sum$SDI and ΔBA, but not for ΔTPA. The two stands that differed were Kab1 ($p = 0.002$) and Coco4 ($p = 0.109$) (Figure 3.5).

Is there less inter-tree competition around a bark beetle-killed tree compared with a similarly sized live tree?

We found little evidence that competition was lower around bark beetle-killed trees compared with the paired live tree in either stand type. Specifically, we did not find significant differences between the bark beetle-killed and paired live tree means within treated or within untreated stands for Δ∑SDI (treated, p = 0.728; untreated, p = 0.532), ΔBA (treated, p = 0.703; untreated, p = 0.494), and ΔTPA (treated, p = 0.768; untreated, p = 0.361) (Table 3.3, Figure 3.6). There were also no significant differences between treated and untreated stands (Δ∑SDI, p = 0.699; ΔBA, p = 0.900; ΔTPA, p = 0.873) (Table 3.3, Figure 3.6). While no significant differences were found among overall means, there were some significant differences within individual stands. In Coco1, the mean competition surrounding the bark beetle-killed tree was lower than for the paired live tree (Δ∑SDI, p = 0.032; ΔBA, p = 0.042; ΔTPA, p = 0.019) (Table 3, Figure 7). While not statistically significant, two other untreated stands had lower mean competition surrounding a bark beetle-killed tree for ΔBA (Coco3u, p-value = 0.058; Coco5u, p-value = 0.052) and one also had lower Δ∑SDI (Coco3u, p-value = 0.057) (Table 3.3). Other stands also had lower levels of competition surrounding the bark beetle-killed tree, although the differences were not significant (p > 0.05).

Overall, treated stands had higher variation compared with the untreated stands. Like the stand-scale variation calculations, there was more variation on the Coconino NF in the live means for ∑SDI and BA, but not TPA (Table 3.4). In the untreated stands, all competition proxy mean CVs were higher in plots surrounding bark beetle-killed trees than around live trees (Table 3.4). On the Kaibab NF, the same trend was found as the Coconino NF in untreated stands. The treated stands on the Kaibab NF had higher CVs in the bark beetle-killed means for ∑SDI and BA, which was different from the Coconino NF (Table 3.4).

Is there less competition around a bark beetle-killed tree compared with the overall stand-scale competition?

We found no evidence that competition differed between bark beetle-killed and stand-scale means in either stand type. We tested the difference between the bark beetle-killed and stand-scale mean by assessing if the competition values for the bark beetle-killed was less than the stand-scale. We found no significant difference in $\Delta\sum$SDI (treated, $p = 0.419$; untreated, $p = 0.259$), ΔBA (treated, $p = 0.869$; untreated, $p = 0.4707$), and ΔTPA (treated, $p = 0.756$; untreated, $p = 0.628$) (Figure 3.8) or between treated and untreated stands ($\Delta\sum$SDI, $p = 0.671$; ΔBA, $p = 0.744$; ΔTPA, $p = 0.997$) (Figure 3.8). Like the individual tree- and stand-scale comparisons, we found a notable amount of variation (as assessed by CV), treated stands having more variation than untreated, and the bark beetle-killed variation higher than the stand-scale (Table 3.4). This trend for the bark beetle-killed and stand-scale comparison was seen in both NF's and across competition proxies, except for treated TPA (Table 3.4).

Is tree size influencing bark beetle-caused tree mortality?

We found no significant difference between paired individual tree-scale QMDs in treated ($p = 0.905$) or untreated stands ($p = 0.767$) (Tables 3.2 and 3.3, Figure 3.3). Individual tree-scale plot center paired trees had to be within 10% DBH and therefore this was as expected. We found no significant difference in bark beetle-killed (range: 5.6 – 22.7 inches) and stand-scale (range: 9.4 – 17.4 inches) QMDs in treated ($p = 0.498$) or untreated stands ($p = 0.845$) (Figure 3.3), but there were individual stands where the bark beetle-killed mean QMD trended higher than at the stand-scale. The bark beetle-killed mean QMD (treated = 19.7 inches; untreated = 15.4 inches) was higher than the stand-scale (treated = 14.3 inches; untreated = 12.9 inches). Although they were not statistically significant, these differences suggest that bark beetles are attacking trees that larger in diameter than the stand average and are practically important for management.

Is site productivity an influencing factor in tree competition and overall bark beetle-caused tree mortality?

We found no significant correlation between the ∑SDI, BA, and TPA that surrounded a bark beetle-killed tree and site index (∑SDI , treated r = -0.491, p = 0.154, untreated r = 0.109, p = 0.764; BA, treated r = -0.212, p = 0.560, untreated r = 0.188, p = 0.602; TPA, treated r = -0.353, p = 0.318, untreated r = 0.134, p = 0.713) or between bark-beetle killed TPA and site index (treated r = -0.170, p = 0.639, untreated r = 0.094, p = 0.796).

DISCUSSION

Correlated with climate change, bark beetle outbreaks have increased spatially and temporally across the Western US and as a result, tree mortality from bark beetles has increased (Bentz et al. 2010, Raffa et al. 2008). To mitigate these effects, density reduction treatments are implemented to reduce competition and increase resilience and resistance (Fettig et al. 2007), and research supports that such treatments are effective (Sartwell 1971, Feeney et al. 1998, Negrón & Popp 2004, Fettig et al. 2007, Gaylord et al. 2010, Hood et al. 2016, Negrón et al. 2017). Previous research has been conducted at the stand-scale, but has rarely addressed the individual tree-scale and how competition directly surrounding trees impacts bark beetle-caused tree mortality (but see Zausen et al. 2005, Kane & Kolb 2010, 2014, Ferrenberg et al. 2022, Hood et al. 2022). In northern Arizona on the Coconino and Kaibab National Forests, treatments are implemented to reduce susceptibility to disturbances, preserve large trees, and emulate historical forest conditions, which results in a landscape with complex spatial patterns (Kaufmann et al. 1994, Waltz et al. 2003, Roccaforte et al. 2009, Reynolds et al. 2013). In this study our aim was to examine how bark beetles were interacting with individual trees within complex spatial patterns. Although no statistically significant results were found when comparisons were made among all sampled stands, there were some significant differences within stands at the individual tree-scale, which warrants further discussion and could inform future research.

Stand-scale

We found that density was generally lower in treated stands, but unexpectedly, not all pairs shared this pattern. Untreated stands treated earlier (i.e. outside of the 15 year window; criteria for this study) which did not respond to the treatment with increased growth or regeneration could have continued to have similar stand characteristics as treated stands. Additionally, pre-harvest structures were unknown, but could have influenced the results in some way. Although unlikely, elevation could have been a factor as there were some significant differences found. Seven out of the ten paired stands had a significant difference in elevation between treated and untreated stands (mean difference = 119.7ft) (Table 3.1). A mean difference of approximately 120 feet is likely not large enough to have an influence on bark beetle-caused tree mortality, but future research may consider including an elevation parameter because lower elevation has been associated with bark beetle-caused tree mortality due to increasing temperatures (Amman et al. 1973, Hansen 1996, Fettig et al. 2005, Williams et al. 2008, Negrón et al. 2009). Although it did not impact bark beetle-caused tree mortality, site index could have played an indirect role in bark beetle tree-selection in at least some stands, especially in the three stands that had significant differences (Table 3.1). This is because site index can impact tree growth (lower site index values = lower site productivity) and trees with slower growth rates often are killed by bark beetles (Kane and Kolb 2010, 2014). Treated stands were treated 6-15 years ago. This range could have been affecting the QMDs and diameter distribution as treated stands could have not yet responded to treatments (i.e. increased growth). Differences in QMD between treated and untreated stands were not large, which was not expected because treated stands typically have higher QMDs (due to less competition for resources and therefore increased growth), and because the prescriptions put an emphasis on retaining the old growth trees (Table A1). In both plot types, there was more variation in treated stands compared with untreated stands, which links to the increased heterogeneity; because treatments are creating complex spatial patterns that result in varying levels of density, there is greater variation. While we did not measure spatial patterns, the CV values, along with the diameter distributions, confirm that we did sample stands with complex structures, and therefore assessing how bark beetles were interacting with them was appropriate.

Individual tree-scale

Few studies have documented the relationship between individual tree competition and bark beetles (but see Zausen et al. 2005, Kane & Kolb 2010, 2014, Ferrenberg et al. 2022, Hood et al. 2022). In our study, we did not find many significant differences in competition surrounding live and beetle-killed trees, although some individual stands had less competition surrounding bark beetle-killed trees, and there was a notable amount of variation (as assessed from the CVs) in individual tree-scale data that could be leading to the lack of differences. Previous research shows strong support that bark beetles kill trees in denser stands with high levels of competition at the stand-scale (Sartwell 1971, Feeney et al. 1998, Negrón & Popp 2004, Fettig et al. 2007, Gaylord et al. 2010, Hood et al. 2016, Negrón et al. 2017). At the individual tree-scale, competition has been shown to negatively impact trees attacked by bark beetles (Zausen et al. 2005, Ferrenberg et al. 2022), but there is recent research that suggests these trends could be changing (Hood et al. 2022). In some cases, our study supports the finding that competition negatively impacts trees attacked by bark beetles; in 40% of the stands, trees killed by bark beetles had more competition around them (Figure 3.7). Of the remaining stands, 15% had approximately equal competition and 45% had less competition around the bark beetle-killed trees (Figure 3.7). Less competition around bark-beetle killed trees does not align with results from previous research. Ferrenberg et al. (2022) paired bark beetle killed and live trees in New Mexico and found that trees killed by bark beetles had more competition (BA) surrounding them, which in-turn impacted their rates of growth and resin duct production. Two studies in northern Arizona examined tree growth and defenses in relation to tree mortality and found that live trees had more annual growth, resin ducts (measure of defense) were larger and more abundant, and that declines in short- and long-term growth increased the likelihood of bark beetle-caused tree mortality (Kane and Kolb 2010, 2014). Another study in northern Arizona assessed the effects of thinning and burning on bark beetle-caused tree mortality (Zausen et al. 2005). They found that tree competition was negatively correlated with tree growth and phloem thickness, and tree competition and water stress were positively correlated, indicating that higher competition increases tree stress, and therefore susceptibility to, and mortality from, bark beetles (Zausen et al. 2005). A study outside of the Southwest examined the effects of radial thinning around large diameter trees (Hood et al. 2022). Radial thinning (also called crop tree release, daylighting, free thinning) removes vegetation around a focal tree to reduce competition and increase resilience (of the focal tree). The study found that there was no clear benefit of radial thinning and of the trees that died in the study, mountain pine beetle was responsible for most of the mortality (Hood et al. 2022). They conclude that radial thinning treatments are effective in increasing heterogeneous structures, but are unlikely to meet the goal of retaining large trees on the landscape (Hood et al. 2022). Historically, trees that survived bark beetle attacks or didn't get attacked typically had high vigor (i.e. the ability for a tree to defend itself from a bark beetle), faster growth rates, lower surrounding competition, and ample resources (Larson et al. 1983, Kolb et al. 1998, Fischer et al. 2010). In our study, we did not include climatic variables or growth rates, quantify resin ducts, or identify bark beetle species, and including these factors would allow further assessment of tree competition on bark beetle-caused tree mortality and give insight into why bark beetles were successful. Although some of our results differ from previous research (high densities = increased bark beetle-caused tree mortality) and show that bark beetles can sometimes kill trees with less competition around them, a significant amount of research is needed at the individual tree-scale to draw further conclusions.

Bark beetle-killed vs. stand-scale

Tree density and competition affecting bark beetle-caused tree mortality is commonly studied at the stand-scale. There are few studies that examine the individual tree-scale, and comparing the individual tree- and stand-scales, to our knowledge, has not been done. Typically, the mean stand-scale density is applied to the entire stand. While stand-scale averages likely work well where spatial complexity is low, stands with high spatial complexity should be assessed at multiple scales. We examined multiple scales in our study and compared overall mean bark beetle-killed and stand-scale values, and although there were no significant findings, competition in some stands trended lower around bark beetle-killed trees (Tables 3.2 and 3.3). Erickson and Waring (2014) examined old growth trees, competition, and tree mortality in northern Arizona and found that treatments are effective at retaining old growth trees, even with drought and other stressors. Some of our results deviate from this and therefore, we suggest further assessment at the individual tree-scale in future research which may determine if competition in conjunction with bark beetles matters at a fine-scale.

Bark beetle-selection and tree size

To select trees, bark beetles use a combination of visual, olfactory, tactile, and gustatory signals, and external cues, or it can be random (Borg & Norris 1969, Wood 1972, Raffa & Berryman 1982, Pureswaran et al. 2006). Selection is dependent on bark beetle species, population sizes, tree size, and pheromones (Mitchell & Preisler 1991). Pheromones released (by bark beetles) attract bark beetles to the host tree and nearby trees that the pheromones reach, resulting in groups of trees to be attacked (Mitchell and Preisler 1991). Like previously stated, untreated stands are considered more susceptible than treated stands because of increased tree stress (Fettig et al. 2007, Negrón et al. 2009, Kolb et al. 2019). Within treated stands with complex spatial patterns, it has been suggested that groupings of trees are more susceptible to bark beetle-caused tree mortality because of higher densities and thus more competition compared to trees left in openings (Olsen 1996, Negrón et al. 2001, Negrón 2020). In our study, we found bark beetle-killed trees within groups in some cases, but not always; sometimes the stand-alone trees were dead. This finding was intriguing because when treatments occur, the microclimate around these trees change; there are changes in temperature, increased water and nutrient availability, increased soil moisture, and reduced canopy cover (Flathers et al. 2016), and therefore, the larger trees left in the openings should have increased vigor and likelihood of tree survival. Because some of our results indicated that bark beetles killed trees with less competition around them, it suggests that tree competition may not be the main driving factor in tree mortality from bark beetles in northern Arizona.

When populations shift from endemic to epidemic, bark beetles tend to select healthier trees with more resources because as population densities increase, the ability to overcome tree defenses increases, and when population densities allow it, bark beetles prefer larger trees because of improved food quality and quantity (thicker phloem) (Ryan et al. 2015). Negrón et al. (2009) suggest that trees in Arizona are resilient to bark beetles if QMD falls outside of the 25.4 - 88.9 inch range. At the stand-scale, the QMDs from this study fall outside of the suggested range. The individual tree-scale tree's QMDs are higher than the stand-scale and closer to the range from Negrón et al. (2009) which may be why bark beetles were attacking and killing those trees. Larger QMDs at the individual tree-scale indicate that bark beetles are selecting trees larger than the stand average size, particularly considering the number of live-dead tree pairs was limited by the number of dead trees we were able to locate and not by our upper limit (5) in most stands (Table 3.3).

Site productivity

The link between site productivity and bark beetle outbreaks is not commonly addressed. Akkuzu et al. (2017) found that areas with lower site productivity had higher levels of bark beetle populations compared with sites with higher productivity. Our study showed that site productivity and bark beetle-caused tree mortality were uncorrelated. It has been shown that bark beetles attack stressed trees that have lower annual growth (Kane & Kolb 2010), and because site productivity impacts tree growth, we postulated that it could be an influencing factor, although our results imply otherwise. Although no correlation was found between site productivity and bark beetle-caused tree mortality, site productivity varied among stands and between treated and untreated stands. This could have implications for tree growth and should be further examined in future research because tree growth is often correlated with bark beetle-caused tree mortality (see Larsson et al. 1983, Kolb et al. 1998, Fischer et al. 2010, Kane & Kolb 2010, 2014, Ferrenberg 2022).

Conclusion

Silvicultural treatments in ponderosa pine forests across the Western US are implemented with multiple objectives, including restoration, increasing resistance and resilience, and mitigating the effects of disturbance (Churchill 2020). In this study, we asked if complex spatial patterns resulting from such treatments were impacting bark beetle-caused tree mortality at an individual tree-scale. Our results were variable; however, we did find that in some cases bark beetles were killing large trees that had less competition around them. If implemented treatments are no longer promoting large tree survival, as intended, the question arises as to why these changes are happening and what can be done about them. Unfortunately, there is not one clear answer, but there is evidence that the climate is changing, and this is correlated with increased bark beetle outbreaks (Bentz et al. 2010). Managers should be proactively managing for an uncertain future (Mina et al. 2022) by monitoring and using adaptive forest management strategies (Allen et al. 2011, Nagel et al. 2017).

The deviations from historical patterns presented here indicate that bark beetle-caused tree mortality patterns may be more difficult to predict now and in the future, potentially due to change in bark beetle selection processes related to densities and spatial patterns, and climate change is likely further exacerbating these effects. While some studies have been conducted at the individual tree-scale and found higher competition around bark beetle-killed trees (Zausen et al. 2005, Kane and Kolb 2010, 2014, Ferrenberg et al. 2022), one recent study did not (Hood et al. 2022). If more studies had included data collected at both scales, perhaps the research would have found more mixed results or there would have been more variation in the results on the interaction between competition and bark beetle-caused tree mortality. Regardless, additional research is needed to fully address these questions. We suggest future research evaluates the effects of climatic variables, growth rates, and the size and frequency of resin ducts, and that bark beetle species are identified, and includes stands from across a wider geographic range.

Tables and Figures

Table 3.1. Summary of stand-scale abiotic variables from paired treated and untreated stands. Elevation and site index are reported as means (standard error); Coco = Coconino National Forest; Kab = Kaibab National Forest. Different letters denote significant differences between paired treated and untreated stands. A paired t-test was conducted for elevation and site index; significance was determined with an $\alpha = 0.05$. Other variables were not included in statistical tests.

Stand	**Elevation (ft)**		**Landform**		**Site Index (ft)***		**Treatment type**	**Treatment year(s)**
	Untreated	**Treated**	**Untreated**	**Treated**	**Untreated**	**Treated**		
Coco1	7018.9^{A} (6.2)	7079.5^{B} (4.8)	Side hill	Flat	65.5^{A} (2.4)	71.6^{A} (1.9)	Individual tree selection; prescribed fire	2008; 2015
Coco2	7023.1^{A} (8.4)	7029.3^{A} (4.8)	Flat/Side hill	Flat	74.5^{A} (2.3)	71.5^{A} (2.4)	Group selection; prescribed fire	2008; 2015
Coco3	7025.7^{A} (4.8)	7007.4^{B} (20.1)	Flat/Side hill	Flat	81.0^{A} (5.5)	56.8^{B} (3.6)	Precommercial thin	2012
Coco4	6981.1^{A} (14.0)	6988.3^{A} (17.1)	Flat	Side hill	77.0^{A} (4.0)	78.3^{A} (7.4)	Group selection; prescribed fire	2010; 2015
Coco5	7103.0^{A} (6.4)	6893.3^{B} (3.8)	Flat	Flat	67.4^{A} (2.7)	76.1^{B} (4.3)	Group selection; prescribed fire	2010; 2015
Coco6	6815.9^{A} (75.0)	7194.6^{B} (10.7)	Side hill	Flat/Side hill	80.3^{A} (2.8)	62.3^{B} (3.2)	Precommercial thin	2012
Kab1	7924.9^{A} (42.6)	7789.0^{B} (9.8)	Side hill	Flat	67.4^{A} (5.3)	68.9^{A} (1.8)	Thin from below	2006
Kab2	7201.1^{A} (8.5)	7402.9^{B} (12.7)	Flat	Side hill	71.6^{A} (5.7)	63.8^{A} (2.5)	Individual tree selection	2007
Kab3	7396.4^{A} (7.8)	7276.4^{A} (60.0)	Side hill	Flat/Side hill	66.9^{A} (6.0)	66.9^{A} (3.1)	Individual tree selection	2006
Kab4	6910.5^{A} (16.1)	6858.0^{B} (11.7)	Flat	Flat	84.4^{A} (7.0)	88.9^{A} (13.6)	Individual tree selection	2008
Coco Mean	**6994.6** **(19.1)**	**7032.1** **(10.2)**	n/a	n/a	**74.3** **(3.3)**	**69.4** **(3.8)**	n/a	n/a
Kab Mean	**7379.3** **(18.8)**	**7331.6** **(23.6)**	n/a	n/a	**72.6** **(6.0)**	**72.1** **(5.3)**	n/a	n/a
Overall mean	**7140.1**^{A} **(19.0)**	**7151.9**^{A} **(15.6)**	n/a	n/a	**73.6**^{A} **(4.4)**	**70.5**^{A} **(4.4)**	n/a	n/a

*Base age 100

Table 3.2. Summary of stand-scale biotic variables from paired treated and untreated stands (calculated from the stand-scale plots). Stand density index, basal area per acre, live trees per acre, dead trees per acre, and quadratic mean diameter are reported as means (standard error); $\sum$ = summation; Δ = the difference between the treated and untreated stands; Coco = Coconino National Forest; Kab = Kaibab National Forest; Δ^{A} = a significant difference was found between treated and untreated stands; significance was determined with an $\alpha = 0.05$. Differences were not calculated between mean dead TPA or QMD.

Stand	**$\sum$Stand density index**			**Basal area per acre (ft^2/ac)**			**Live trees per acre**			**Dead trees per acre**		**Quadratic mean diameter (in)**	
	Untreated	**Treated**	**Δ**	**Untreated**	**Treated**	**Δ**	**Untreated**	**Treated**	**Δ**	**Untreated**	**Treated**	**Untreated**	**Treated**
Coco1	153.0 (16.9)	66.9 (11.4)	86.1^{A} (20.1)	98.3 (11.9)	46.3 (8.9)	52.0^{A} (14.7)	102.9 (12.3)	48.6 (17.4)	54.3^{A} (23.1)	5.0 (0.0)	5.0 (0.0)	13.2 (1.1)	13.4 (2.1)
Coco2	205.4 (19.0)	52.0 (10.8)	153.3^{A} (23.1)	136.8 (12.7)	37.1 (9.2)	99.7^{A} (16.1)	120.7 (8.5)	27.9 (7.2)	92.9^{A} (12.7)	10.0 (0.0)	5.0 (0.0)	14.4 (0.7)	16.3 (1.8)
Coco3	164.8 (16.3)	130.8 (15.8)	34.1 (23.4)	103.1 (10.5)	80.9 (10.0)	22.2 (14.1)	138.6 (16.7)	138.6 (28.6)	0.0 (23.5)	22.5 (8.7)	15.0 (5.0)	10.6 (0.8)	10.5 (1.1)
Coco4	201.2 (21.9)	123.3 (10.5)	78.9^{A} (28.4)	141.8 (16.2)	86.6 (7.8)	55.1^{A} (17.8)	106.4 (18.1)	66.4 (17.6)	40.0 (29.1)	5.0 (0.0)	8.8 (2.4)	15.3 (1.1)	15.3 (1.6)
Coco5	268.1 (25.2)	64.2 (10.2)	203.9^{A} (29.6)	161.9 (15.6)	44.9 (8.7)	117.0^{A} (19.4)	244.3 (26.7)	51.4 (17.3)	192.9^{A} (36.3)	20.0 (4.4)	5.0 (0.0)	11.0 (0.3)	12.5 (3.0)
Coco6	232.7 (31.2)	93.6 (11.7)	139.1^{A} (31.2)	143.5 (18.3)	60.3 (8.2)	83.2^{A} (18.2)	189.3 (40.8)	94.3 (13.2)	95.0^{A} (46.5)	18.8 (7.5)	10.8 (2.0)	11.7 (1.1)	11.0 (0.9)
Kab1	123.1 (15.5)	94.4 (23.0)	28.7 (32.7)	71.9 (10.0)	69.8 (16.8)	2.2 (23.8)	152.1 (28.0)	30.0 (7.4)	122.1^{A} (26.8)	13.3 (3.3)	8.8 (2.4)	9.4 (0.8)	19.6 (1.1)
Kab2	171.5 (12.3)	107.5 (4.2)	64.1^{A} (18.5)	110.0 (2.2)	69.4 (11.8)	40.6^{A} (11.9)	115.0 (9.9)	60.0 (10.1)	55.0^{A} (16.1)	8.8 (2.0)	7.5 (2.5)	13.1 (0.6)	14.5 (1.1)
Kab3	160.7 (39.6)	99.4 (12.3)	61.3 (36.3)	102.3 (21.4)	64.6 (9.7)	37.7 (19.9)	112.9 (52.1)	68.6 (7.5)	44.3 (53.8)	5.0 (0.0)	5.0 (0.0)	12.4 (1.6)	13.1 (1.3)
Kab4	59.3 (12.6)	75.2 (11.1)	-15.9 (8.0)	43.7 (10.3)	53.2 (9.7)	-9.5 (5.8)	27.1 (8.2)	45.7 (8.0)	-18.6 (9.4)	5.0 (0.0)	15.0 (5.8)	17.4 (3.0)	14.1 (2.0)
Coco Mean	**204.2 (21.2)**	**88.5 (11.6)**	**115.9 (25.1)**	**130.9 (14.0)**	**59.4 (8.9)**	**71.5 (16.7)**	**150.4 (22.1)**	**71.2 (18.1)**	**79.2 (28.5)**	**13.6 (3.4)**	**8.3 (1.6)**	**12.7 (0.9)**	**13.2 (1.8)**
Kab Mean	**128.7 (20.3)**	**94.1 (12.9)**	**34.6 (23.6)**	**82.0 (11.0)**	**64.3 (12.5)**	**17.8 (15.4)**	**101.8 (24.6)**	**51.1 (8.3)**	**50.7 (26.3)**	**8.0 (1.3)**	**9.1 (2.7)**	**13.1 (1.3)**	**15.3 (1.4)**
Overall mean	**174.0 (20.9)**	**90.7 (11.9)**	**83.4 (24.7)**	**111.3 (12.9)**	**61.3 (10.0)**	**50.0 (16.8)**	**130.9 (20.1)**	**63.2 (14.1)**	**67.8 (29.1)**	**11.3 (2.6)**	**8.59 (2.0)**	**12.9 (1.0)**	**14.3 (1.6)**

Table 3.3. Summary of biotic variables from paired treated and untreated stands (calculated from individual tree-scale plots). Stand density index, basal area per acre, trees per acre, and quadratic mean diameter are reported as means (standard error). There was a total of 42 individual tree-scale plots among untreated stands and 35 individual tree-scale plots among treated stands; individual tree-scale plots per stand are listed within table, T = treated stand, U = untreated stand. ∑ = summation; Δ = the difference between the bark beetle-killed mean and paired live tree mean; B = bark beetle-killed; L = paired live tree; Coco = Coconino National Forest; Kab = Kaibab National Forest; Δ^A = a significant difference was found; significance was determined with an $\alpha = 0.05$. Differences were not calculated between QMDs.

Stand	**∑Stand density index**						**Basal area per acre (ft^2/ac)**						**Trees per acre**						**Quadratic mean diameter (in)**			
	Treated			**Untreated**			**Treated**			**Untreated**			**Treated**			**Untreated**			**Treated**		**Untreated**	
	B	L	Δ	B	L	Δ	B	L	Δ	B	L	Δ	B	L	Δ	B	L	Δ	B	L	B	L
Coco1 T, n = 4 U, n = 5	33.4 (5.4)	55.8 (10.3)	22.4^A (5.9)	178.9 (12.5)	131.2 (12.1)	-47.7 (15.8)	20.0 (3.4)	36.9 (6.9)	16.9^A (5.3)	107.7 (8.0)	80.5 (8.1)	-27.1 (9.3)	30.0 (10.0)	46.7 (8.8)	16.7^A (3.3)	166.0 (21.6)	146.0 (34.7)	-20.0 (31.9)	22.7 (15.2)	21.6 (14.3)	11.7 (5.9)	11.6 (5.8)
Coco2 T, n = 5 U, n = 3	94.1 (12.4)	99.4 (29.5)	24.1 (45.4)	193.2 (85.7)	78.0 (24.0)	-115.2 (99.0)	61.9 (9.7)	66.6 (21.7)	17.2 (33.0)	131.7 (51.2)	52.6 (21.0)	-79.1 (64.9)	46.0 (14.7)	46.0 (10.5)	12.0 (21.5)	106.7 (51.7)	56.7 (8.8)	-50.0 (45.1)	16.3 (8.3)	18.3 (7.5)	20.7 (4.8)	21.6 (5.7)
Coco3 T, n = 5 U, n = 5	110.0 (21.7)	58.5 (18.2)	-51.2 (14.0)	116.6 (39.1)	104.7 (58.7)	69.7 (34.6)	70.1 (13.2)	35.4 (8.9)	-34.7 (11.8)	72.0 (30.5)	118.2 (35.8)	46.2 (23.1)	126.0 (37.0)	76.0 (56.1)	-50.0 (63.0)	142.0 (41.2)	158.0 (71.4)	16.0 (90.8)	17.7 (5.2)	19.8 (6.0)	22.3 (5.6)	23.4 (6.7)
Coco4 T, n = 3 U, n = 3	104.2 (44.2)	63.8 (17.0)	-27.0 (61.2)	135.4 (26.7)	125.3 (28.6)	-10.1 (55.4)	69.7 (37.4)	41.3 (5.8)	-18.9 (44.5)	93.2 (25.8)	88.7 (21.8)	-4.4 (45.4)	90.0 (0.0)	85.0 (65.0)	-3.3 (44.8)	66.7 (21.9)	70.0 (26.5)	3.3 (20.3)	27.8 (3.9)	26.2 (1.8)	19.3 (10.7)	18.4 (7.9)
Coco5 T, n = 2 U, n = 4	82.6 (37.7)	43.3 (41.2)	-39.3 (3.5)	196.1 (85.6)	311.6 (60.0)	115.5 (58.4)	67.2 (31.8)	33.5 (32.8)	-33.7 (1.1)	112.9 (18.4)	190.2 (33.3)	77.4 (33.6)	20.0 (10.0)	20.0 (0.0)	0.0 (10.0)	220.0 (61.0)	290.0 (52.9)	70.0 (59.9)	17.5 (14.4)	16.8 (13.7)	11.5 (4.8)	10.9 (5.6)
Coco6 T, n = 2 U, n = 5	109.0 (50.6)	71.3 (37.8)	-37.6 (12.8)	150.6 (51.9)	165.0 (38.6)	14.4 (44.9)	59.4 (23.1)	44.2 (24.8)	-15.2 (1.7)	86.3 (29.4)	97.3 (23.7)	11.0 (26.0)	270.0 (180.0)	75.0 (5.0)	-195.0 (185.0)	152.0 (58.3)	152.0 (35.6)	0.0 (46.9)	20.3 (7.8)	20.3 (7.8)	11.0 (3.8)	10.7 (3.3)
Kab1 T, n = 2 U, n = 5	143.0 (44.7)	82.0 (58.6)	-102.0 (3.9)	110.6 (19.9)	98.6 (11.5)	-12.0 (12.5)	106.7 (33.6)	62.9 (44.9)	-72.3 (2.2)	65.2 (10.8)	57.1 (6.8)	-8.1 (8.0)	60.0 (0.0)	20.0 (4.3)	-50.0 (10.0)	104.0 (27.7)	102.0 (19.8)	-2.0 (26.7)	20.6 (4.7)	20.9 (4.3)	12.9 (1.8)	12.7 (1.8)
Kab2 T, n = 4 U, n = 5	66.1 (16.2)	150.5 (80.7)	9.2 (62.4)	161.6 (29.6)	130.4 (32.9)	-31.1 (9.6)	49.4 (14.4)	108.4 (64.7)	4.7 (48.8)	111.0 (18.7)	88.2 (22.0)	-22.8 (10.0)	22.5 (4.8)	55.0 (15.0)	5.0 (15.5)	72.0 (19.3)	74.0 (27.7)	2.0 (17.7)	23.4 (6.6)	22.3 (8.9)	20.8 (3.5)	20.1 (2.6)
Kab3 T, n = 3 U, n = 2	85.2 (47.5)	72.0 (5.7)	-13.2 (52.8)	282.2 (122.5)	310.2 (96.3)	28.0 (26.1)	59.0 (34.2)	46.5 (7.7)	-12.5 (41.9)	164.9 (63.6)	181.8 (47.6)	16.8 (16.0)	40.0 (15.3)	70.0 (30.6)	30.0 (20.8)	310.0 (220.0)	320.0 (160.0)	10.0 (60.0)	18.6 (6.2)	19.5 (6.9)	5.6 (0.6)	5.4 (1.1)
Kab4 T, n = 5 U, n = 5	58.4 (14.5)	110.7 (46.4)	30.2 (49.0)	84.7 (16.4)	106.7 (17.3)	12.6 (20.9)	34.9 (8.5)	73.6 (28.0)	24.0 (29.2)	55.2 (10.8)	80.4 (11.8)	18.2 (12.7)	56.0 (15.7)	72.5 (40.1)	2.0 (44.9)	50.0 (10.0)	32.5 (7.5)	-20.0 (15.8)	12.2 (6.1)	12.3 (6.3)	18.0 (5.3)	18.5 (5.4)
Coco Mean	**88.9 (32.5)**	**65.4 (25.7)**	**-9.5 (23.8)**	**161.8 (50.8)**	**152.6 (36.6)**	**30.3 (51.4)**	**58.1 (18.5)**	**43.0 (16.8)**	**-6.1 (16.2)**	**100.6 (29.1)**	**104.6 (24.5)**	**8.9 (33.7)**	**77.0 (51.2)**	**58.1 (24.2)**	**-40.3 (54.6)**	**119.4 (69.3)**	**135.5 (36.7)**	**3.2 (49.2)**	**20.4 (9.1)**	**20.5 (8.5)**	**16.1 (5.9)**	**16.1 (5.8)**
Kab Mean	**88.2 (30.7)**	**103.8 (47.9)**	**-20.0 (42.0)**	**159.8 (47.1)**	**161.5 (39.8)**	**-0.6 (17.3)**	**62.5 (22.7)**	**72.9 (36.3)**	**-14.5 (30.5)**	**99.1 (26.0)**	**101.9 (22.1)**	**7.4 (11.7)**	**44.6 (9.5)**	**54.4 (22.5)**	**-3.3 (22.3)**	**134.0 (37.8)**	**132.1 (53.8)**	**-2.5 (30.1)**	**18.7 (5.9)**	**18.8 (6.6)**	**14.3 (2.8)**	**14.2 (2.7)**
Overall mean	**88.6 (29.9)**	**80.7 (34.5)**	**-9.0 (31.2)**	**161.0 (47.4)**	**156.2 (37.0)**	**21.1 (38.72)**	**59.8 (20.9)**	**54.9 (24.6)**	**-13.0 (22.0)**	**100.0 (25.2)**	**103.5 (21.9)**	**2.8 (25.9)**	**86.1 (32.9)**	**56.6 (23.5)**	**-25.7 (41.9)**	**129.4 (52.7)**	**148.9 (55.9)**	**6.3 (41.5)**	**19.7 (7.8)**	**19.8 (7.8)**	**15.4 (4.7)**	**15.3 (4.6)**

Table 3.4. Coefficient of variation (CV) (%) for individual tree- and stand-scale means. Higher CV values indicate higher deviation from the mean. ∑ = summation; Coco = Coconino National Forest; Kab = Kaibab National Forest; S = stand-scale mean; B = individual tree-scale, bark beetle-killed mean; L = individual tree-scale, paired live tree mean.

Stand	**∑Stand density index**						**Basal area per acre (ft^2/ac)**						**Trees per acre**					
	Treated			**Untreated**			**Treated**			**Untreated**			**Treated**			**Untreated**		
	S	B	L	S	B	L	S	B	L	S	B	L	S	B	L	S	B	L
Coco Mean	38.4	48.1	69.1	28.2	52.5	45.8	43.5	50.1	66.5	28.9	55.9	48.6	69.1	56.2	59.2	35.5	62.7	55.9
Kab Mean	44.8	61.4	57.6	40.3	46.5	39.7	49.3	64.4	63.0	39.9	43.2	37.2	46.3	42.8	49.4	68.5	82.7	61.0
Overall mean	40.9	53.4	65.2	33.0	50.1	43.4	45.8	65.3	65.3	33.3	44.0	60.0	60.0	50.9	55.3	48.7	70.7	58.0

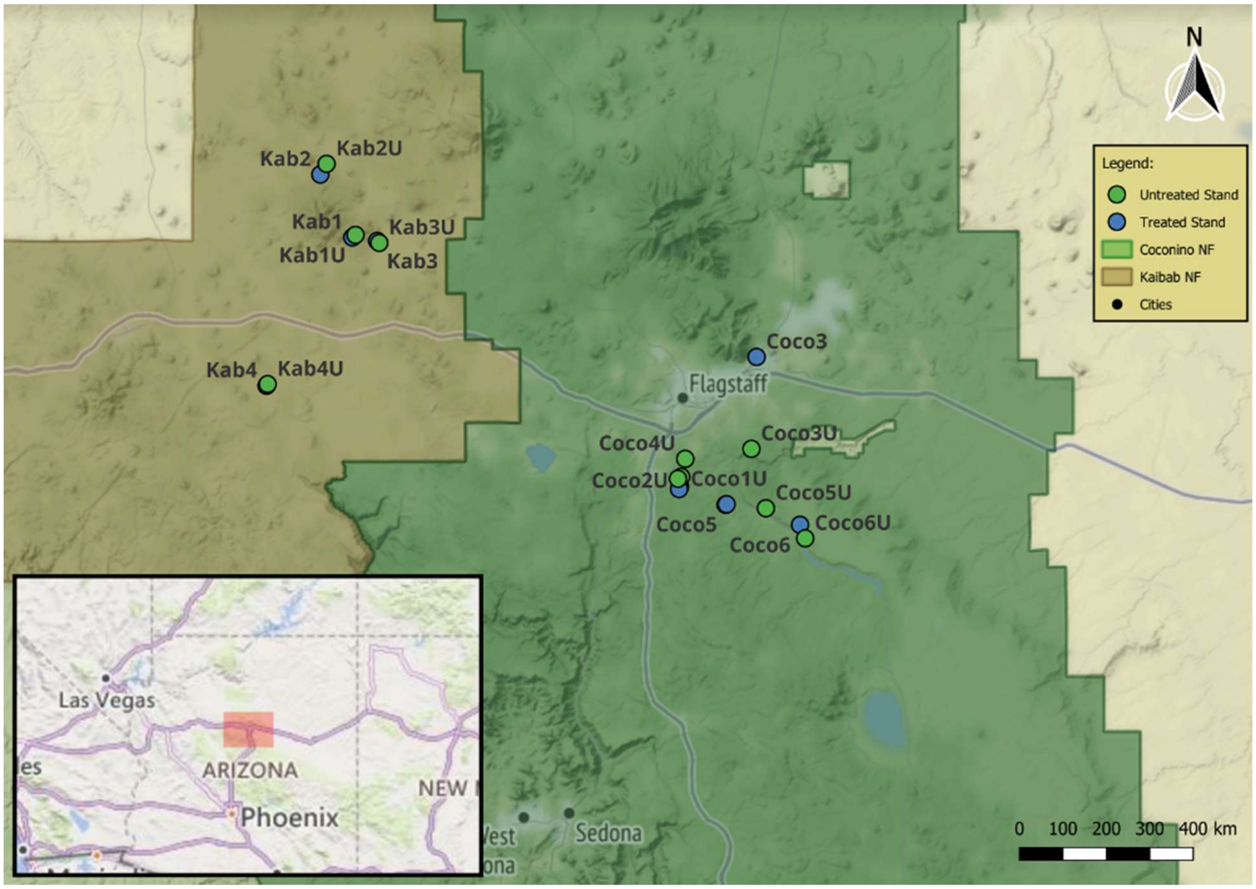

Figure 3.1. Paired stand locations in northern Arizona, USA. Treated stands indicated with blue dots and untreated stands indicated with green dots. The Coconino National Forest (NF) is in dark green and the Kaibab NF is in brown. Stands were 25-100 acres. Coco = Coconino NF; Kab = Kaibab NF; U indicates untreated stands. For detailed site descriptions, see Methods and Materials.

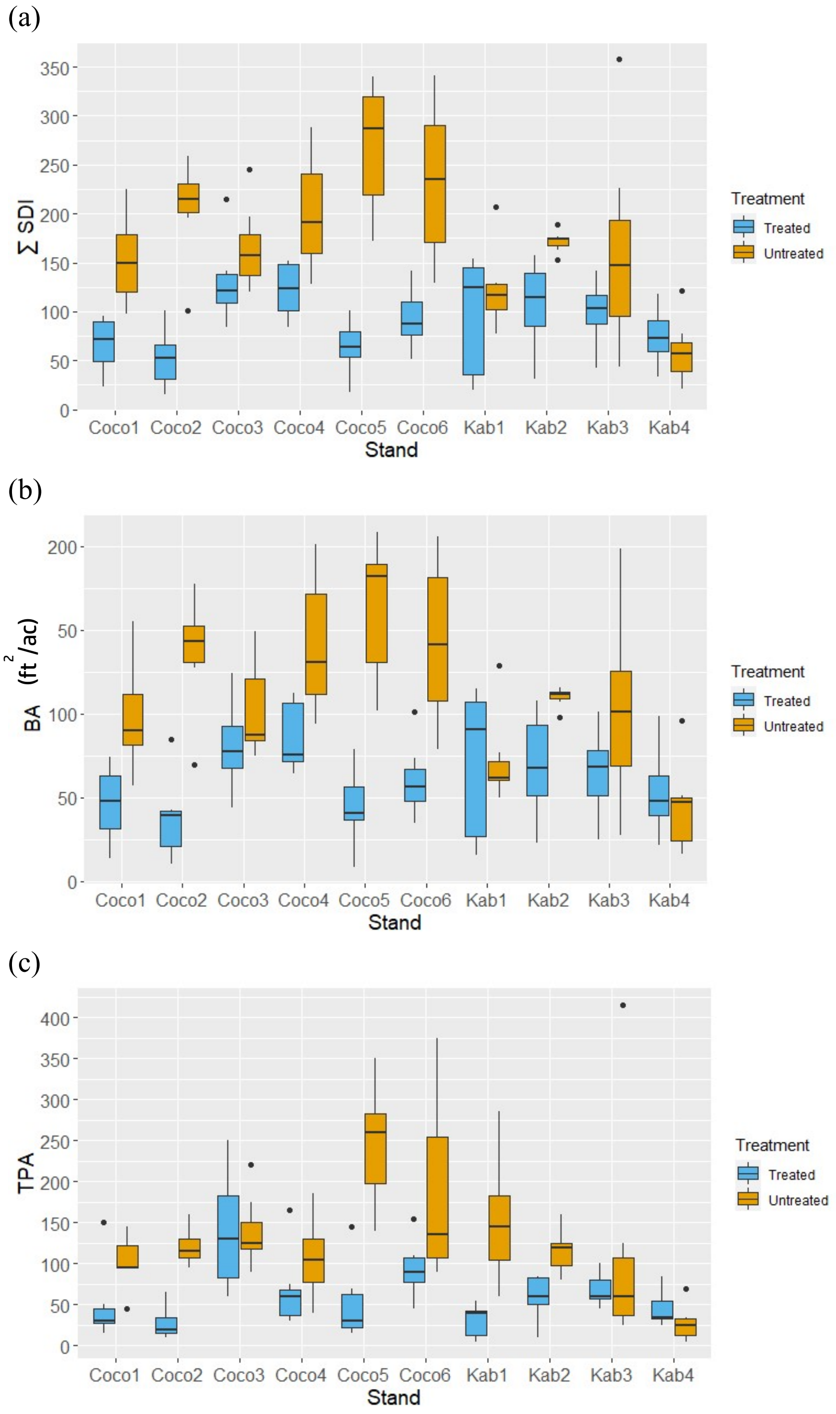

Figure 3.2. Summation stand density index (∑SDI), basal area per acre (BA), and trees per acre (TPA) in treated and untreated stands (calculated from the stand-scale plots). Treated stands generally had less density compared to the untreated stands. Coco = Coconino National Forest; Kab = Kaibab National Forest.

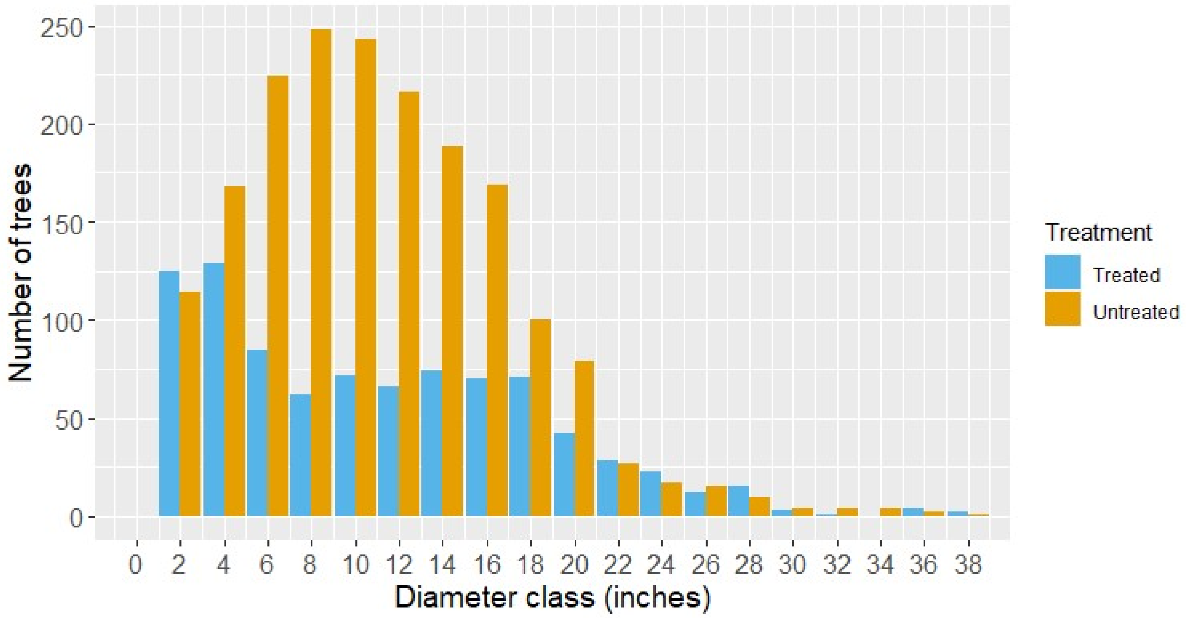

Figure 3.3. Number of trees by diameter class across all treated and untreated stands by 2-inch size class. The number of trees is the sum of all trees in each diameter class by treated and untreated stands. Treated stands diameter distribution approximated uneven-sized stands with higher structural complexity; untreated stands approximated a normal distribution with a more distinct size class and less structural complexity.

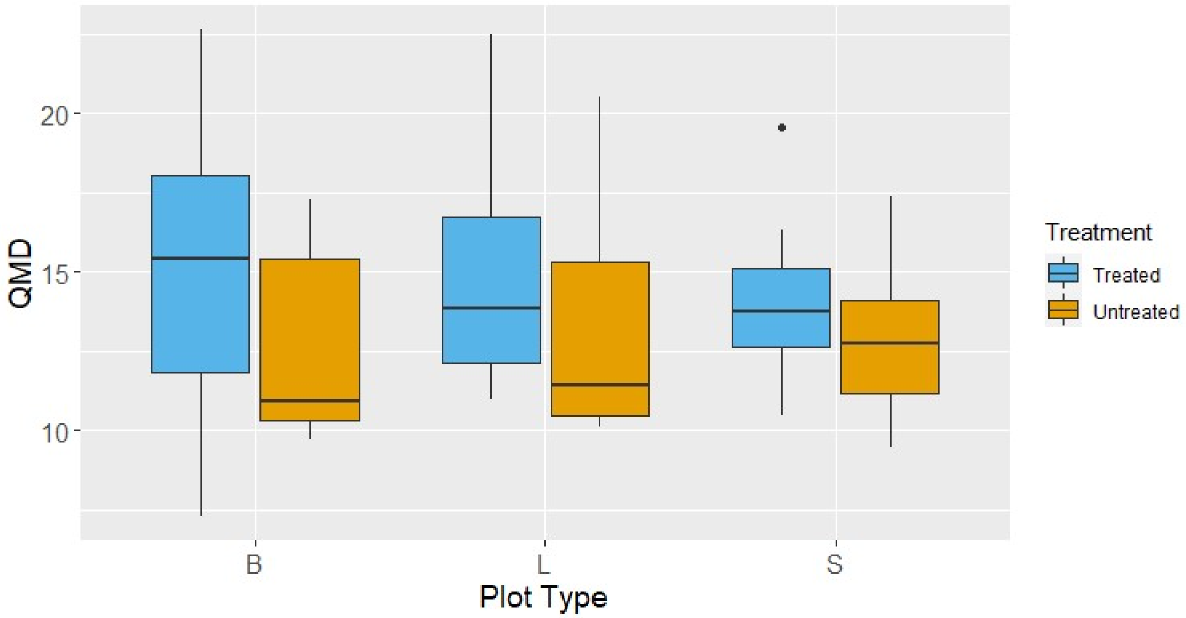

Figure 3.4. Quadratic mean diameter (QMD) (in) for the individual tree- and stand-scale means. No significant differences ($p > 0.05$) found among individual tree-scale or stand-scale means. Plot type = the type of plot the data were derived from; B = individual tree-scale, bark beetle-killed; L = individual tree-scale, live; S = stand-scale. See Methods & Materials and result sections for more details.

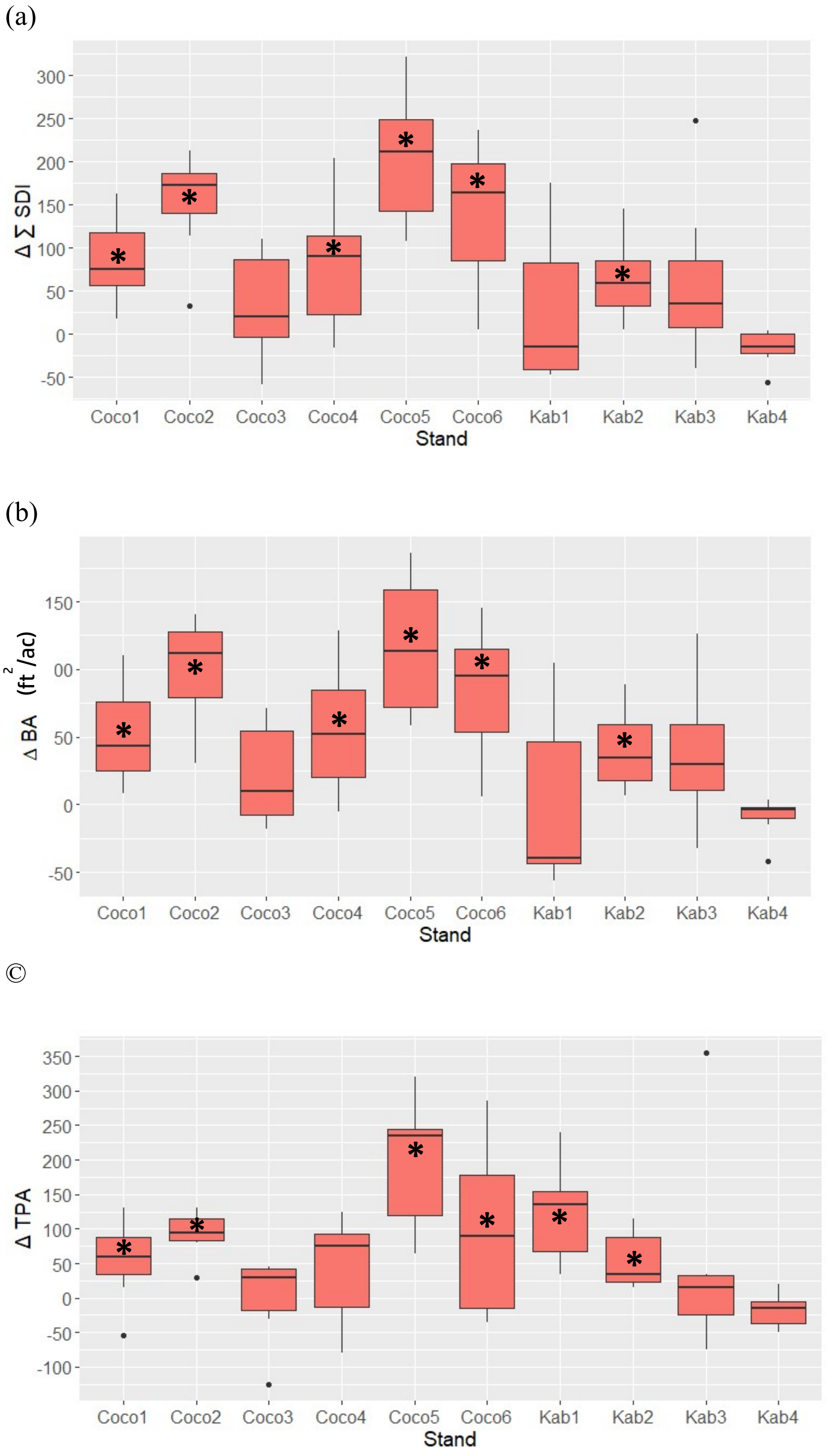

Figure 3.5. Mean differences in (a) summation stand density index (Δ∑SDI), (b) basal area per acre (ΔBA), and (c) trees per acre (TPA) between treated and untreated stands (calculated from the stand-scale plots). Significant differences ($p < 0.05$) indicated with *. Coco = Coconino National Forest; Kab = Kaibab National Forest. See results section for more details.

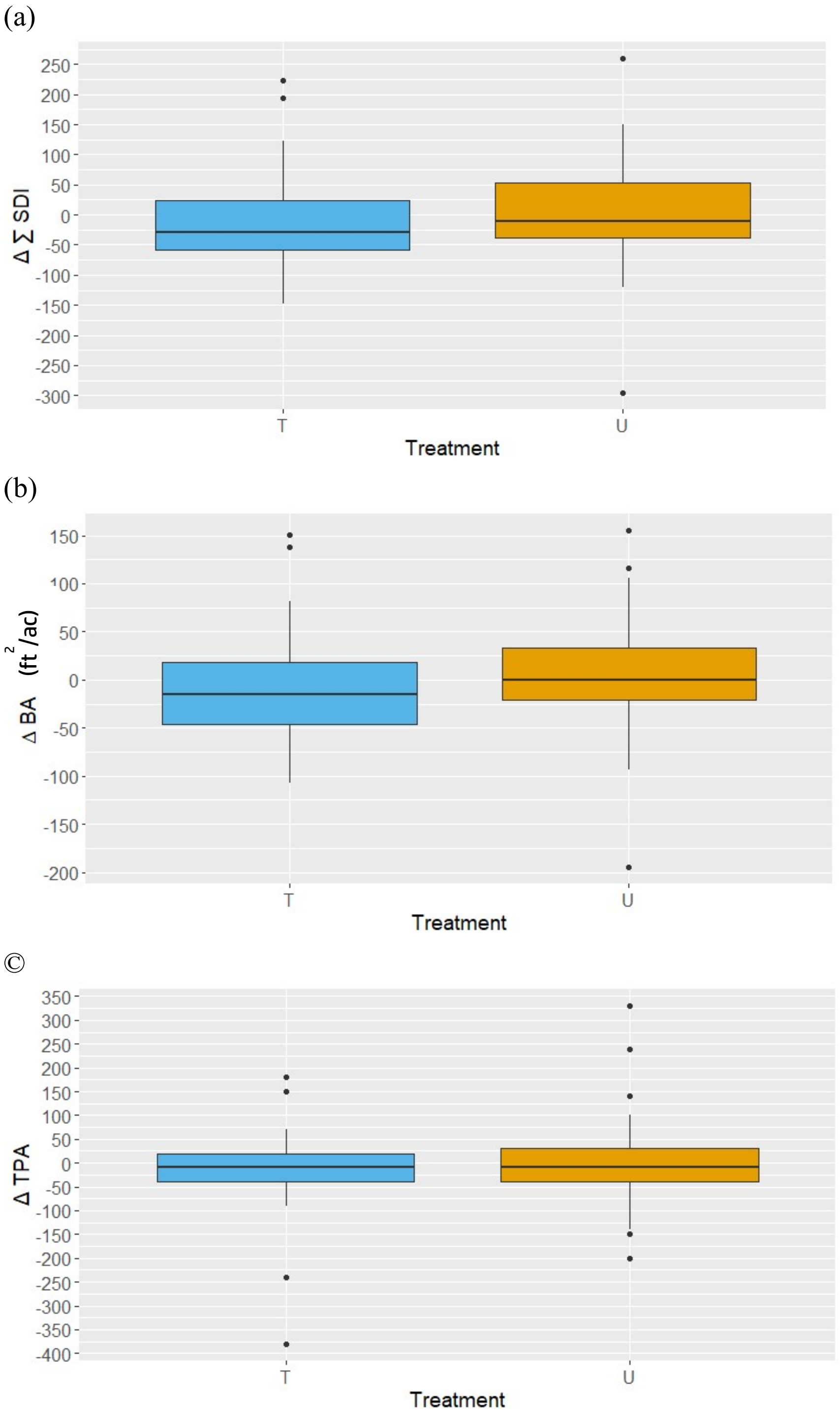

Figure 3.6. Mean differences in (a) summation stand density index (Δ∑SDI), (b) basal area per acre (ΔBA), and (c) trees per acre (TPA) between individual tree-scale means. No significant differences ($p > 0.05$) were found between the bark beetle-killed and paired live tree means within treated or within untreated stands for Δ∑SDI, ΔBA, and ΔTPA, or between paired treated and untreated stands.

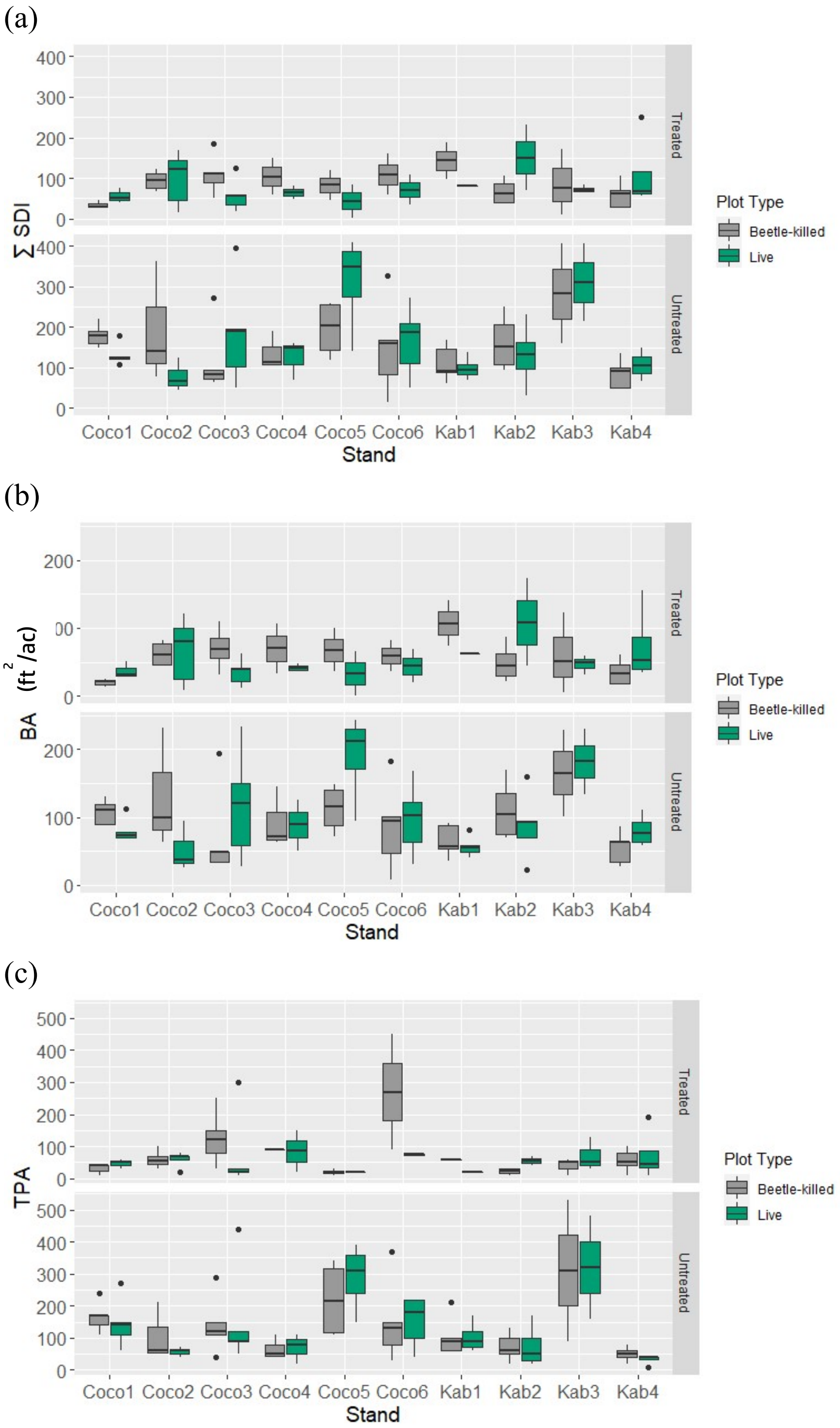

Figure 3.7. (a) Summation stand density index, (b) basal area per acre, and (c) trees per acre in treated and untreated stands (calculated from the individual tree-scale plots). Treated stands generally had less density compared to the untreated stands and bark beetle killed-means generally have higher values compared to the paired live mean. Coco = Coconino National Forest; Kab = Kaibab National Forest.

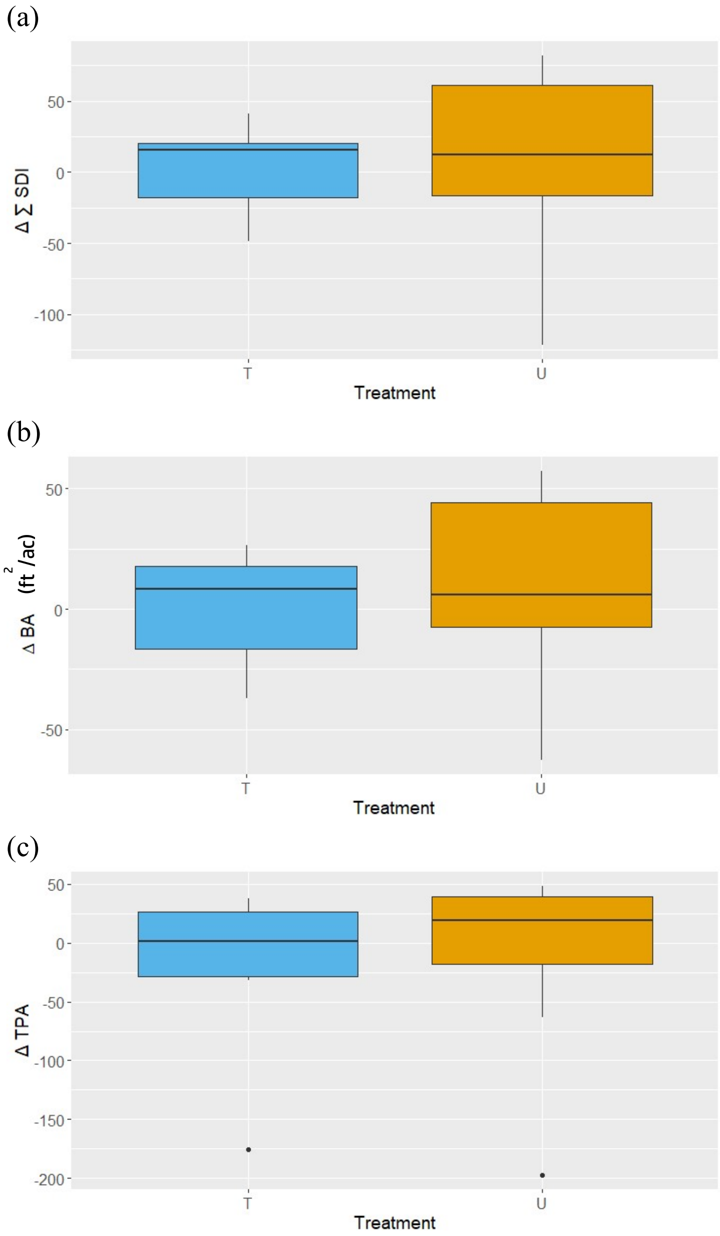

Figure 3.8. Mean differences in (a) summation stand density index (Δ∑SDI), (b) basal area per acre (ΔBA), and (c) trees per acre (TPA) between the individual tree-scale, bark beetle and stand-scale means. No significant differences ($p > 0.05$) were found between the individual tree-scale, bark beetle-killed and stand-scale means within treated or within untreated stands for Δ∑SDI, ΔBA, and ΔTPA, or between paired treated and untreated stands.

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CHAPTER 4

MANAGEMENT IMPLICATIONS

In the face of climate change, the Southwestern United States (US) forests are threatened by biotic and abiotic disturbances. The severity of bark beetle outbreaks has already begun to increase in space and time and therefore management to increase forest resilience and minimize susceptibility is critical (Bentz et al. 2010). As outlined in Chapter Three, the goals of this thesis were to analyze how bark beetles interact with complex spatial patterns and assess if there were differences in competition at the individual tree- and stand-scales that impacted bark beetle-caused tree mortality. Using proxies for competition, we made comparisons using t-tests to assess if there was less competition around trees killed by bark beetles compared with a similarly sized live tree (individual tree-scale comparisons) and the overall stand-scale metrics from treated and untreated stands. Although no statistically significant results were found when comparisons were made among all sampled stands, there were some significant differences within stands at the individual tree-scale, and recently published work showed that eliminating competition (other trees) to increase large tree survival was ineffective (Hood et al. 2022).

Across the Western US, forests were impacted by Euro-American settlement; most are now dense, overstocked, and have altered disturbance regimes (Churchill 2020). Conditions like these can be found in northern Arizona on the Coconino and Kaibab National Forests (Cooper 1960, Covington & Moore 1994a, Covington and Moore 1994b, Covington et al. 1997, Churchill 2020). Treatments are implemented to emulate forest conditions prior to Euro-American settlement when forests were far less dense and "park-like" in structure (Woolsey 1911, Kaufmann et al. 1994, Waltz et al. 2003, Roccaforte et al. 2009, Reynolds et al. 2013). Within the treatments, there is a strong emphasis on retention of large, old growth trees to create a heterogenous structure and provide other ecosystem services (Allen et al. 2002, Kolb et al. 2007). How bark beetles interact with treated and untreated landscapes is commonly addressed at the stand-scale but not at the individual tree-scale, with a few exceptions. Kane and Kolb (2010, 2014) paired bark beetle-killed trees with live trees in northern Arizona. They found that the live trees had more annual growth and larger and more abundant resin ducts, but that declines in short- and long-term growth increased the likelihood of bark beetle-caused tree mortality (Kane and Kolb 2010, 2014). Another study in northern Arizona showed that tree competition was negatively correlated with tree growth and phloem thickness, and tree competition and water stress were positively correlated, indicating that higher competition increased tree stress, and therefore susceptibility to, and mortality from, bark beetles (Zausen et al. 2005). More recently, Ferrenberg et al. (2022) paired bark beetle-killed and live trees in New Mexico and found that trees killed by bark beetles had more competition (basal area) surrounding them, which in-turn impacted their rates of growth and resin duct production. These results support the well-stated hypothesis that increased competition results in higher levels of bark beetle-caused tree mortality. In contrast, a study from southwest Oregon where silvicultural treatments put a similar emphasis on large diameter trees where Hood et al. (2022) examined the effects of radial thinning around large diameter trees. Radial thinning (also called crop tree release, daylighting, free thinning) removes vegetation around a focal tree to reduce competition and increase resilience (of the focal tree). They found that there was no clear benefit of radial thinning, and of the trees that died in the study, mountain pine beetle was responsible for most of the mortality (Hood et al. 2022). They concluded that radial thinning treatments are effective in increasing heterogeneous structures but are unlikely to meet the goal of retaining large trees on the landscape (Hood et al. 2022). Our study supports a similar hypothesis as we found that bark beetles are sometimes killing larger trees with less competition surrounding them.

Across the West, management objectives include creating a heterogeneous structure and retaining large, mature trees (Churchill 2020). Williams et al. (2013) reiterated the importance of mature trees, stating that their loss will result in less regeneration, which increases the risks of forest structural and compositional changes. In our study and Hood et al. (2022), there is some evidence that large, mature trees are dying from bark beetles. If implemented treatments are no longer promoting large tree survival like as intended, we need to ask why these changes are happening and what we can do about them? Unfortunately, there is no single, clear answer, however, there is evidence that our climate is changing, and bark beetle outbreaks are correlated with it (Bentz et al. 2010). As managers, we should be proactive and understand that such changes may lead to even greater uncertainty that should be considered (Mina et al. 2022).

Defined by Walters (1986), adaptive management is a philosophical approach that acknowledges uncertainty and that we have incomplete knowledge, but as managers, we must make decisions based on what we do know and what we have learned. Adaptive management, alongside resistance and resilience, have become terms that are integrated into forest management (Allen et al. 2011, DeRose and Long 2014). Evidence supports density reduction to alleviate bark beetle-caused tree mortality (Sartwell 1971, Feeney et al. 1998, Negrón & Popp 2004, Fettig et al. 2007, Gaylord et al. 2010, Hood et al. 2016, Negrón et al. 2017), and these treatments also increase resilience, reduce competition, and fire hazard. Large tree survival is an important component of treatments, and results from this study indicate that bark beetles are sometimes killing large trees that are often targeted for retention in silvicultural treatments. We suggest monitoring old growth trees and using adaptive management, such as a modified treatment, where large old growth trees are not the only tree left in openings. Long-term monitoring will help managers recognize patterns that can then allow them to further adapt or use nontraditional approaches to try and overcome changes (Allen et al. 2011, Nagel et al. 2017). As a result of this study, we support continued use of density reduction treatments to reduce bark beetle-caused tree mortality and treatments that create complex spatial patterns to increase resilience and resistance, while simultaneously experimenting with modifications of current treatments and monitoring for changes.

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APPENDIX

SUPPLEMENTAL TABLES AND FIGURES

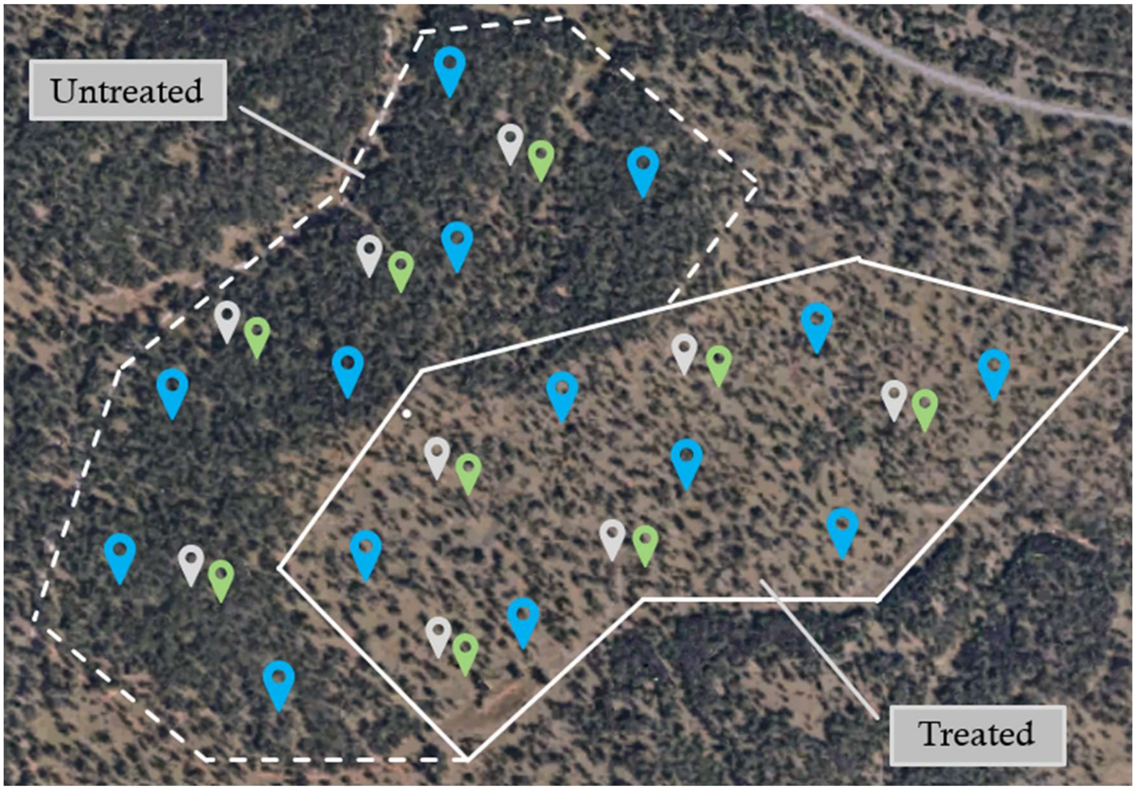

Figure A1. Example of the two plot networks within a treated and untreated stand. Blue points = stand-scale plots. Grey and green points = individual tree-scale paired plots. Stand-scale plots were randomly located in each stand to measure stand structure, density, and abiotic characteristics. Individual tree-scale plots were implemented to measure individual tree competition by pairing a bark beetle-killed tree and similarly-sized live tree. For more details, see Chapter 3, Methods and Materials.

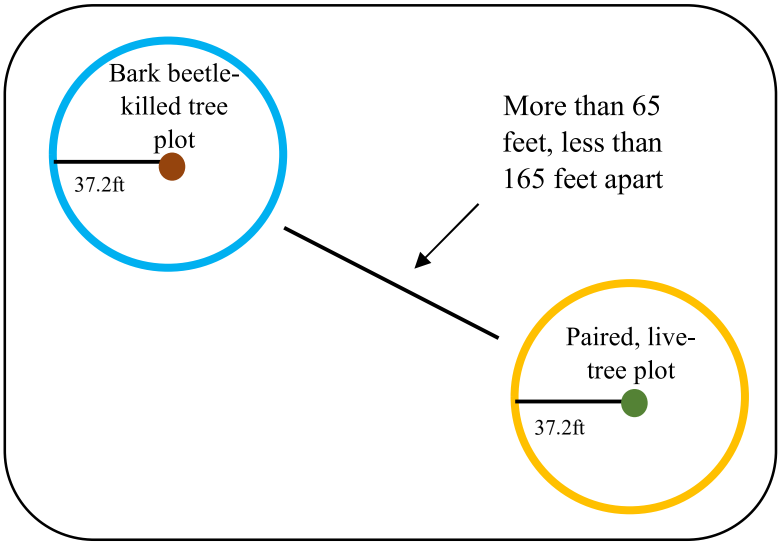

Figure A2. A diagram of the individual tree-scale circular plots (r = 37.2 ft). Plots were paired and comprised of one bark beetle-killed tree (brown dot) and one live tree (green dot) of similar size (within 10% DBH). To ensure plots did not overlap one another and were under similar conditions, they were more than 65 feet but less than 165 feet apart.

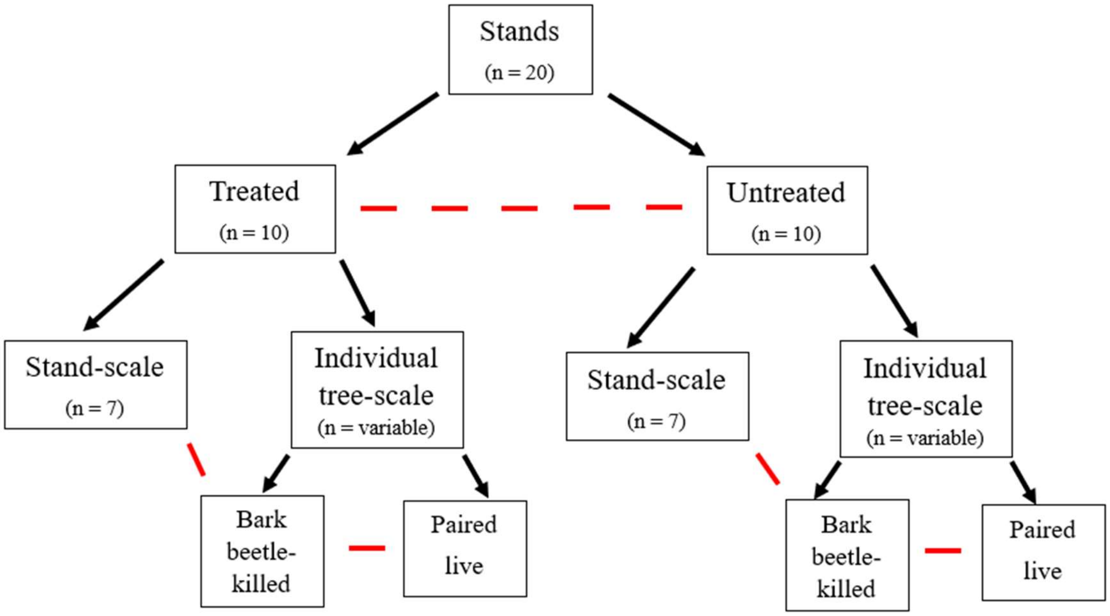

Figure A3. Study design and statistical comparisons. We had a total of 20 stands, 10 treated and 10 untreated. Comparisons were made between treated and untreated stands at both the individual tree- and stand scale, between the individual tree-scales, and between the stand-scale and individual tree-scale, bark beetle-killed. Red dashed lines show comparisons. A combination of t-tests, paired t-tests, weighted t-tests, one-way t-tests were used. For more details, see Chapter 3, Methods and Materials.

Table A1. Silviculture prescriptions from treated stands on the Coconino and Kaibab National Forests. Prescriptions were obtained from local National Forest silviculturists. N/A = variable not included in a prescription.

Stand	Future Conditions/Objectives			Treatment prescribed	Treatment type & year	Prescribed burn?
	Structure & Spatial Patterns	Density	Fire & Forest Health			
Coco1	Clumpy, uneven-aged, multi-storied PIPO forest structure that emulates conditions prior to 1870 Canopy closure average = 30%	BA = 0-40 ft^2/ac	Fire risk reduction Reintroduction of frequent ground fires	Individual tree selection	Commercial Cut 2008	Yes, 2015
Coco2	Decrease canopy cover Retain and increase a variety of age/size classes Reduce canopy closure to ~40% averaged across clumps and openings to increase spacing between crowns Canopy closure will be variable with a stand average of 40% Create 20% openings for natural regeneration between clumps	Basal area = 60-120ft2 within clumps	Reduce torching risk Increase tree health, growth, and vigor, decrease the height to which firebrands are lofted and the distance at which spot fires would occur, reduce torching	Group selection	Commercial cut 2008	Yes, 2015
Coco3		Reduce density of existing PIPO to improve the health and vigor of PIPO and Gamble oak	Reduce the potential for a wildfire from crowning and spotting		Cut 2012	No
Coco4	Uneven-aged, clumpy structure that closely resembles pre-settlement forest conditions. Retain and increase a variety of age/size classes	Basal area variable, range from 80-120 ft2 within clumps, openings between clumps Canopy closure variable, stand average across clumps and openings = 50%	Reduce fire torching and likelihood of spot fires Open, healthy, vigorous PIPO forest structure that has low fire hazard and conducive to the reintroduction of low intensity surface fire	Group selection	Commercial cut 2010	Yes 2015

			Increase tree health, growth, vigor			
Coco5	Uneven-aged, clumpy structure that closely resembles pre-settlement forest conditions. Retain and increase a variety of age/size classes Increase spacing between crowns	Basal area variable, range from 80-120 ft2 within clumps, openings between clumps Canopy closure variable, stand average across clumps and openings = 50%	Reduce fire torching and likelihood of spot fires Open, healthy, vigorous PIPO forest structure that has low fire hazard and conducive to the reintroduction of low intensity surface fire Increase tree health, growth, vigor	Group selection	Commercial cut 2010	Yes 2015
Coco6		Cut all ponderosa pine up to 12” DBH; all junipers up to 14” DRC; all snags up to 18” DBH Do not cut oaks or shrubs	Branches of large junipers may be pruned to reduce ladder fuels		PCT 2012	No
Kab1	No yellow pine will be removed Irregular spacing of trees Leave trees are to be left individually and in groups of 2-6 trees.	Mean BA 70ft2/ac	N/A		Thin from below, retaining larger diameter dominant and co-dominant trees; 2006	
Kab2	Retain all yellow pines Remove mistletoe infected conifers Heavily thin (0-20BA/ac) blackjacks less than 16” DBH within one chain of yellow pine or yellow pine groups Create ½ to 2 acre forage openings in 20% of unit; if opening is 1 acre or less, remove all PIPO; in openings >1 acre, include one group of 3-5 largest pines, free of mistletoe	Average BA = 60ft2/ac	Reduce fire risk in wildland urban intensive zone by reducing tree density and breaking up continuous fuels		Commercial irregular thin with forage openings 2007	

Kab3	Improve vigor and longevity of and retain all yellow pines Remove all mistletoe infected blackjack ponderosa pine Irregular spacing of trees Leave trees are to be left individually and in groups of 2-6 trees. If average diameter is between 5 and 9”, average spacing = 25’x25’	Mean BA 70ft2/ac if the average diameter leave tree is > 12” dbh Mean BA = 50ft2/ac if average diameter is 9-12” dbh	Reduce fire risk in wildland urban intensive zone by reducing tree density and breaking up continuous fuels		Commercial Irregular Thin 2006	
Kab4	Improve diversity of vegetative size, density, and structure Increase vigor and longevity of and retain yellow pines Divide the area into ¼ to 1 acre groups Irregular spacing within groups to be thinned	Heavily thin (0 to 20 BA/ac) blackjacks less than 18” dbh within 60’ of yellow pine or yellow pine groups 1/3 of the area to low density – 20 BA/ac 1/3 of the area to moderate density – 50 BA/ac 1/3 of the area to high density – 80 BA/ac	Reduce fire risk Increase tree growth, vigor, and crown development		Irregular thin 2008	