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

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# FEEDBACK REQUESTED

Here is what I could use feedback on:

1. terminology:
2. journal?
3. framing of introduction
4. flow/structure/grammatical
5. interpretation of figures & captions
6. major methodological issues
7. results from RF in appendix?

# Abstract

Key findings

# Keywords

# Introduction

Many studies have sought to understand how biodiversity influences interactions between natural enemies and their resources. In the case of plant-herbivore interactions, greater plant diversity often reduces the effects herbivory (i.e., ‘associational resistance,’ Barbosa et al. 2009), particularly when herbivores are specialists capable of rapid population growth (**otway\_resource\_2005?**). Associational resistance is commonly hypothesized to occur due to several non-mutually exclusive mechanisms. First, herbivory may be lower in more diverse systems if herbivores are less likely to encounter, stay, and reproduce in areas where their hosts are less abundant (i.e., ‘resource concentration hypothesis,’ Root 1973). Second, reductions in herbivory may occur if insects are less likely to find their hosts due to chemical or visual masking by heterospecific neighbors (**castagneryrol\_effects\_2014?**), Third, heterospecific neighbors may increase the abundance of herbivore natural enemies Staab and Schuldt (2020).

While increases in plant diversity may decrease the effects of herbivore species on plants, it also hypothesized to increase herbivore richness (‘resource specialization hypothesis,’ **keddy\_plant\_1984?**).

\*\*\* something about the potential effects of \*\*\*

Yet little research has examined the effects of plant diversity on community-level outcomes of herbivory. This is particularly true in natural systems, where the number of potential interactions is high and effects of different herbivores on their focal host populations often differ greatly, due to differences in herbivore population biology and susceptibility and quality of plant host communities. Further, change in community composition may co-occur with changes in host quality, further complicating the effects of plant diversity on herbivore effects at he community scale (Jactel et al. 2021). Critically community-level outcomes may drive ecosystem processes, such as carbon sequestration, especially when plant diversity is low (but not monospecific) and herbivores are capable of rapid population growth. Thus where management goals are focused on ecosystem processes, an understanding of the effects of plant diversity on herbivory is critical.

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 ultimately cause tree death (**raffa\_natural\_2015?**). Conifer defense against bark beetles consists primarily of resin exudation that physically expels the beetle and allelochemicals, which repel or kill beetles (Christiansen et al. 1987). To overcome these defenses and colonize live trees, bark beetles rely on a mass-attack strategy, where pioneering beetles emit aggregation pheromones that attract other beetles 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 (Raffa et al. 2008). During severe outbreaks, bark beetles may cause severe and extensive mortality (**rodman\_effects\_20201?**).

In the western United States, there are more than 25 native bark beetle species. However over the past two decades, the mountain pine beetle (MPB; *Dendroctonus ponderosae*), spruce beetle (SB; *Dendroctonus rufipennis*), and western balsam bark beetle (WBBB; *Dryocoetes confusus*) collectively have caused over 70% of the bark beetle-attributed tree mortality, most of which has occurred in high elevation forests (**hicke\_chacterizing\_2020?**).

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 use this system to ask:

1. How often do stand conditions suitable for multiple bark beetle species occur?
2. Given stand stand conditions susceptible for multiple bark beetles species, does the occurrence or severity of cumulative bark beetle activity increase with the host species richness?
3. Does the co-occurrence of multiple bark beetle species result in more severe 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. F

When stand conditions are suitable for multiple bark beetle species, we expect the occurrence of bark beetle-driven tree mortality will be greater (i.e. resource specialization hypothesis), but severity will be lower (i.e. associational resistance).

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

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 forests with lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) that are located in the Intermountain West (i.e., Arizona, New Mexico, Colorado, Utah, Nevada, Idaho, Montana, and Wyoming). Our study area was constrained to the Intermountain West due to regional differences in data collection that exist within the FIA program (Burrill et al. 2017).

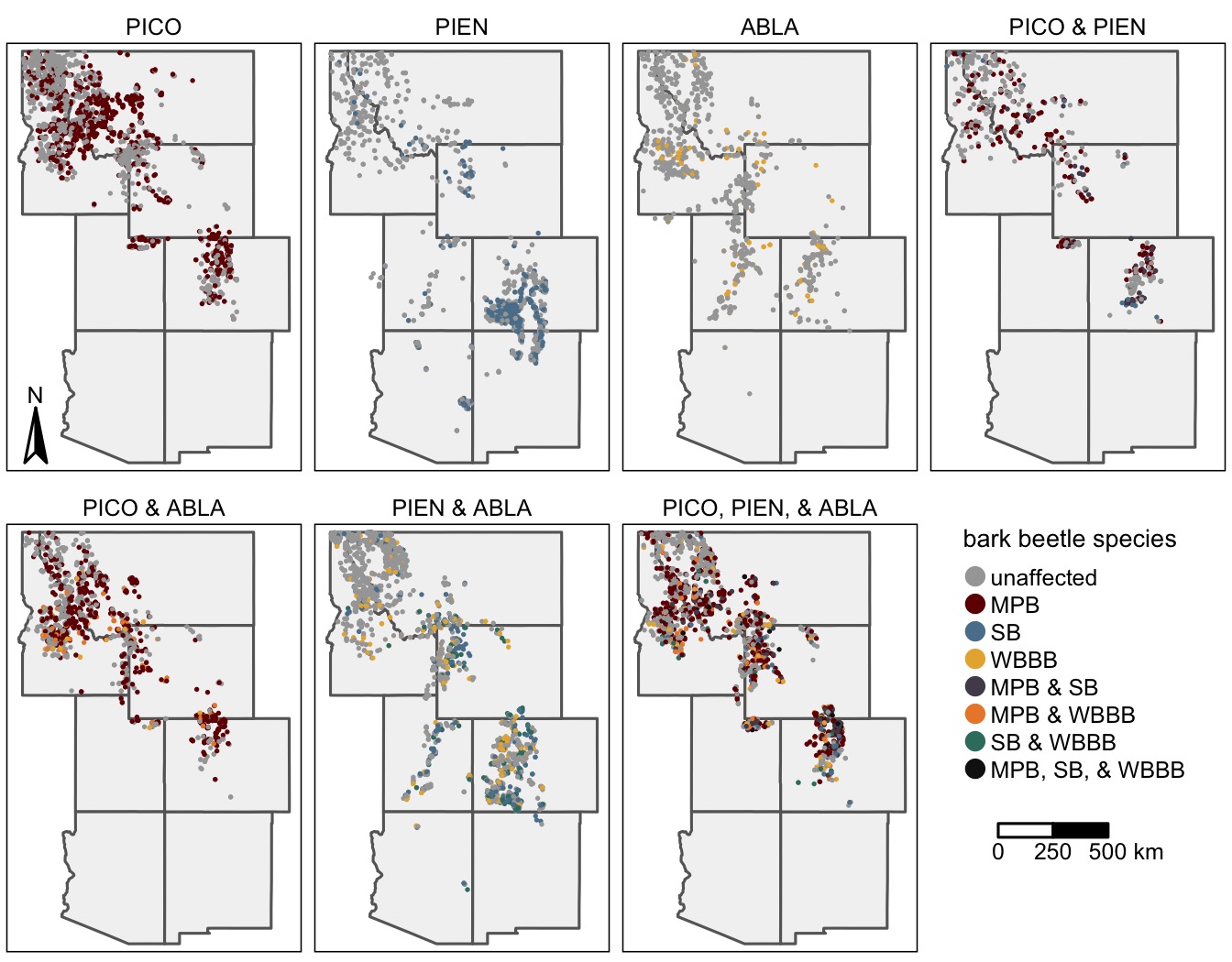


Figure 1: a caption

## Data

To understand interactions between subalpine tree and bark beetle communities, we used data from the FIA program. The FIA program inventories all public and private forested land using a spatially and temporally distributed sampling design, making it useful for the study of tree species distributions (e.g., Iverson and Prasad 1998, Rehfeldt et al. 2006) and tree demography DeRose et al. (2013). In the Western US, all plots are visited once every ten years (Gray et al. 2012). At each plot, field crews collect data within four 7.32 m radius subplots arranged in a fixed pattern. For each tree within the plot, field crews record the species, size (diameter at breast height; DBH), and status (live or dead) for trees (>= 12.7 cm DBH).For each live tree, field crews additionally record up to three damaging agents (e.g. MPB), defined as any agent 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). For dead trees that were alive at the previous visit, the proximate cause of death is also collected for any tree that was alive at the previous visit and at revisit is dead using visible evidence (e.g., fire scars, bark beetle galleries). Because identifying the mortality agent is more challenging cause of death codes are broad (e.g., “insect” or “disease”).

We acquired all FIA data for the Intermountain West, but restricted our analyses to the most recent inventory for plots that contained a focal host species and where all subplots were inventoried. We then characterized stand structure and composition using only live and recently killed (i.e. killed within the past ~10 years) trees. each plot we calculated the basal area, quadratic mean diameter (QMD), and basal area dominance (% total basal area) for each host species. Additionally, we characterized the presence (i.e., at least one tree infested) and severity of bark beetle activity (% total basal area) by bark beetle species. For live Engelmann spruce, we listed the presence of SB when the agent was listed as a general bark beetle or SB specifically. Similarly, we listed the presence of MPB in lodgepole when agent was listed as a general bark beetle or MPB specifically. For live subalpine fir, we listed the presence of WBBB when the damaging was recorded as, subalpine fir decline, a general bark beetle, or WBBB specifically. Finally, we assumed the mortality of lodgepole pine, Engelmann spruce, and subalpine fir that was attributed an insect, was caused by the MPB, SB, and WBBB, respectively.

## Analyses

To determine how frequently co-occurrence of multiple bark beetle species was likely to occur, we first calculated the proportion of plots where multiple host species were present.

Then we identified the stands where host species were susceptible to bark beetle infestation while accounting for variation in host size, basal area, and dominance (% host basal area). To do so we used a random forest modeling framework (Breiman 2001), a distribution-free approach useful for modeling nonlinear relationships and complex interactions characteristic of ecological systems (Cutler et al. 2007). We constructed separate models for the presence of MPB, SB, and WBBB and as predictor variables included host QMD, host basal area, and host dominance, which have been commonly linked to increased risk of bark beetle activity (REFERENCE). Because most stands in our dataset were unaffected by bark beetles, we used a synthetic minority oversampling technique (SMOTE) to deal the imbalance in the response (**chawla\_smote\_2002?**). Briefly, the SMOTE approach oversamples the minority class by synthesizing new cases from the minority class (here affected stands). Models were fit in R (Team 2020) using the **Tidymodels** package (**kuhn\_tidymodels\_2020?**). We then assumed that each host species were susceptible to infestation when the predicted probability of occurrence of the focal bark beetle species was greater than 0.5.

### How often do stand conditions suitable for multiple bark beetle species occur?

### Given stand stand conditions susceptible for multiple bark beetles species, does the occurrence or severity of cumulative bark beetle activity increase with the host species richness?

We used a one-sided proportion test to determine if the proportion of plots affected by any bark beetle species was significantly greater (p <0.05) than the proportion affected by an individual species.

### Does the co-occurrence of multiple bark beetle species result in more severe cumulative bark beetle mortality?

To determine if the severity of cumulative bark beetle-driven tree mortality greater in stands with multiple susceptible hosts

# Results

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

Across the 10,439 FIA plots with one of the target host species, 66% (n=5,850) contained at least two species (Fig. 2). Subalpine fir was most likely to occur with other target host species (50% of plots), followed by Engelmann spruce (45% plots), and lodgepole pine (36% of stands).

However, random forest models predicted that only 21% of all plots (n=2,163) were suitable for more than one bark beetle species. However, MPB, SB, and WBBB were only present in 23.4% (n=2,441), 9.9% (n=1034), and 7.8% (n=813) of plots, respectively.

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).

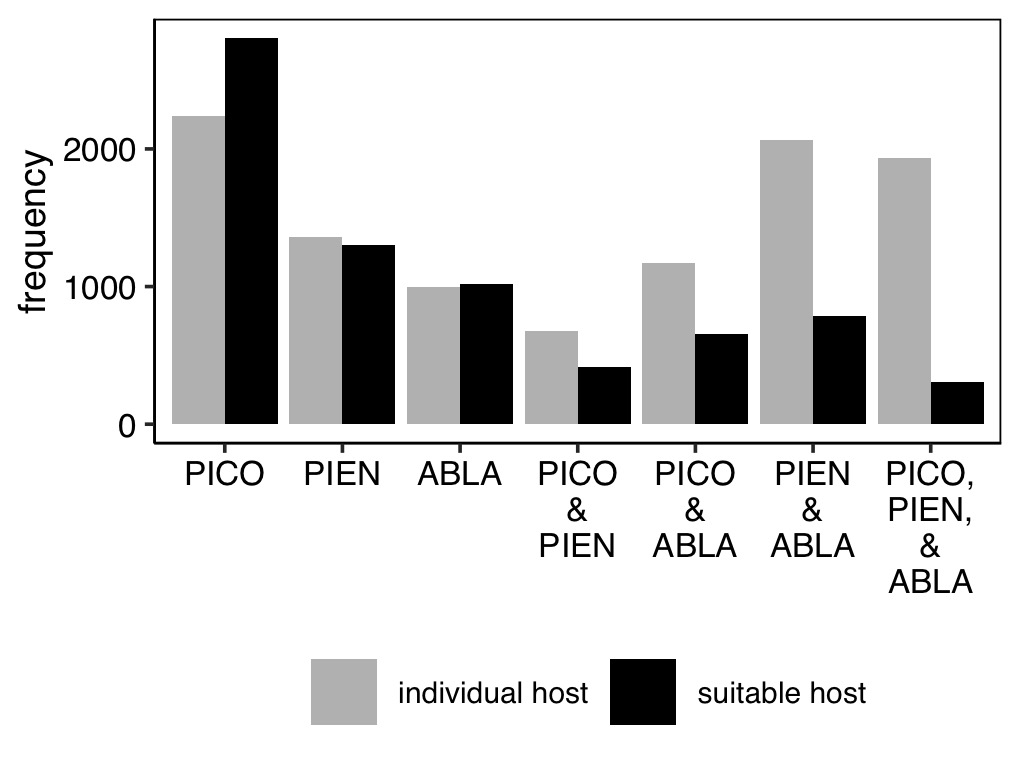


Figure 2: The frequency of plots by host identity. Gray bars indicate host species were present (i.e., at least one individual of the focal species was present within the plot). Black bars indicate stand structure and composition conditions were conducive to bark beetle infestation in focal tree species. For host identities, PICO is lodgepole pine, PIEN is Engelmann spruce, and ABLA is subalpine fir.

### Given stand stand conditions susceptible for multiple bark beetles species, does the occurrence or severity of cumulative bark beetle activity increase with the host species richness?

Given suitable stand conditions for multiple bark beetle species, the probability of occurrence of bark beetle activity was significantly greater than the probability of a single bark beetle species 3.

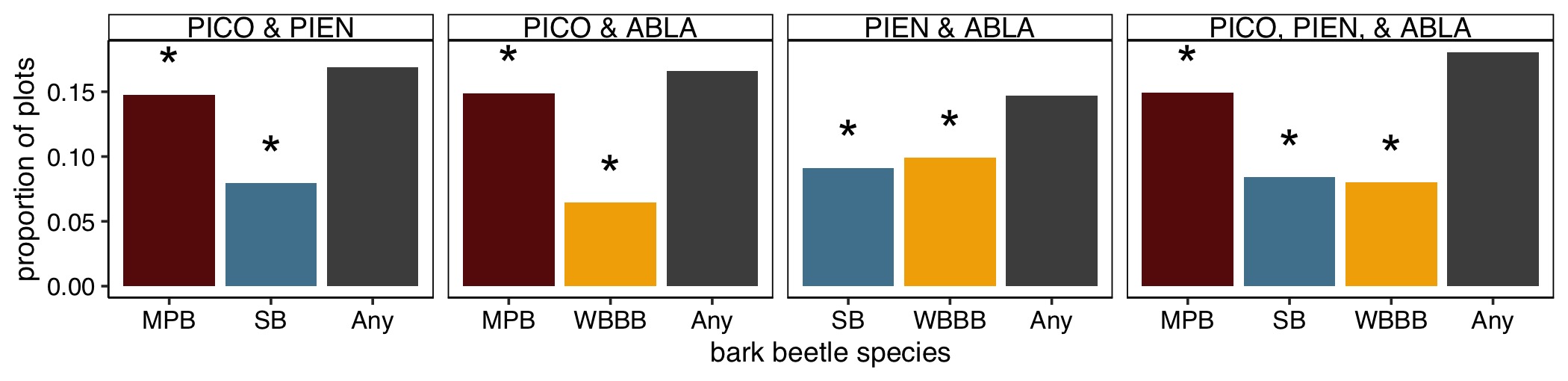


Figure 3: The proportion of plots affected by the mountain pine beetle (MPB), spruce beetle (SB), western balsam bark beetle (WBBB), or any bark beetle (i.e., MPB, SB or WBBB) by the identity of hosts species susceptible to bark beetle infestation. For host identities, PICO is lodgepole pine, PIEN is 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.

However, the effect of the number of susceptible hosts on the severity of bark beetle activity depended upon the identity of host species. In stands susceptible to all three hosts, the proportion of trees affected by bark beetles was greater than the activity due to a single bark beetle species (Fig. 4. 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). Specifically significant differences did not exist between severity attributed to all bark beetles and the most commonly occurring bark beetle, but the proportion of the basal area affected by the other bark beetle was significantly lower than the cumulative severity (Fig. 4.

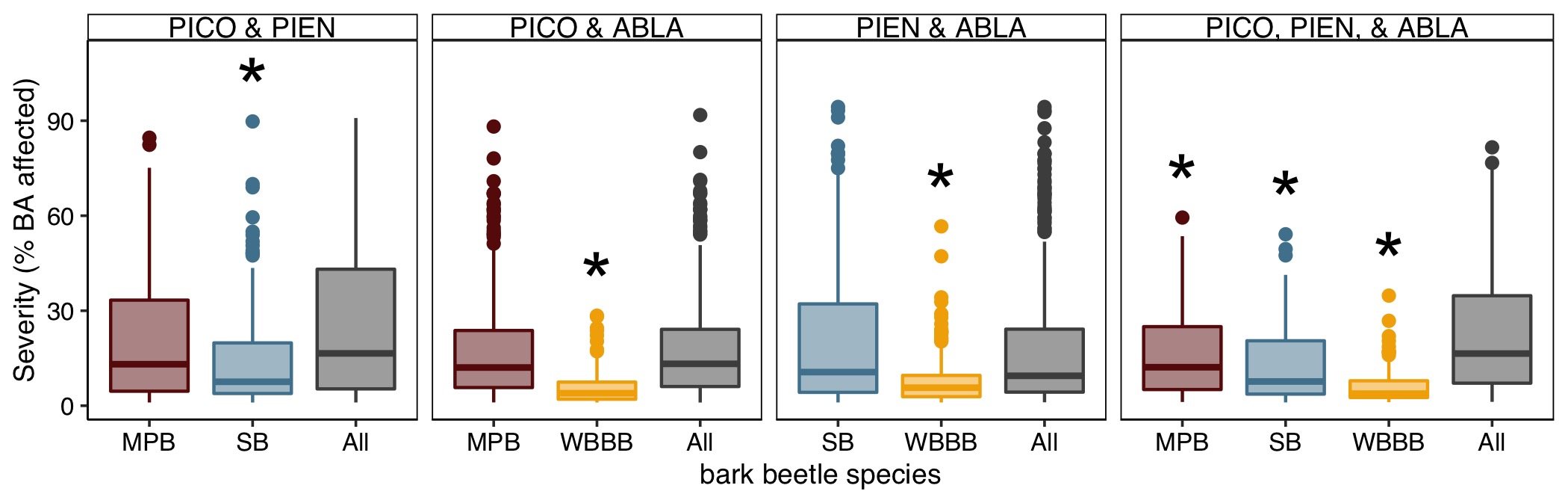


Figure 4: Boxplots illustrating the severity of mortality (% of total basal area) attributed to the mountain pine beetle (MPB), spruce beetle (SB), western balsam bark beetle (WBBB), or all bark beetles (i.e., cumulative mortality due to MPB, SB and WBBB) by the identity of hosts species susceptible 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.

## Does the co-occurrence of multiple bark beetle species result in more severe cumulative bark beetle mortality?

Across all 10,439 FIA plots, only 5.3% (n=539) were affected by multiple bark beetle species.

Given the 2,163 plots where multiple tree species were susceptible to bark beetle infestation, 56.7% (n=1,227) were affected by at least one bark beetle species and 21.3% (n=461) were affected by multiple bark beetle species. The most commonly occurring agent was the MPB (n=768, 35.5% of plots), followed by the WBBB (n=503, 23.3%) and the SB (n=461, 21.3%). The most commonly occurring combination of bark beetle species was MPB and SB (33.2% of cases; n=153), followed by MPB and WBBB (31.2% of cases; n=144) and 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 bark beetle species?

When plots contained two tree species susceptible to bark beetles, the presence of both bark beetle species increased activity 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 beetle activity, the highest rates of bark beetle activity 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).

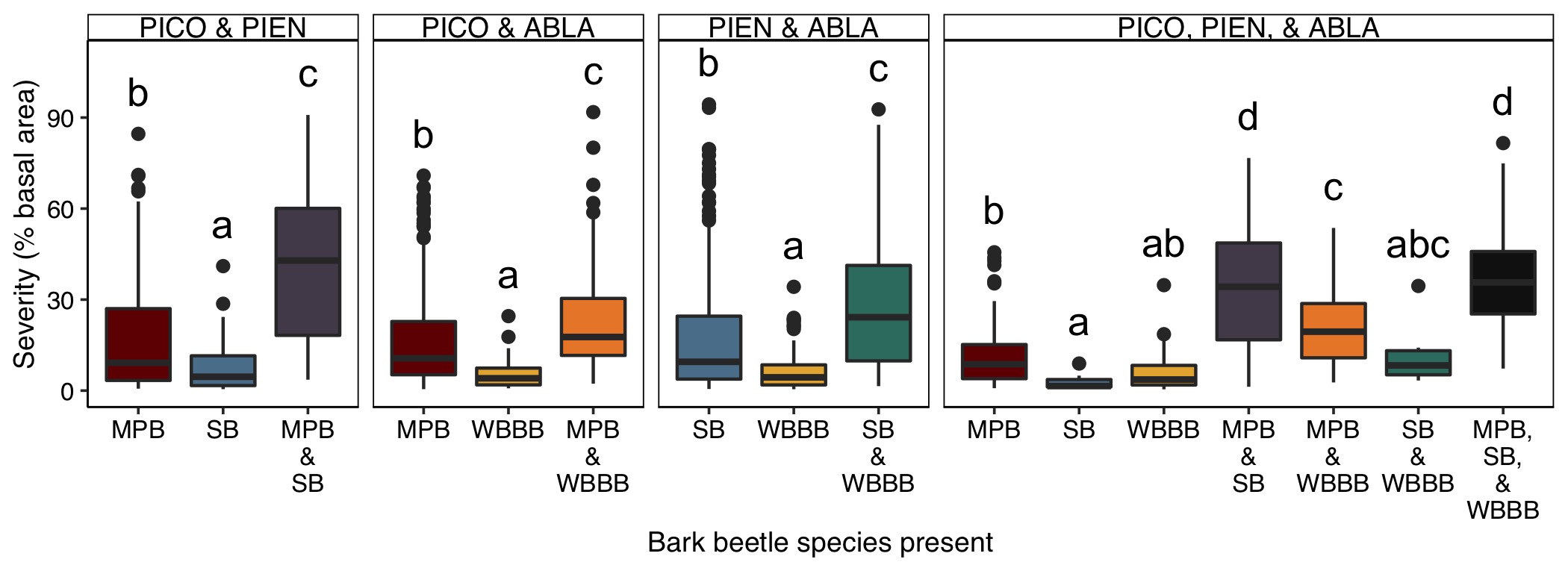


Figure 5: The severity of bark beetle mortality in plots with multiple tree species susceptible to bark beetles (columns) by the combinatin of bark beetle species present. Letters above boxes indicate significant (p < 0.05) differences between groups as determined by a Dunn test, a nonparametric rank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

# Acknowledgements

# Author contributions

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## Supplement

### Random Forest Modeling

Consistent with existing stand hazard ratings, the probability of each bark beetle species occurring generally increased with host basal area, quadratic mean diameter, and percent basal area (Fig. 6). However, both MPB and WBBB exhibited a slight decrease in the probability of outbreak at very high basal areas and all three bark beetle species exhibited a lower probability of outbreak in stands where host trees were very large (i.e. high QMD values). WBBB also exhibited a decline in the probability of outbreak when subalpine fir comprised a relatively high proportion of the basal area.

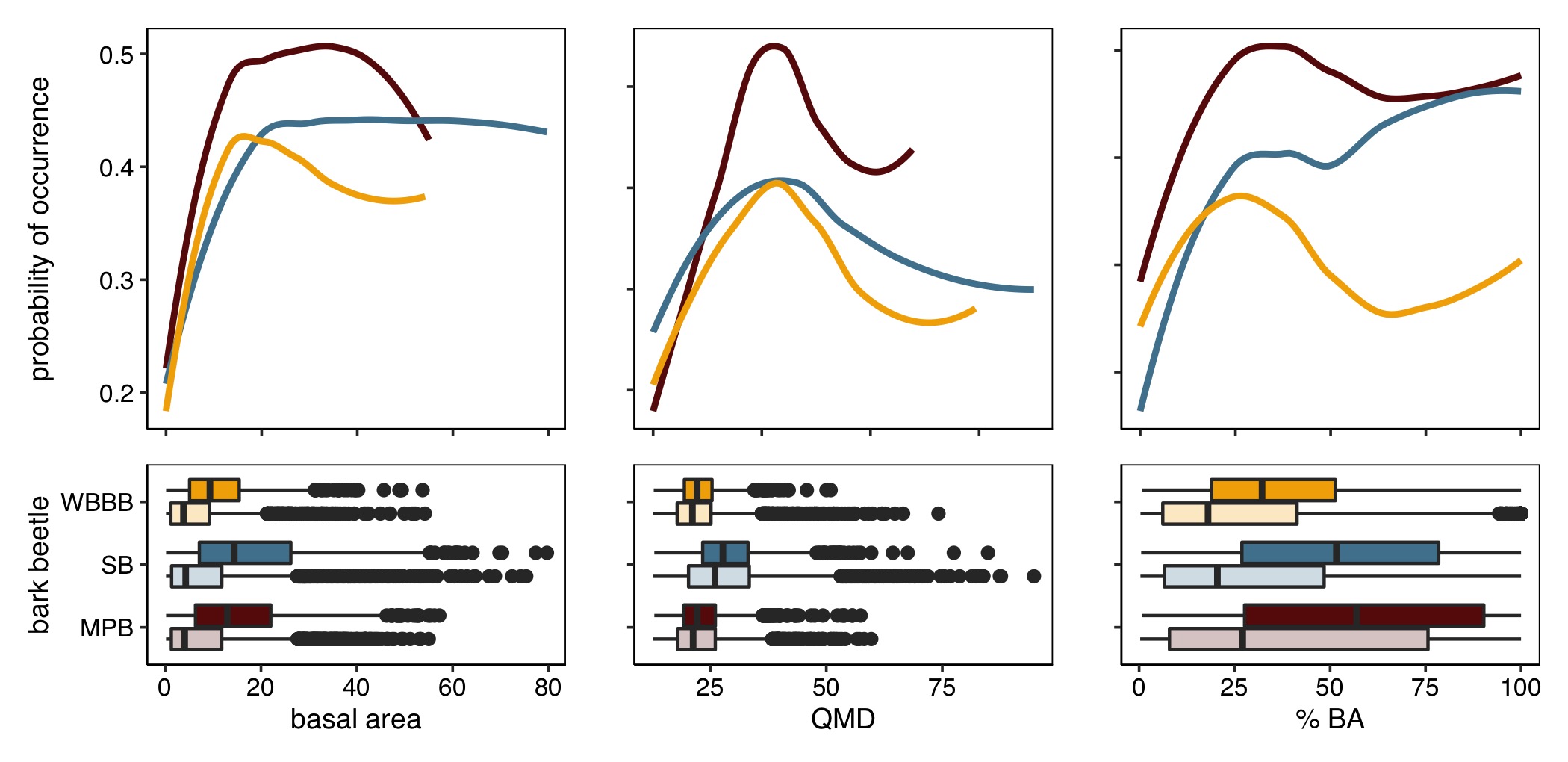


Figure 6: The associations between the probability of occurrence of the mountain pine beetle (MPB; red), spruce beetle (SB; blue); and western balsam bark beetle (WBBB; yellow) and three common measuree of stand suceptibility to bark beetl beetle outbreak, basal area (BA), quadratic mean diameter (QMD), and host dominace (% BA). The top row illustrates smoothed partial dependence results from Random Forest modeling, while in the bottom row boxplots illustrate the distribution of values for stands affected (dark colors) and unaffected (light colors) by each bark beetle species.

### Maps

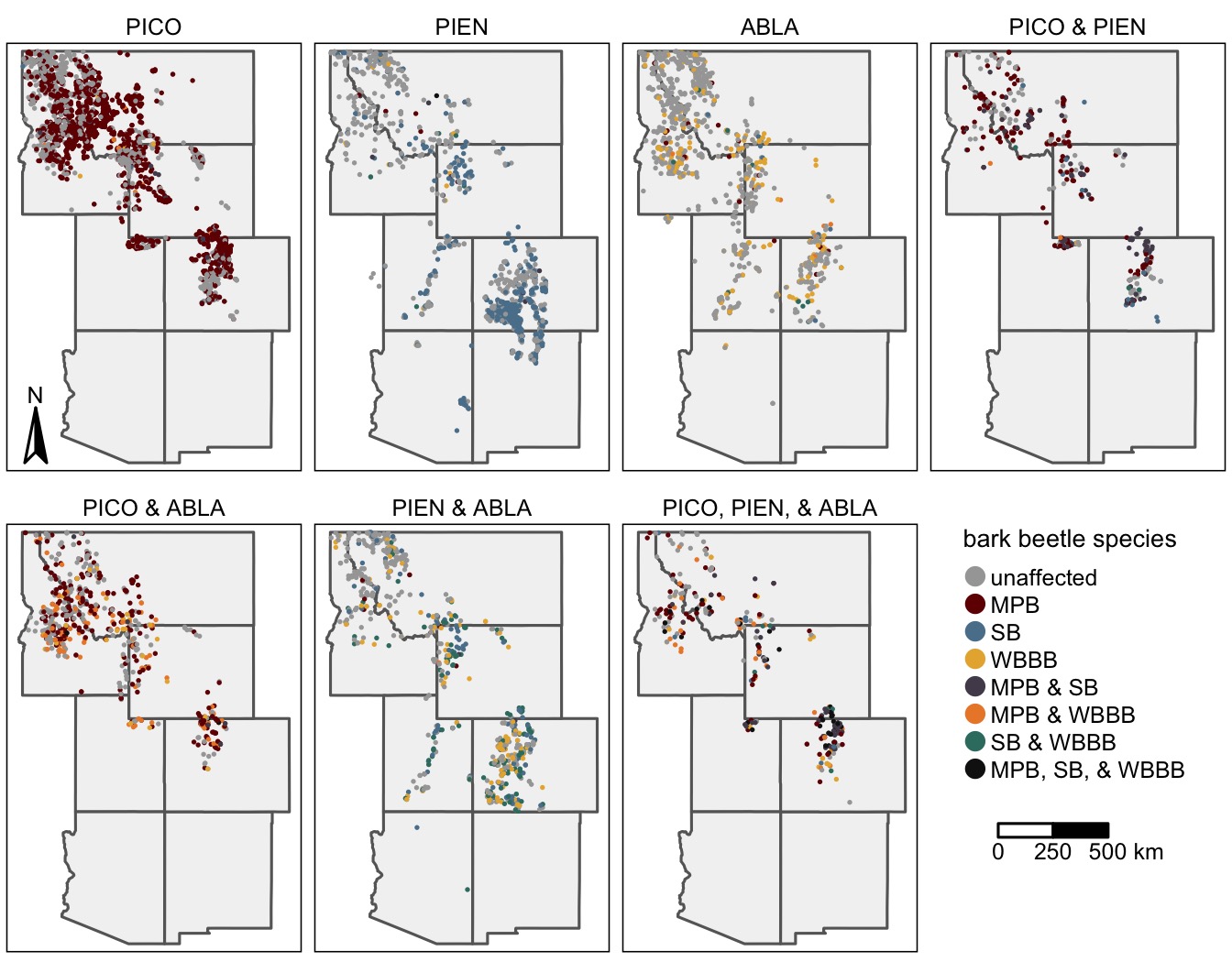


Figure 7: a caption

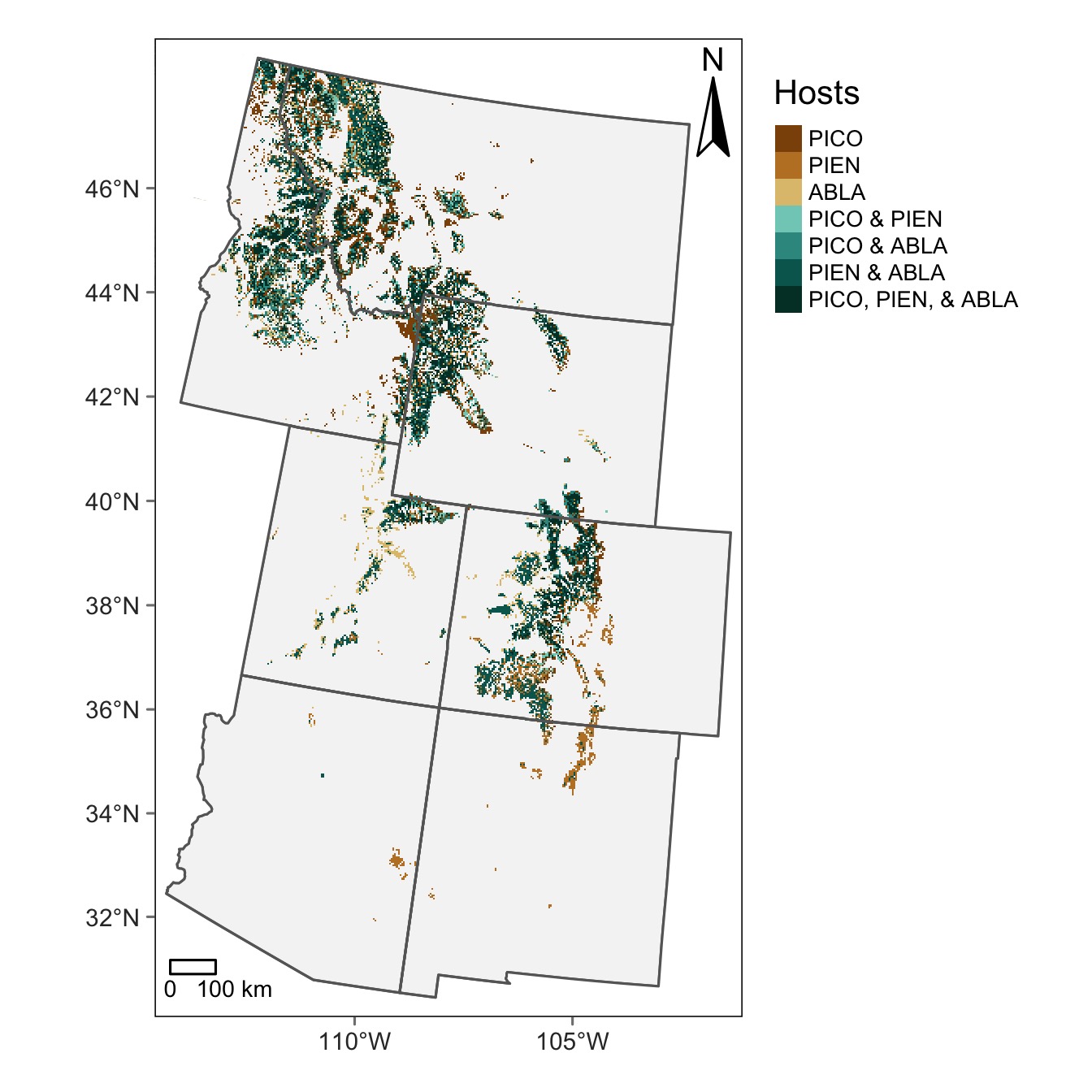


Figure 8: The distribution of host species presence across the study area. Data are from the Individual Tree Species Atlas (Ellenwood et al. 2015) and represent conditions in ca. 2002.