Host richness increases the occurrence but not the severity of bark beetle-induced tree mortality

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# Abstract

Key findings

# Keywords

# Introduction

Paragraph 1: Theoretical context - plant & insect interactions

Many studies have sought to understand how community diversity influences interactions between natural enemies and their resources. In the case of plant-herbivore interactions, greater plant diversity often reduces herbivory on plants at both the individual and population level (i.e., ‘associational resistance,’ Barbosa et al. 2009). This is hypothesized to occur when insect herbivores, particularly specialists, are less likely to find and stay in areas where their hosts are less abundant (i.e., ‘resource concentration hypothesis,’ Root 1973). This may occur if insects are less likely to encounter their host due to decrease in host frequency or abundance [i.e. ‘host dilution effect’, @], heterospecific neighbors chemically mask host trees (i.e. ‘host apparency hypothesis,’ **castagneryrol\_effects\_2014?**), mixed stands favor greater abundance of herbivore natural enemies Staab and Schuldt (2020). However, increased tree diversity may also result in an increase in herbivore richness (‘resource specialization hypothesis,’ **keddy\_plant\_1984?**). Yet little research has examined community-level outcomes, which are often hard to quantify because of the number of potential interactions increases dramatically with increasing community diversity, particularly when natural enemies are generalists. Further, the effects of different natural enemies on their focal host populations often differ greatly, due to differences in susceptibility and mortality rates and the availability and quality (as viewed by their natural enemies) of resource communities. Critically, community-level outcomes may drive ecosystem processes, particularly when community diversity is low and plant-herbivore relationships are highly dynamic. In this context there is a particular need to understand the effects of tree diversity on outbreaks of irruptive insects, which in recent years (2003-2012) have affected 85 million hectares of forest globally, or ca. 18 million hectares more than wildfire (Lierop et al. 2015), resulting in widespread changes in carbon sequestration (e.g., Kurz et al. 2008), timber production (e.g. **schowalter\_insect\_2012?**), and water quality (e.g., **Mikkelson\_bark\_2013?**), among other things.

Paragraph 2: Bark beetles

Bark beetles (Curculionidae: Scolytinae) are among the few native insect species that can kill large numbers of trees in a single year. For instance in the western United States, recent outbreaks of native bark beetles have killed 3.8 billion trees [1997-2018; Hicke et al. (2020)]. Bark beetles bore through the bark, where they mate and oviposit their eggs. Concurrently, bark beetles introduce pathogenic fungi Larvae feeding upon the phloem and fungal spread stop the translocation of water and nutrients and cause tree death. Conifer defense against bark beetles consists primarily of resin exudation that physically expels the beetle and allelochemicals, which repel or kill beetles. To overcome these defenses and colonize live trees, bark beetles rely on a mass-attack strategy, where pioneering beetles emit aggregation pheromones that call conspecifics to the tree. Typically bark beetles exist at low population levels and attack weakened trees, but as populations increase bark beetles attack increasingly better defended trees. Such severe mortality occurs only during outbreaks when pheromone-mediated mass-attack allows bark beetles to overcome tree defenses.

For instance, a primary goal of the Western Bark Beetle is to promote resilience of forests to bark beetle outbreaks by increasing the diversity of age classes and tree species.

Paragraph 3: Bark beetles

To better understand how community diversity influences interactions between bark beeetles and their resources, we use a natural system with inherently low tree and bark beetle diversity. Specifically our research focuses on tree mortality due to three bark beetle species, the mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*D. rufipennis*), and western balsam bark beetle (*Dryocoetes confusus*), which in subalpine forests of Western North America predominantly attack lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), respectively. We use this system to ask:

1. Is co-occurrence of multiple trees susceptible to bark beetle attack common?
2. How often do stand conditions susceptible to multiple bark beetles occur?
3. Given stand stand conditions susceptible to multiple bark beetles, does the the occurrence or severity of cumulative bark beetle mortality

We expect that co-occurrence of trees of different host species will be common, but co-occurrence of stand conditions suitable for multiple bark beetle species will not. Given stands where conditions are suitable for multiple bark beetle species, occurrence of bark beetle-driven tree mortality will be greater (i.e. diversity begets diversity), but severity will be lower (i.e. resource concentration).

host tree richness or identity influence the occurrence and severity of tree mortality due to bark beetles at the community-scale?

To test these hypotheses, we used a large dataset consisting of XXX,XXX plots established by the United States Forest Service Forest Inventory and Analysis Program (FIA; <https://www.fia.fs.fed.us/>). Specifically we ask:

We also expected the severity of bark beetle infestation to vary with the number of agents present, but with two alternative hypotheses. If the population dynamics of each bark beetle species are independent, then stands with multiple agents will experience higher tree mortality than stands with only one agent (i.e. additive effects). Alternatively, lower tree mortality may occur if concurrent outbreaks of bark beetles of different species cause semiochemical confusion or if competitive release increases tree defensive capacity.

# Methods

## Study area

The study area consists of subalpine lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) forest in the Intermountain West (i.e., Arizona, New Mexico, Colorado, Utah, Nevada, Idaho, Montana, Wyoming)

## Data

### FIA data

The FIA program is a single inventory program that includes all public and private forested land (>= 0.4 ha in size and >= 10% canopy cover) in the US. In the Western US, all plots are visited once every ten years (Gray et al. 2012). The spatially and temporally distributed probabilistic sampling design is useful studies of the distribution of tree species (e.g., Iverson and Prasad 1998, Rehfeldt et al. 2006), forest insects (e.g., DeRose et al. 2013), and tree mortality (e.g., Shaw et al. 2005)

At each FIA plot, field crews collect data for trees (>= 12.7 cm DBH) within four 7.32 m radius subplots arranged in a fixed pattern. Data on the proximate cause of death is collected for any tree (>= 12.7 cm DBH) that was alive at the previous visit and at revisit is dead using visible evidence (e.g., fire scars, bark beetle galleries).

#### Determination of presence/absence of bark beetle activity

For each live tree (>= 12.7 cm DBH), field crews record up to three damaging agents, which are defined as agents that are likely to prevent the tree from surviving >2 years, reduce the growth of the tree in the near term, or negatively affect the tree’s marketable products (Burrill et al. 2017).

Cause of death codes are very broad (e.g., “insect” or “disease”). Accuracy of FIA data is commonly assessed using blind checks, where two crews perform independent inventories. Agreement between mortality agent codes recorded in the two inventories is generally >80% (Anderegg et al. 2015). Active damage is easier to identify, thus the codes for damaging agents are much more specific.

#### Calculation of stand characteristics

For each plot, we then calculated 1 - basal area by host species 2 - quadratic mean diameter (QMD) 3 - basal area dominance (% total basal area) by species 4 - presence and severity of bark beetle activity (% total basal area) by bark beetle species

#### Selection of plots

We selected all plots that were part of the annual inventory and where all subplots were inventoried.

Within this plots, we characterized stand structure and composition using only live and recently killed (i.e. killed within the past ~10 years) trees greater that 12.7 cm DBH within the subplot.

## Analyses

### Model the suitable stand conditions

However, benefits provided by mixtures are less evident for larger-scale disturbances (Jactel et al. 2021) suggesting that changes in the structure of host communities, rather than biodiversity per se, can explain when a dilution effect should be observed.

Construct random forest models using synthetic minority oversampling technique (SMOTE), an approach for dealing with imbalanced data. The SMOTE approach oversamples the minority class by synthesizing new cases from the minority class. We compared this approach with two other common approaches for dealing with imbalanced data in a random forest framework - balanced and weighted random forests and selected the approach that classified affected plots with the greatest accuracy.

# Results

## Do stand conditions suitable for multiple outbreaks commonly co-occur?

Across the 10,439 FIA plots examined here, 66% (n=5,850) contained at least two of the focal host species (Fig. 1). Subalpine fir was most likely to occur with other hosts (50% of plots), followed by Engelmann spruce (45% plots), and lodgepole pine (36% of stands). However, only 20% of all plots (n=7,294) were suitable for more than one bark beetle species. Conditions suitable for infestation in subalpine fir were most likely to co-occur with conditions suitable for infestation in another tree species (17% of stands).

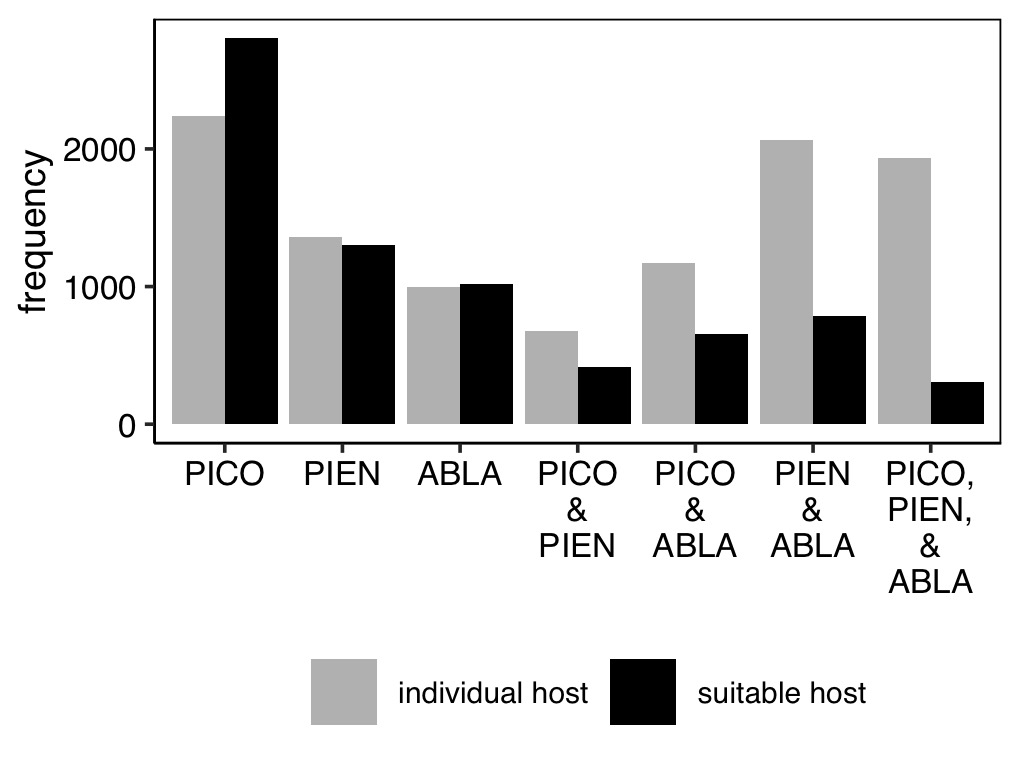


Figure : Figure 1: The frequency of plots by host identity. Gray bars indicate host species were present (i.e., at least one individual of the focal species was present within the plot). Black bars indicate stand structure and composition conditions were conducive to bark beetle infestation in focal tree species. For host identities, PICO is lodgepole pine, PIEN is Engelmann spruce, and ABLA is subalpine fir.

## Is occurrence or severity cumulative bark beetle mortality greater in stands with multiple hosts?

Given suitable stand conditions for multiple agents, the probability of occurrence of bark beetle attributed mortality was significantly greater than the probability of a single bark beetle species ??.

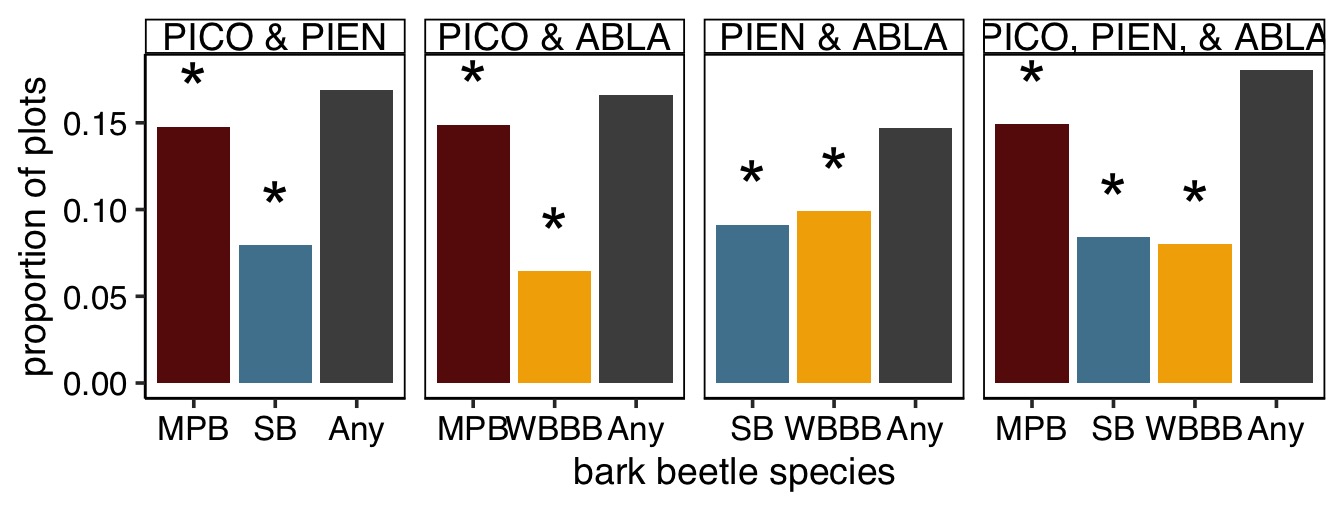


Figure : Figure 2: The proportion of plots affected by the mountain pine beetle (MPB), spruce beetle (SB), western balsam bark beetle (WBBB), or any bark beetle (i.e., MPB, SB or WBBB) by the identity of hosts species susceptible to bark beetle infestation. For host identities, PICO is lodgepole pine, PIEN is Engelmann spruce, and ABLA is subalpine fir. Astericks above bars indiciate that proportion plots affected by the individual bark beelte species was significantly less than the proportion of plots affected by any bark beetle species.

## Is the severity of cumulative bark beetle-driven tree mortality greater in stands with multiple susceptible hosts?

In stands susceptible for all three hosts, cumulative mortality was significantly greater than mortality by a single bark beetle species (Fig. 3. When stand conditions were suitable for only two bark beetles, the severity of cumulative tree mortality was driven by the most commonly occurring agent (MPB > SB > WBBB) and was not significantly different than the cumulative mortality (Fig. 3.

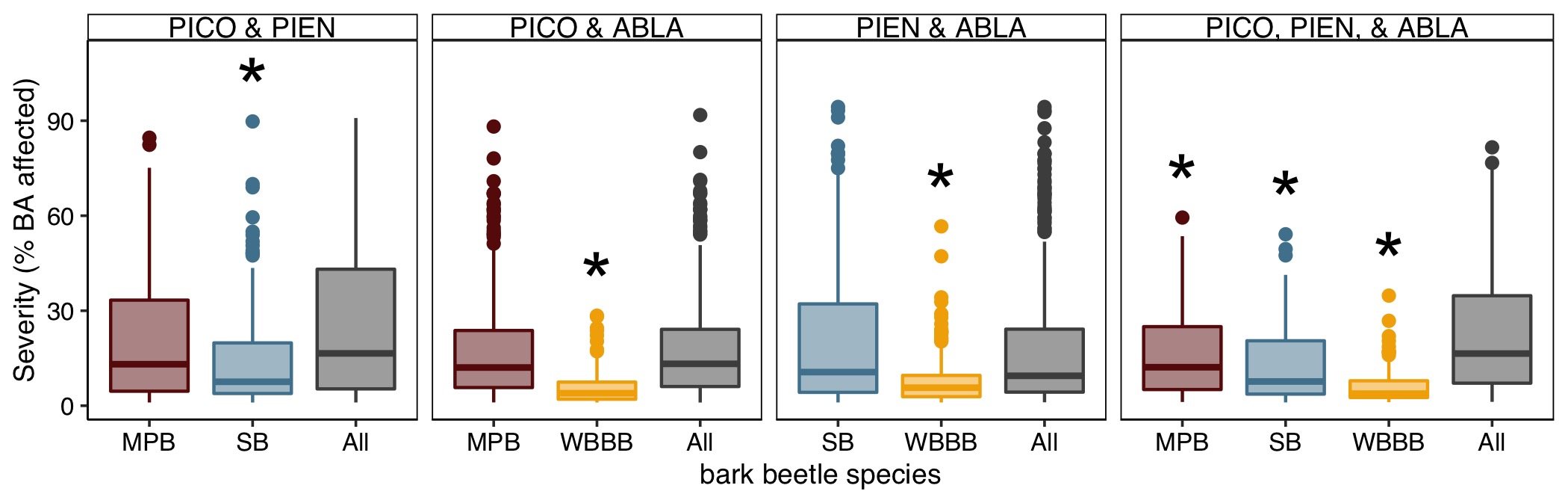


Figure : Figure 3: Boxplots illustrating the severity of mortality (% of total basal area) attributed to the mountain pine beetle (MPB), spruce beetle (SB), western balsam bark beetle (WBBB), or all bark beetles (i.e., cumulative mortality due to MPB, SB and WBBB) by the identity of hosts species susceptible to bark beetle infestation. For host identities, PICO is lodgepole pine, PIEN is Engelmann spruce, and ABLA is subalpine fir. The bottom and top limits of each box are the lower and upper quartiles, respectively; the thick black line within the box is the median; error bars equal ±1.5 times the interquartile range; and points denote outliers, values outside ±1.5 times the interquartile range. Astericks above boxes indicate that severity bark beetle mortality attributed to the individual species was significantly less than the cumulative mortality due to all bark beetles.

## Is the co-occurrence of multiple agents common?

Not really, only 21.3% (n=461) of stands suitable for multiple agents were affected by multiple agents. When multiple agents occur, the most commonly occurring agents was MPB (n=341), followed by SB (n=317) and WBBB (n=308). The most commonly occurring combinations of agents was MPB and SB (33.2% of cases; n=153), followed by MPB and WBBB (31.2% of cases; n=144) and then SB and WBBB (26% of case; n=120). The combination of all three agents was rare (9.5% of cases; n=44).

## Is severity greater in stands with multiple agents?

When plots contained two tree species susceptible to bark beetles, the presence of both bark beetle species increased tree mortality relative to presence of only one bark beetle species (Fig. 4). The increase was greatest for stands that contained both MPB and SB; the median severity of plots with both MPB and SB was 33.7 percentage points greater than MPB alone and 38.3 percentage points greater than SB alone. The median severity of plots with both MPB and WBBB was 7.0 percentage points greater than MPB alone and 13.6 percentage points greater than WBBB alone. The median severity of plots with both SB and WBBB was 14.7 percentage points greater than SB alone and 19.8 percentage points greater than WBBB alone.

Given stand conditions that made all three tree species susceptible to bark beetles, the highest rates of mortality were in plots where both MPB and SB present; whether or not WBBB was also present did not affect mortality severity (~1 percentage point difference in median severity; Fig. 4).

Plots with both SB and WBBB experience similar mortality to plots

The median severity of plots with all three agents was 16.2 percentage points greater than only MPB and WBBB and 27.4% percentage points greater than plots with SB and WBBB.

The median severity of plots with all three agents was most similar to plots affected by both

The median severity of plots with all three agents was 27.0 percentage points greater than MPB alone, 34.2 percentage points greater than SB alone, and 32.0% percentage points greater than WBBB alone.

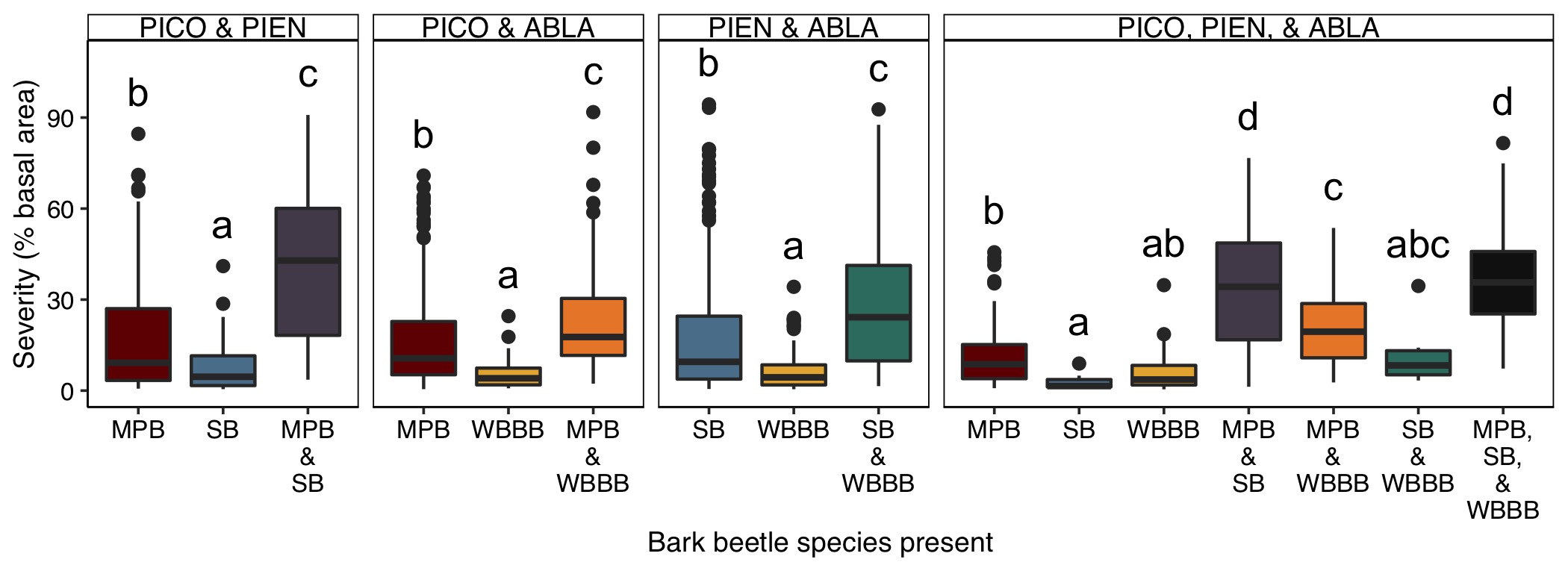


Figure : Figure 4: The severity of bark beetle mortality in plots with multiple tree species susceptible to bark beetles (columns) by the combinatin of bark beetle species present. Letters above boxes indicate significant (p < 0.05) differences between groups as determined by a Dunn test, a nonparametric rank sum test. The bottom and top limits of each box are the lower and upper quartiles, respectively; the thick black line within the box is the median; error bars equal ±1.5 times the interquartile range; and points denote outliers, values outside ±1.5 times the interquartile range.

# Discussion

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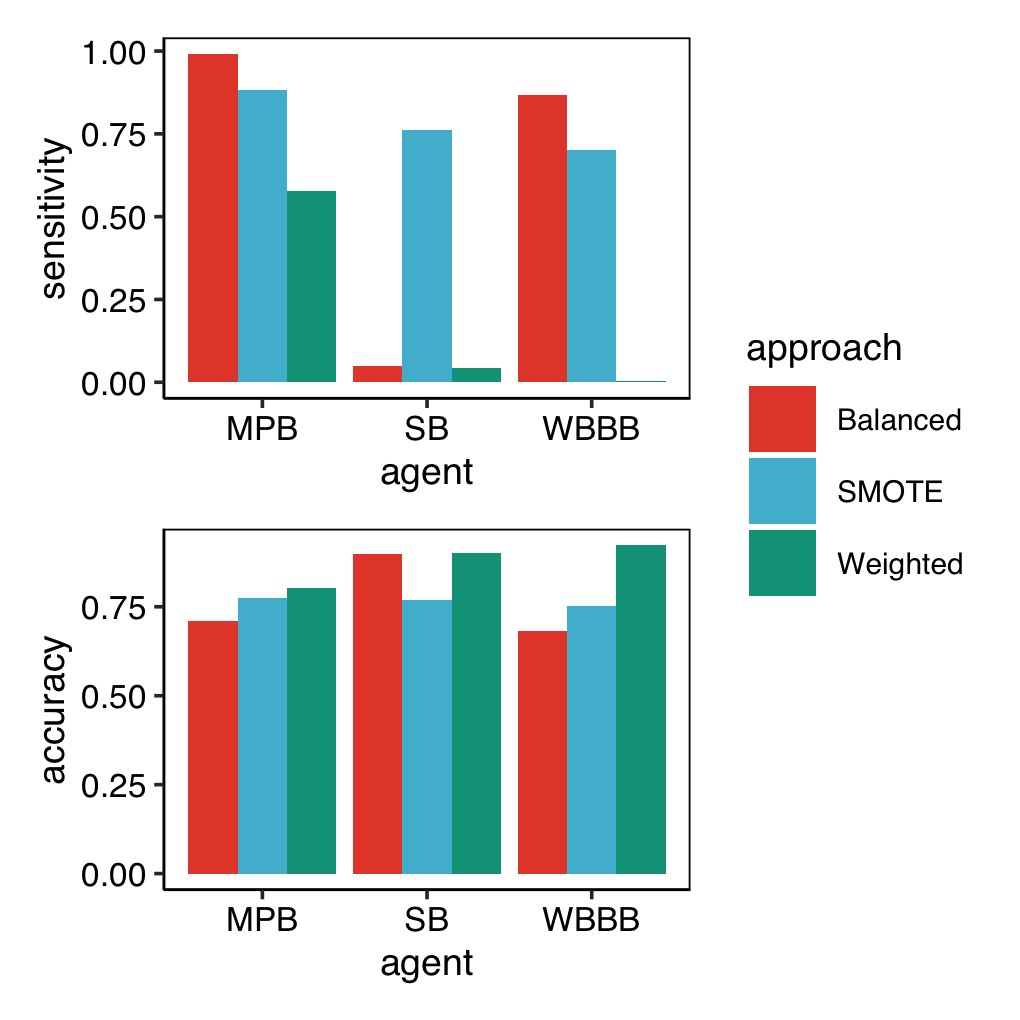
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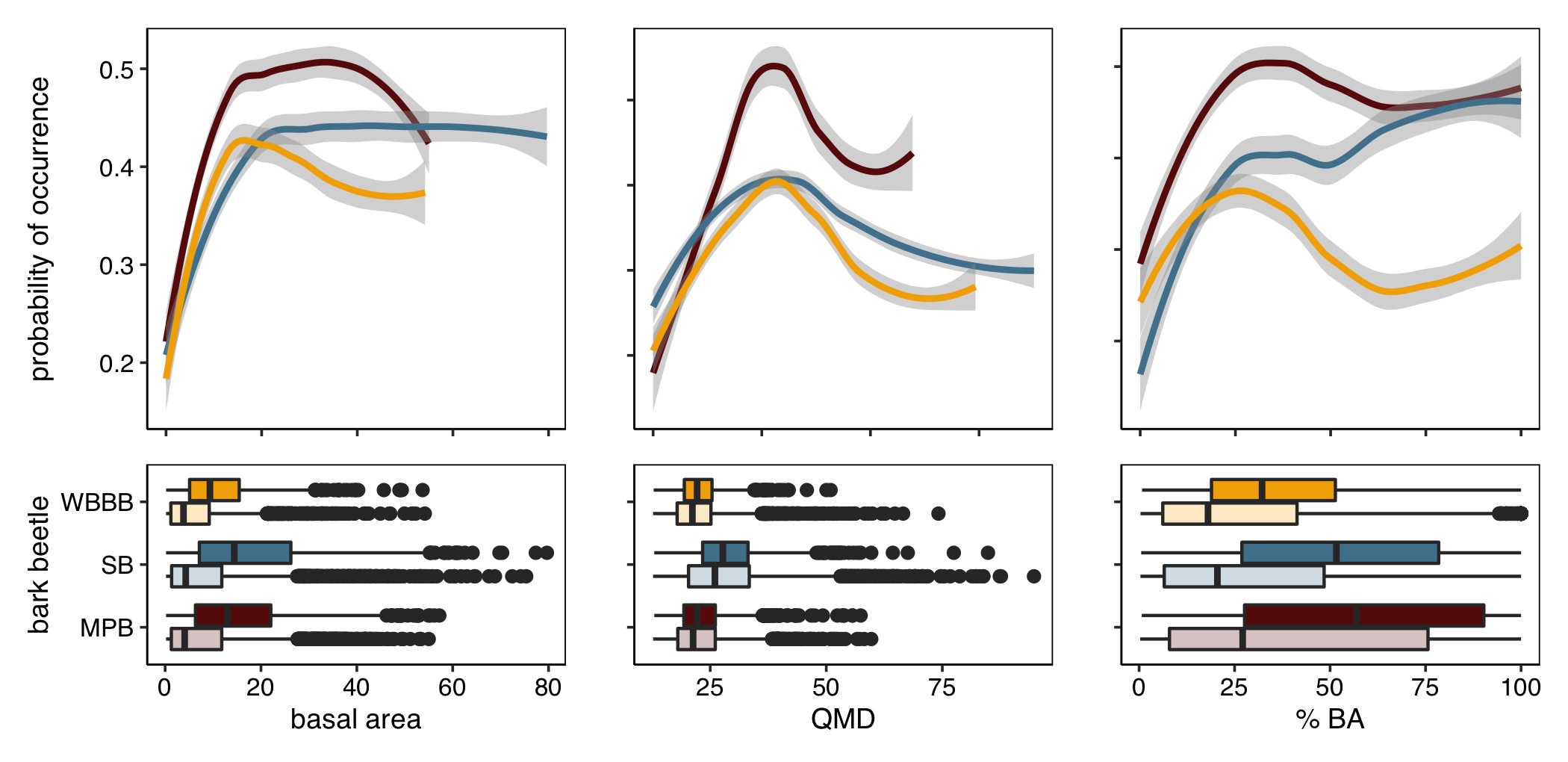
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## Supplement

### Random Forest Modeling



In general, the probability of each bark beetle species occurring increased with host basal area, quadratic mean diameter, and percent basal area. 

### Stand structure and composition in stands

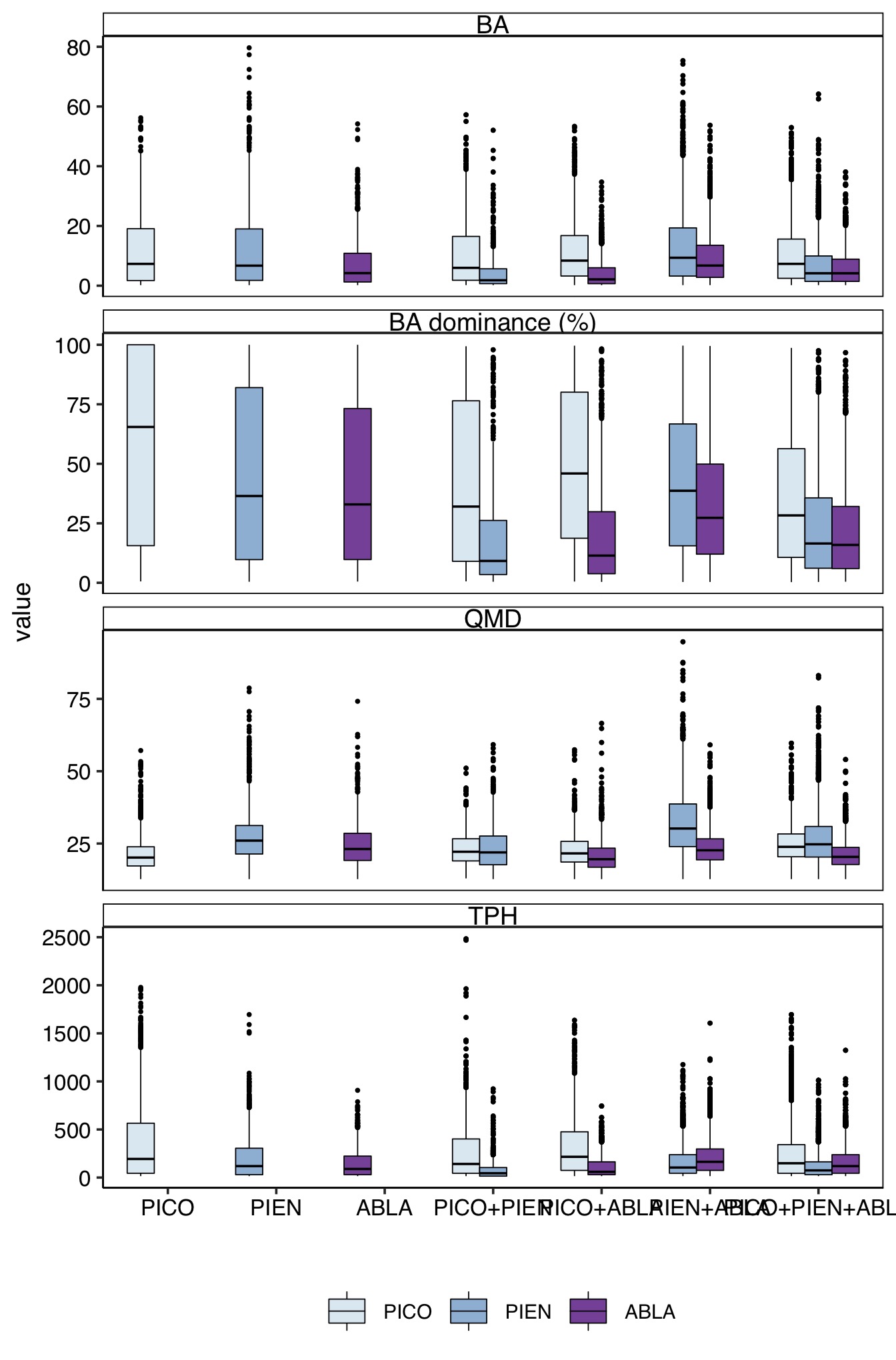


Figure : Figure 5: A caption

### Maps

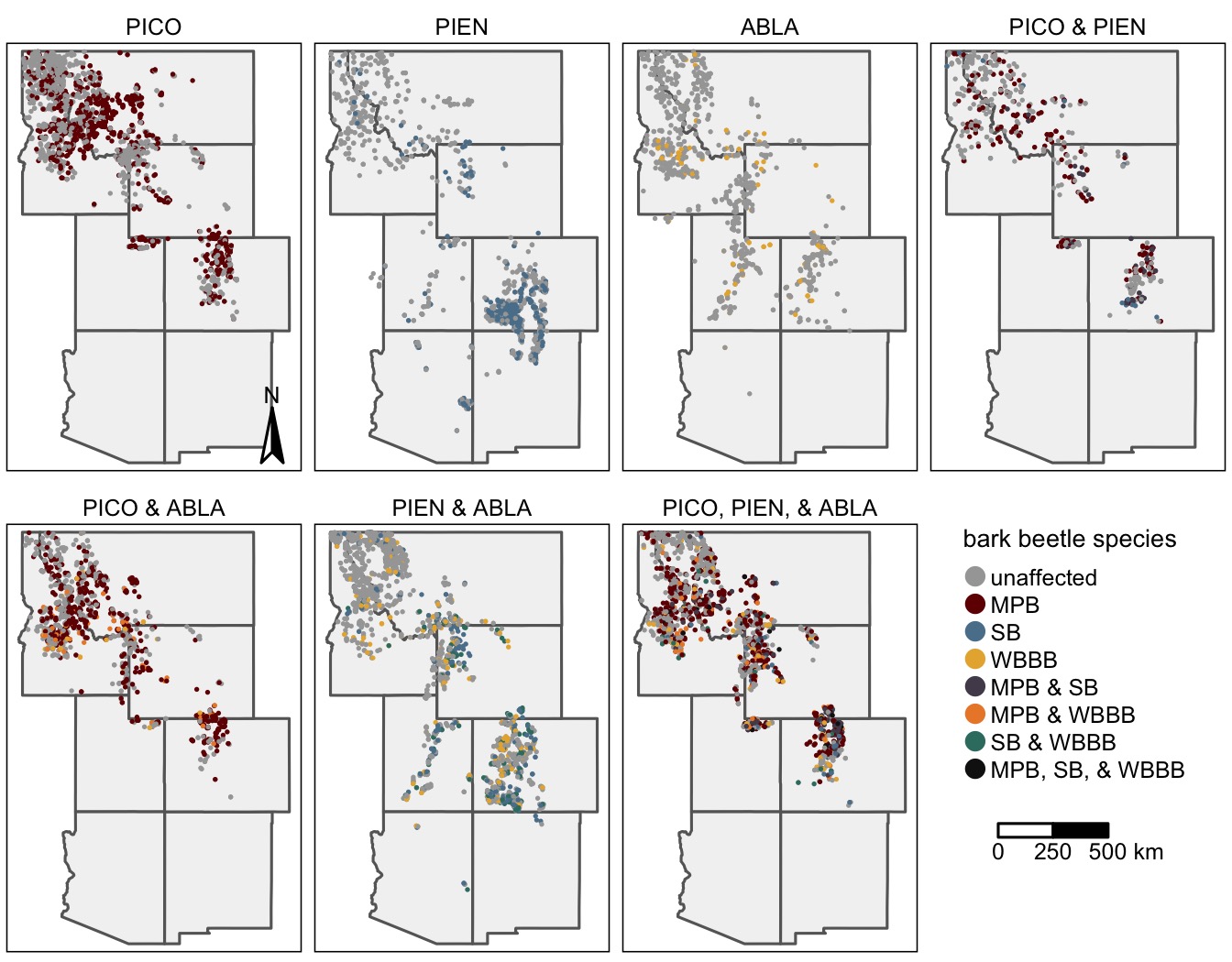


Figure : Figure 6: a caption

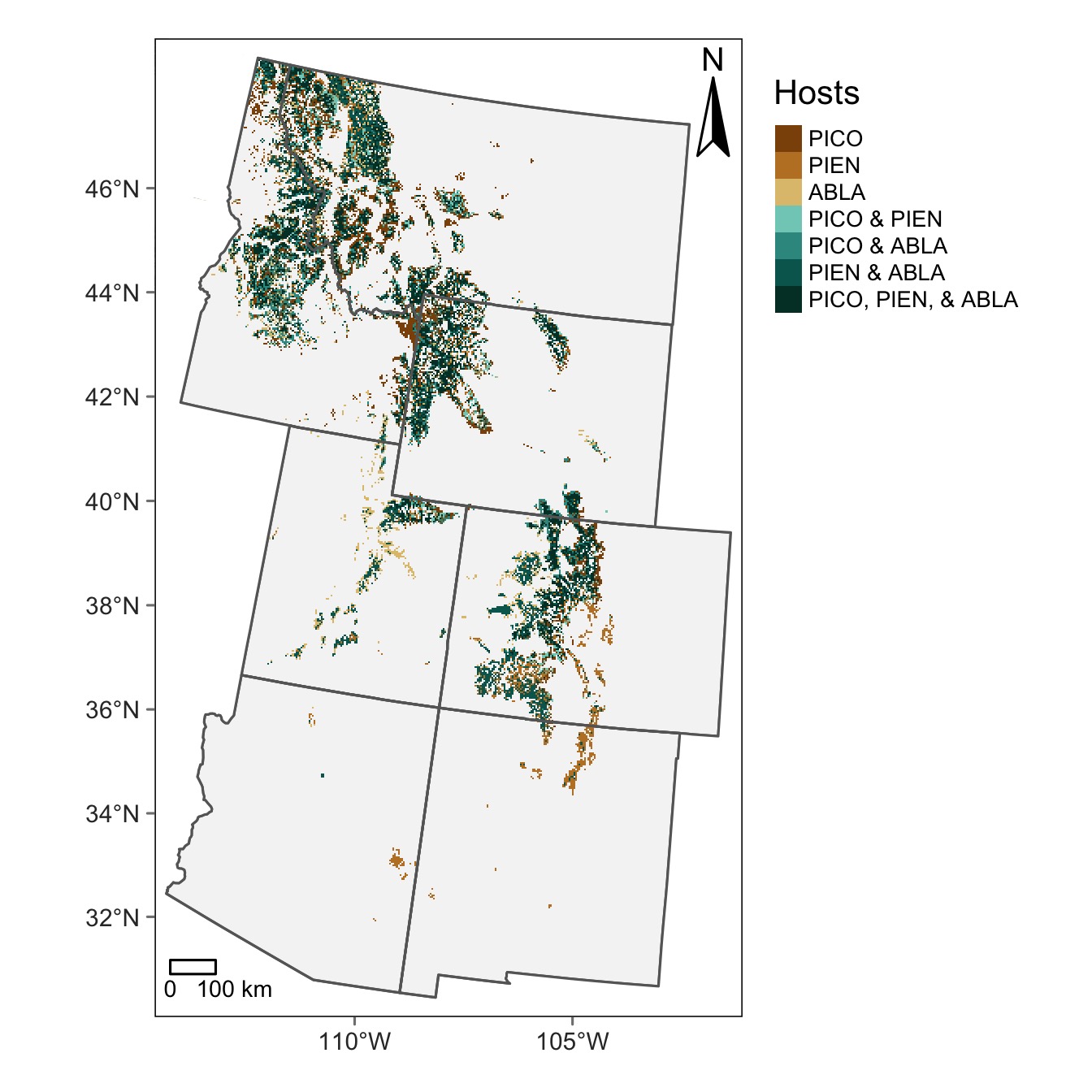


Figure : Figure 7: The distribution of host species presence across the study area. Data are from the Individual Tree Species Atlas (Ellenwood et al. 2015) and represent conditions in ca. 2002.

## Quatile comparison