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

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# Abstract

# Keywords

# Introduction

Paragraph 1: Broad applied context

In this context there is a particular need to understand interactions between 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 (van Lierop et al. 2015).

* insect outbreaks are causing widespread tree mortality in temperate forest worldwide
* future changes in climate are expected to increase tree mortality
* forests provide key ecosystem services
* management

Paragraph 2: Theoretical context - diversity & natural enemies - Many studies have sought to understand how community diversity influences interactions between natural enemies and their resources. - Key hypotheses: 1 - associational resistance - the abundance or damage of herbivores is lower when plant diversity is greater Jactel et al. (2021) hypotheses: 1 - resource concentration: the presence of heterospecific neighbors around a tree of a focal species grown in mixed stands leads to a lower probability of host tree finding by insect herbivores due to lower host abundance or frequency (Root 1973) 2 - host apparency: 3 - decoy: preference for non-host trees

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.

Most studies have focused on individual- or population-level outcomes.

For instance, increased host community diversity may either increase or decrease the susceptibility of individuals to their natural enemies.

At the population-scale these effects may either scale-up or result in counter-intuitive effects. However, 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 natural enemy-resource relationships are highly dynamic.

\*\*\* paragraph about irruptive species and community host diversity\*\*\* - stand scale - landscape scale

To better understand how community diversity influences interactions between natural enemies and their resources, we use a natural system with inherently low resource and natural enemy 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 whether host tree richness or identity influence the occurrence and severity of tree mortality due to bark beetles at the community-scale? We hypothesize that greater host richness will increase the probability of outbreak occurrence

Bark beetles (Curculionidae: Scolytinae) are among the few native insect species that can kill large numbers of trees in a single year. 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.For instance, in the continental western United States bark beetles have killed more than XXXX trees over the past X decades. 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.

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/>).

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).

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

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

## Is co-occurrence of multiple hosts common?

Yes, 66% (n=5,850) FIA plots had at least two host species present. Subalpine fir was most likely to occur with other hosts (50% of stands), followed by Engelmann spruce (45% stands), and lodgepole pine (36% of stands) (Fig. 1).

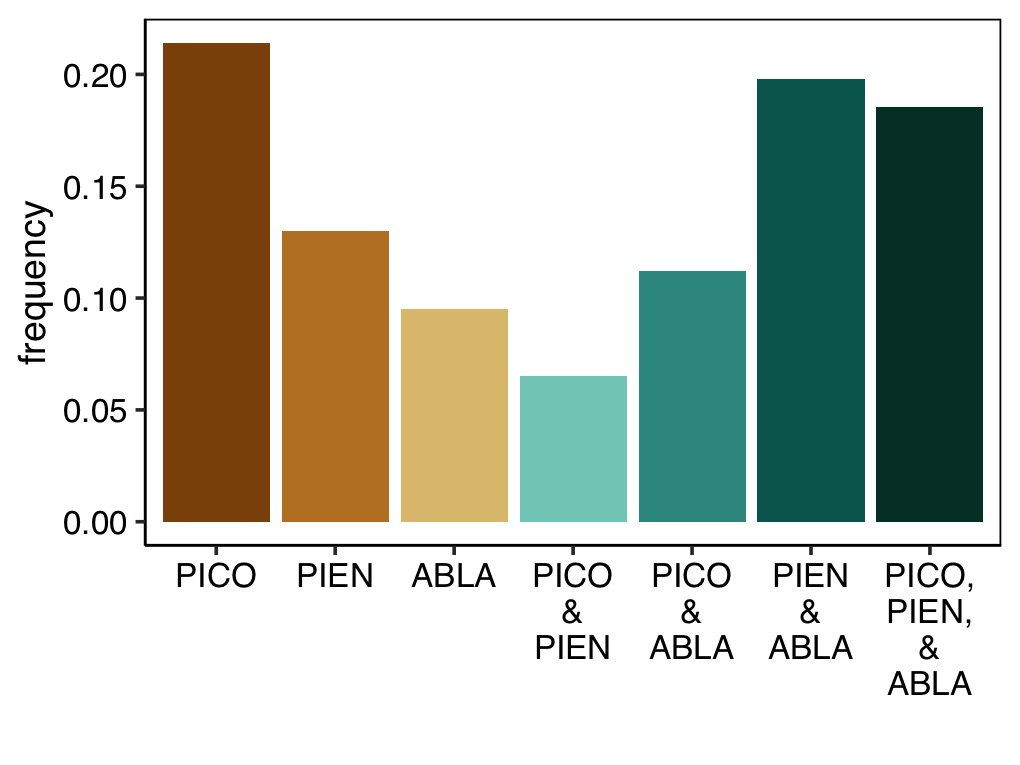


Figure 1: .

## Is co-occurrence of the stands conditions suitable for multiple bark beetle species common?

20% of stands were suitable for more than one bark beetle species. Conditions suitable for WBBB were most likely to co-occur with conditions suitable for another bark beetle (17% of stands)

(Fig. 2).

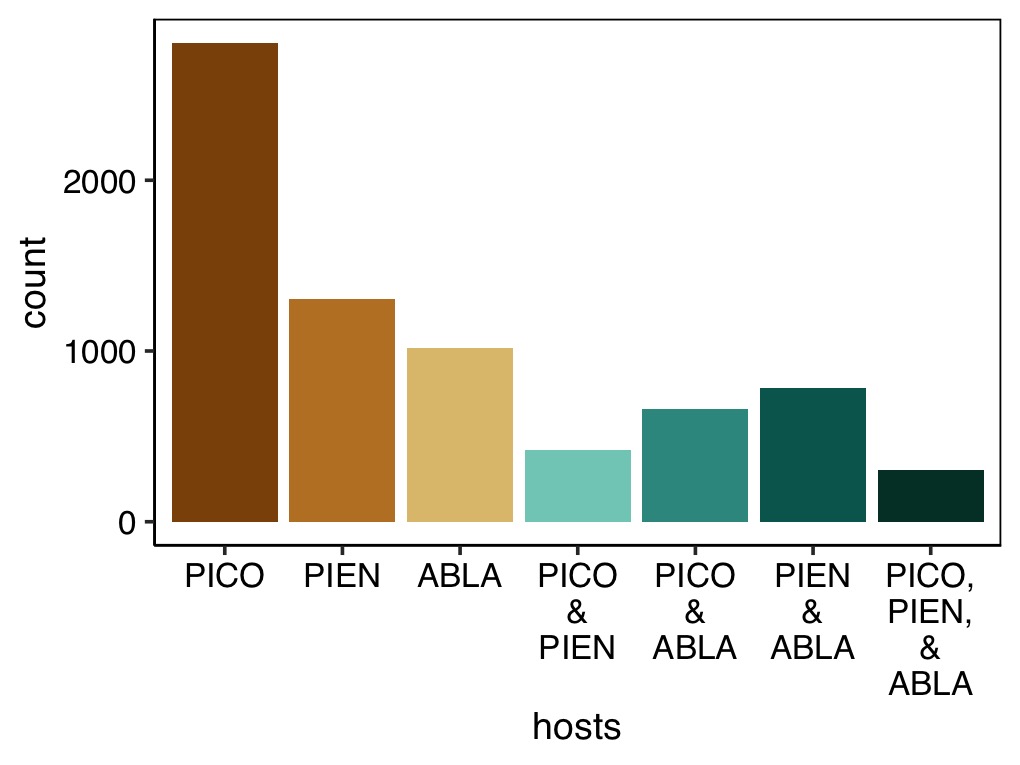
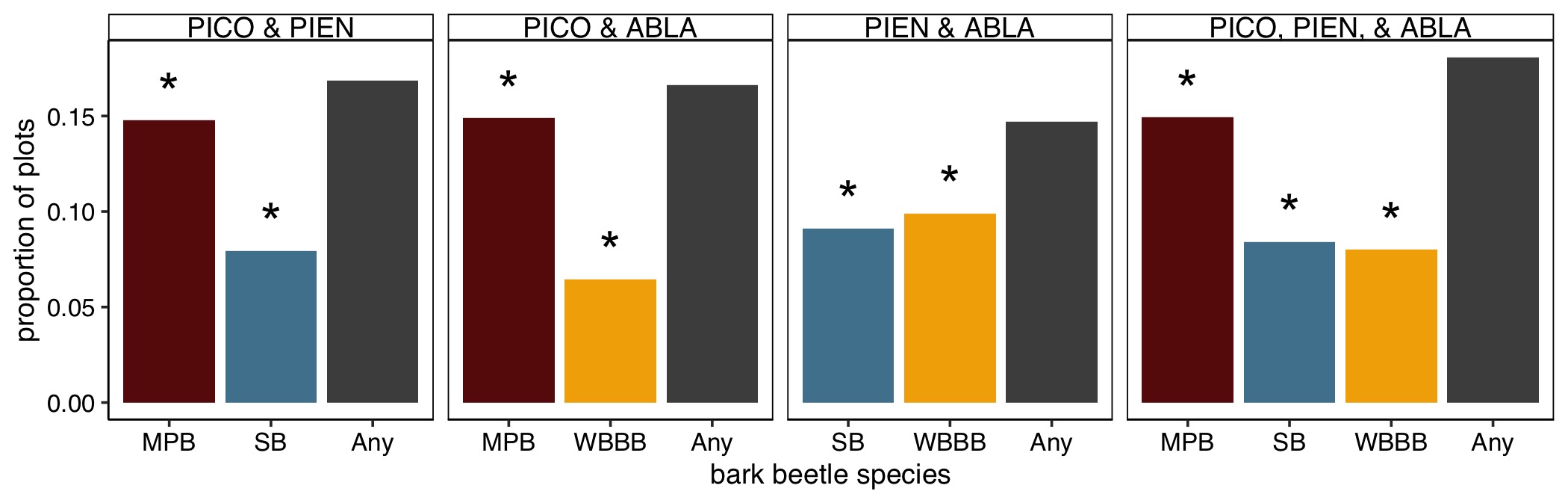


Figure 2: .

## 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 any agent was significantly greater than the probability of a single agent 2. 

Given suitable stand conditions for multiple agents, is the severity of cumulative bark beetle-driven tree mortality greater in stands with multiple hosts?

In stands suitable for all three hosts, cumulative mortality was significantly greater than mortality by a single agent. 4. When stand conditions were suitable for only two bark beetles, the severity of cumulative tree mortality was driven by the most common agent (MPB > SB > WBBB) and was not significantly different than the cummualtive mortality.

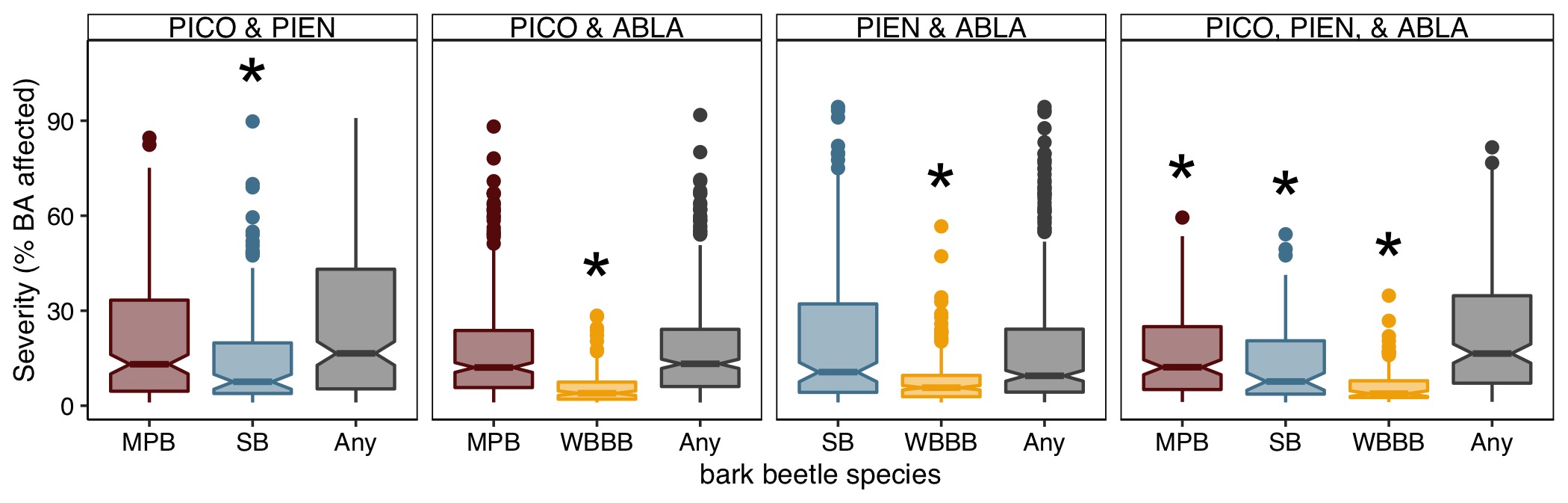


Figure 4: Severity

## Given suitable stand conditions, is 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).

agentsF

n

freq

MPB+SB

153

0.3318872

MPB+WBBB

144

0.3123644

SB+WBBB

120

0.2603037

MPB+SB+WBBB

44

0.0954447

n

2163

## [1] 335

## [1] 0.065893

## [1] 305

## [1] 0.05862003

## [1] 299

## [1] 0.04980843

##   
## MPB MPB+SB MPB+SB+WBBB MPB+WBBB none SB SB+WBBB WBBB  
## PICO 3795 77 0 50 3437 18 0 36  
## PIEN 26 42 4 0 2113 1028 34 38  
## ABLA 68 0 0 23 2187 25 44 493  
## PICO\n&\nPIEN 487 329 8 16 576 96 12 12  
## PICO\n&\nABLA 813 28 20 375 957 4 0 139  
## PIEN\n&\nABLA 24 16 4 4 1324 332 344 407  
## PICO,\nPIEN,\n&\nABLA 248 204 144 128 336 36 24 92

suitablehostsF

agentsFplongrev

n

freq

PICO & PIEN

MPB, SB, & WBBB

6

0.0053715

PICO & PIEN

SB & WBBB

9

0.0080573

PICO & PIEN

MPB & WBBB

12

0.0107431

PICO & PIEN

MPB & SB

238

0.2130707

PICO & ABLA

MPB, SB, & WBBB

15

0.0089392

PICO & ABLA

MPB & WBBB

268

0.1597139

PICO & ABLA

MPB & SB

21

0.0125149

PIEN & ABLA

MPB, SB, & WBBB

3

0.0017943

PIEN & ABLA

SB & WBBB

233

0.1393541

PIEN & ABLA

MPB & WBBB

3

0.0017943

PIEN & ABLA

MPB & SB

12

0.0071770

PICO, PIEN, & ABLA

MPB, SB, & WBBB

108

0.1188119

PICO, PIEN, & ABLA

SB & WBBB

18

0.0198020

PICO, PIEN, & ABLA

MPB & WBBB

96

0.1056106

PICO, PIEN, & ABLA

MPB & SB

153

0.1683168

## Is severity greater in stands with multiple agents?

Generally, yes.

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. 5). 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. 5).

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.

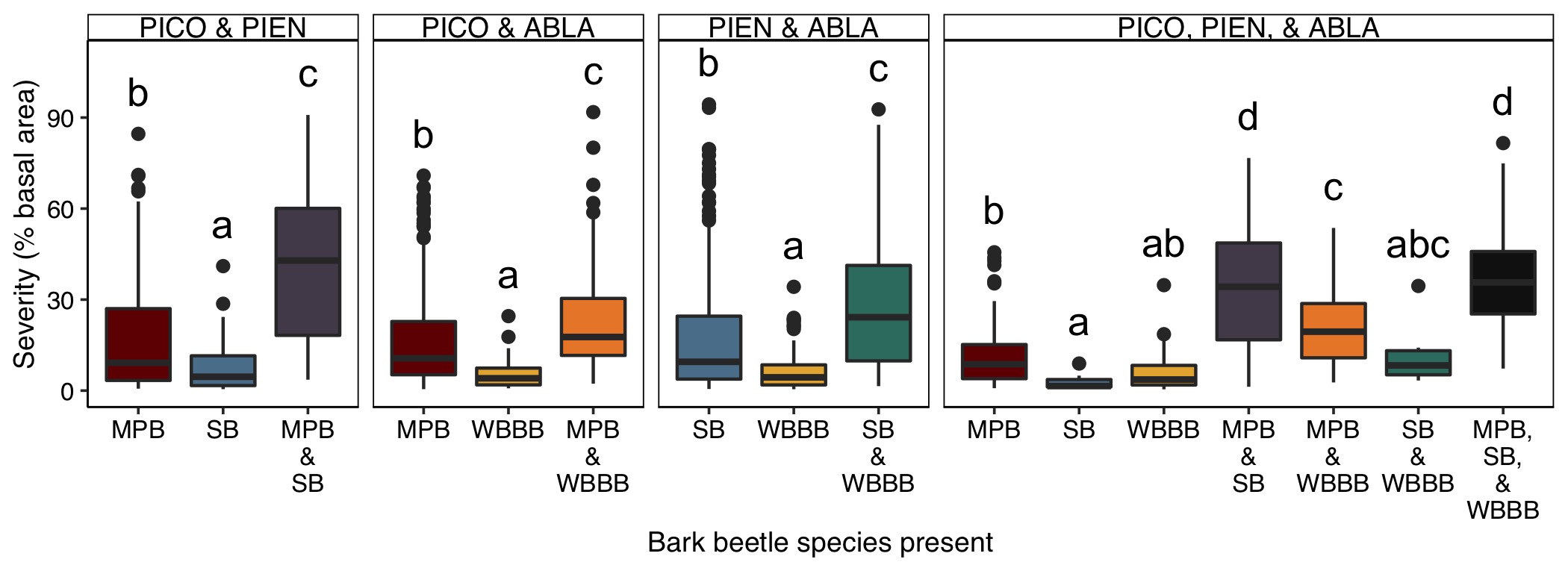


Figure 5: The severity of bark beetle mortality in plots with multiple tree species susceptible to bark beetles (columns) by the combinatin of bark beetle species present. Letters above boxes indicate significant (p < 0.05) differences between groups as determined by a Dunn test, a nonparametric rank 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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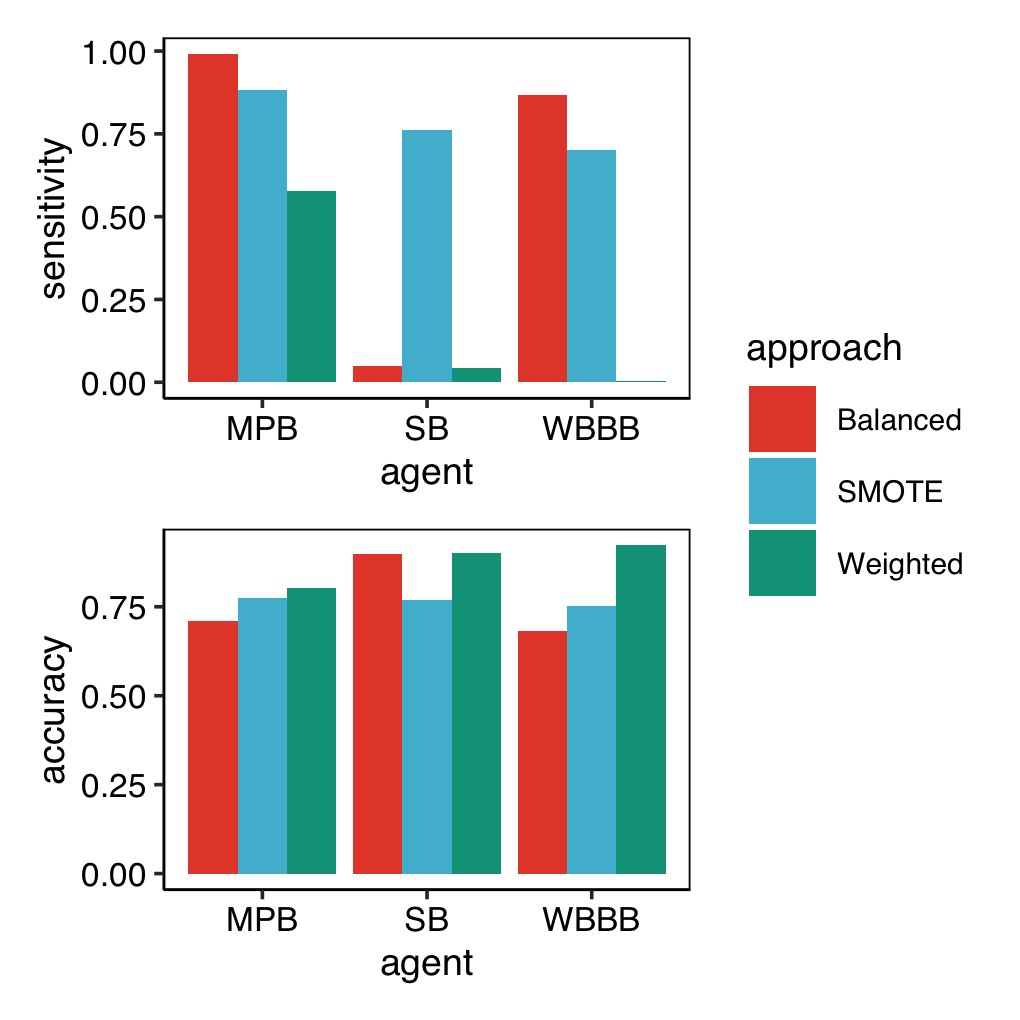
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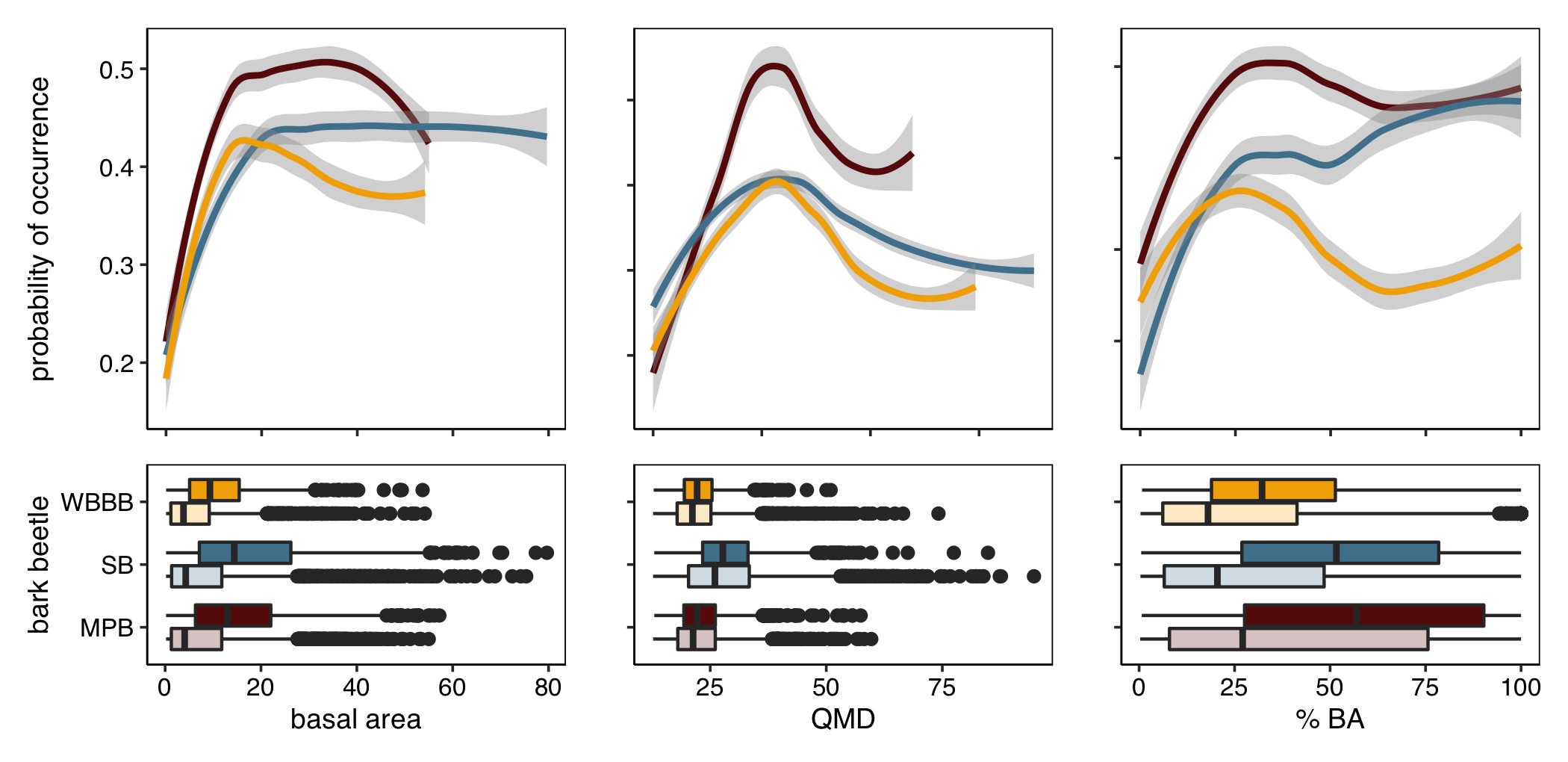
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## Supplement

### 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

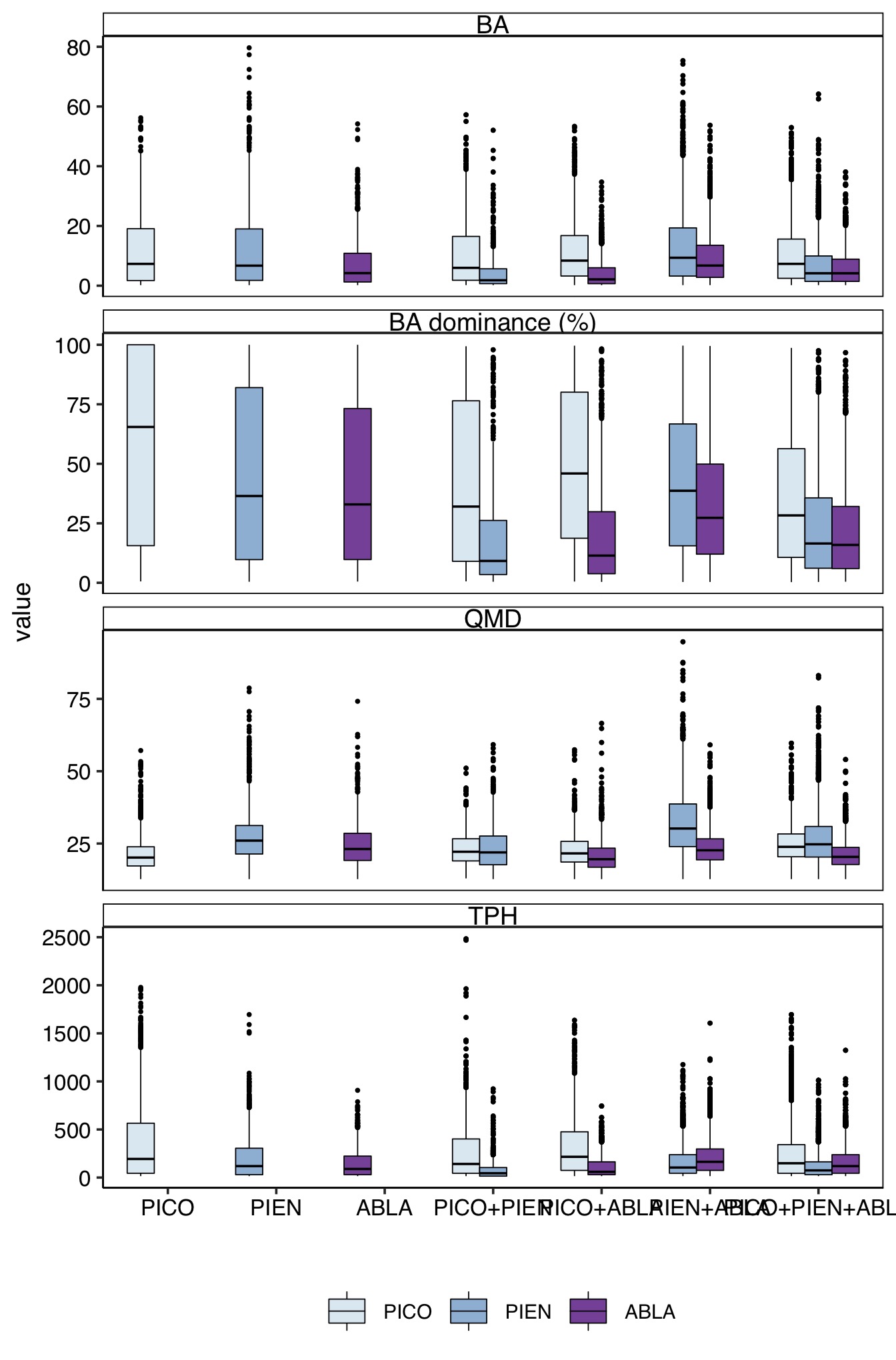


Figure 6: A caption

### Maps

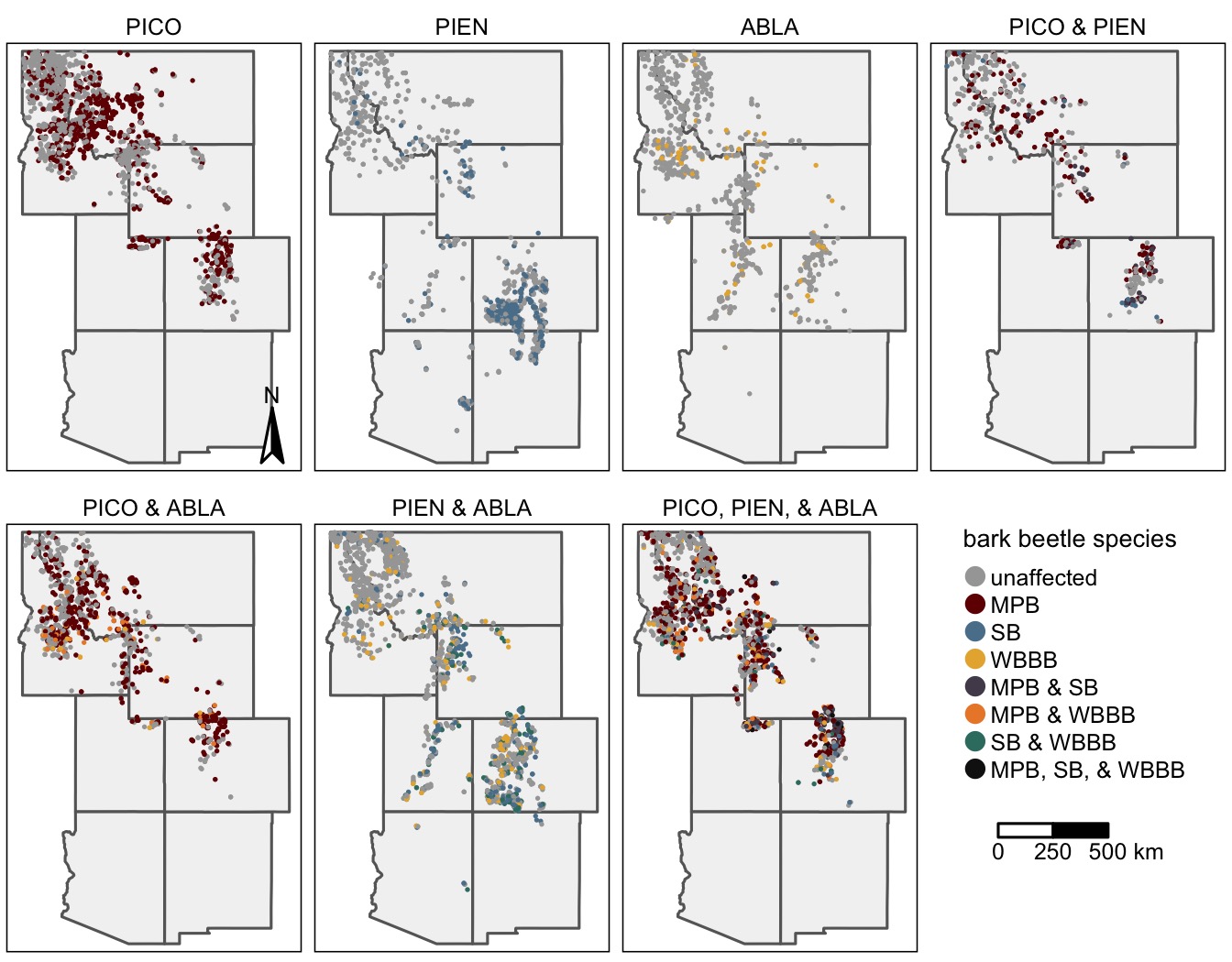


Figure 7: a caption

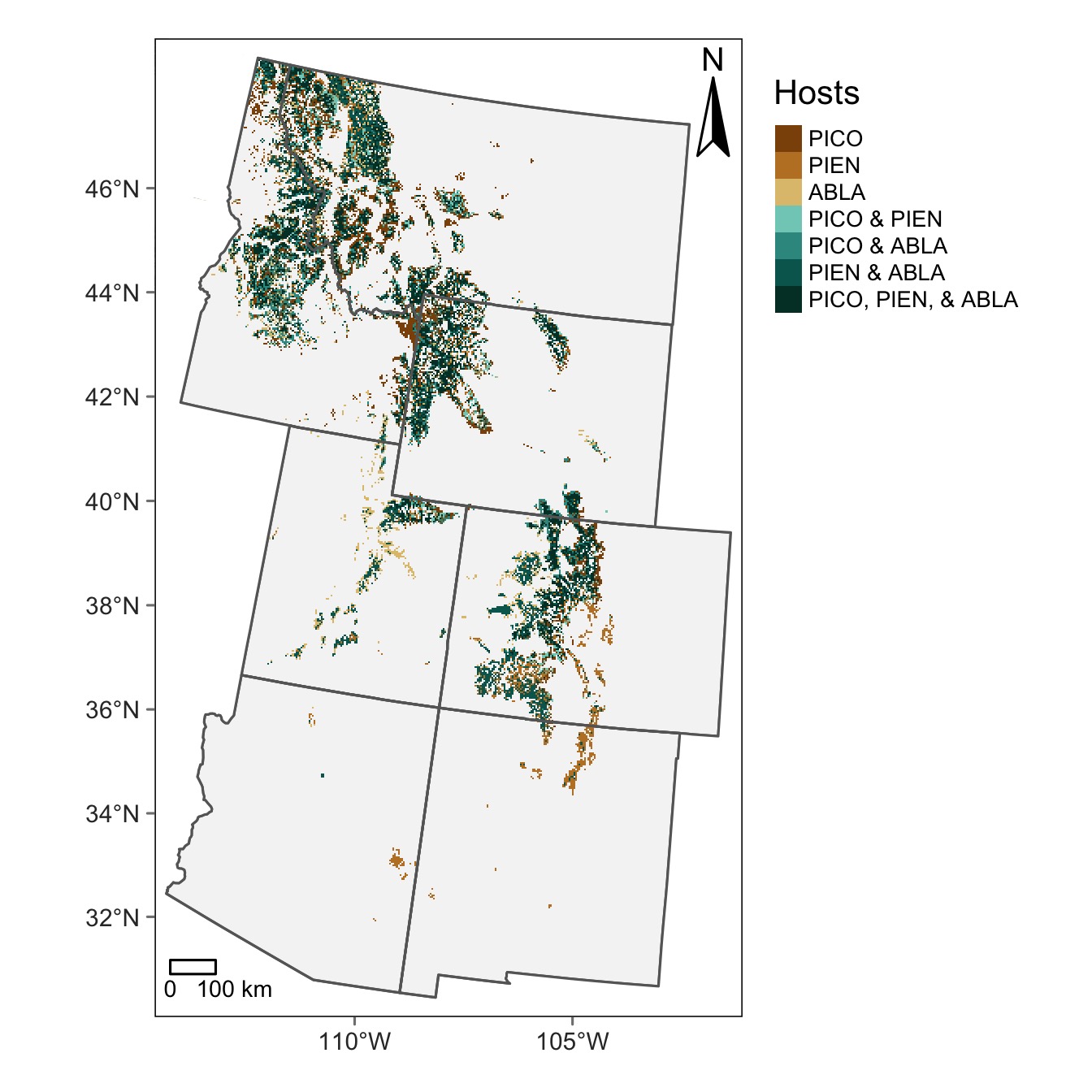


Figure 8: The distribution of host species presence across the study area. Data are from the Individual Tree Species Atlas (Ellenwood et al. 2015) and represent conditions in ca. 2002.

## Quatile comparison