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Aggressive tree killer or natural thinning agent? Assessing the impacts of a globally important forest insect

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Abstract

Invasive insects and pathogens are prominent tree mortality agents in forests around the world, and the magnitude of their impacts is increasing. Comparative studies across multiple populations can be helpful for the development of new insights and innovative management strategies. We used the Sirex woodwasp, *Sirex noctilio* Fabricius, as a model system to compare invasion impacts across a range of ecological contexts around the globe: native woodwasps colonizing native trees, invasive woodwasps in non-native plantation trees, and invasive woodwasps attacking native trees. Across 133 stands of eight pine species on four continents, tree mortality associated with *S. noctilio* attack was positively correlated with stand basal area and stand density, and was mostly confined to smaller, suppressed trees. Larger average tree size and greater distances between trees were linked to lower levels of tree mortality. To more deeply assess the impacts of tree loss due to this pest, we examined mortality in vigorous trees, defined as those with a stem diameter greater than or equal to 90% of the mean diameter for trees in the stand. *Sirex noctilio*- related mortality in vigorous trees was rare, with one exception where *Pinus contorta* stands in Argentina lost as many as 300 vigorous trees ha^{-1}. Pine species varied dramatically in their susceptibility to *S. noctilio*: for example, these losses in *P. contorta* were in stark contrast to very low mortality in *P. ponderosa,* the other pine species grown in Argentina. Surprisingly, location did not alter patterns in the influence of stand basal area on tree susceptibility for individual species: most notably, *Pinus radiata* had the same relationship between basal area and tree mortality when grown in Spain (where *S. noctilio* is native and not considered a meaningful forest pest) and South Africa (where *S. noctilio* is a problematic invasive). Our findings suggest that the availability of optimal pine hosts is a key driver of *S. noctilio*-related tree mortality across continents and management regimes. Important variables that influence host availability include species-specific susceptibility and environmental and management-related factors that promote or limit the number of stressed trees present both within stands and across the regional forest or plantation landscape.

1. Introduction

Non-native insects and pathogens cause elevated tree mortality rates in forest ecosystems around the world (Fei et al., 2019; Wingfield et al., 2015). These impacts are increasing (Boyd et al., 2013) with continuing introduction due to travel and trade (Hulme, 2009; Liebhold et al., 2012) and the rapid climate change of the Anthropocene (Ayres and Lombardero, 2018). These factors exacerbate uncertainty around trajectories for our current forests (Anderegg et al., 2015). It is often unclear how to best define, identify, and respond to the impacts of pests either directly or indirectly via forest management (Ramsfield et al., 2016). Valuation of elevated forest tree damage can vary (Shackleton et al., 2019) across affected forest resource values and this can influence allocation of research funding and the scope of questions investigated. In the study of invasive species, research aims frequently reflect a shifting lens shaped by both ecosystem impacts and management goals. One consequence is that studies tend to be framed more locally than globally with respect to tree species, value systems and economic and ecological context (Kumschick et al., 2015).

One way to improve generalizability of pest impact assessment is through application of methods that facilitate comparison across a range of ecological contexts (Blackburn et al., 2014). The Sirex woodwasp, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), offers a model system for assessing impacts of a forest pest across a wide range of habitats and management contexts (Corley et al., 2018; Slippers et al., 2015). This woodwasp is a well-known invasive killer of many *Pinus spp.* (Bordeaux and Dean, 2012) in Southern Hemisphere plantations (Slippers et al., 2012a), yet in its native Eurasian range, *S. noctilio* is mainly considered a scavenger of dying trees (Ayres et al., 2014; Lombardero et al., 2016). North American interest in the woodwasp has grown since its introduction to the northeastern United States and southeastern Canada around 2005 (Hoebeke et al., 2005). The arrival of *S. noctilio* to North America was unique because it marked the first time that invasive populations could be studied in a region where its favored hosts (*Pinus* spp.) are also native, unlike in the Southern Hemisphere where host trees are non-native and mainly found in plantation settings.

Tree mortality from *S. noctilio* attack varies greatly across the native and non-native range of the insect, as well as regionally and among host species (e.g., Dodds et al. 2010; Ayres et al. 2014). Mounting evidence suggests that host tree susceptibility plays a key role in shaping *S. noctilio* impacts and invasion outcomes. Even in the earliest *S. noctilio* invasions in early 20th century New Zealand, plantation managers recognized that outbreaks tended to occur in overstocked stands with many suppressed trees and that outbreaks could "confer … an inestimable benefit" by thinning stands whose remaining trees might then be released from competition and see increased growth rates a short time later (Rawlings and Wilson, 1949). Under this scenario, *S. noctilio* can be thought of as one of a suite of factors that may exploit trees weakened by competition in stands undergoing self-thinning, acting as a mortality agent that limits stand density as trees increase in size (Westoby, 1984).

Recent studies in North America (Haavik et al., 2015; Krivak-Tetley et al., 2020), South America (Lantschner and Corley, 2015) and the native range of *S. noctilio* (Lombardero et al., 2016) have shown that tree susceptibility is a dominant driver of woodwasp population growth rates. If this is the case, differences among trees due to species identity, genetic provenance, environmental factors, or management might be responsible for observed differences in woodwasp impacts. High levels of susceptibility could promote the development of outbreaks (Cavers and Cottrell, 2015) that may intensify through positive feedbacks and be difficult to control. For example, Lantschner et al. (2019) found that *S. noctilio* outbreaks in southern Argentina were largely incited by regional droughts, in combination with stand-level factors such as high stocking levels that increased tree susceptibility. Subsequent woodwasp population declines were attributable to the depletion of susceptible trees and negative density dependence in woodwasp population dynamics (Lantschner et al., 2019).

Despite the apparent importance of these bottom-up effects, *S. noctilio* management strategies in the Southern Hemisphere have often emphasized the use of classical biological control to prevent and reduce the impacts of outbreaks (Bedding and Iede, 2005; Hurley et al., 2007). Managers broadly recognize that silvicultural practices influence the success of biological control programs; Cameron (2012) described *S. noctilio* management as "a three-legged stool" comprised of silvicultural treatments, nematode application and parasitoid introduction. But in short-rotation pulp production stands, silvicultural treatments such as reducing stand density or selecting more resistant *Pinus* species have often been seen as economically infeasible. Research efforts over the past ten years have focused more attention on the latter two legs of this stool—nematode application and parasitoid introduction—than on the first. Since 2009, relatively few studies of the *S. noctilio* system have interrogated the details of reported stand level impacts and explored resource-related variables as drivers of woodwasp outbreaks. And although reports of eruptive *S. noctilio* population behavior and substantial tree mortality are widespread, these have not been directly compared across continents to offer insight about their relative magnitude and common causes. In fact, the same impact levels are often perceived differently across the native and invaded range: the existence of >5% mortality in a stand is referred to as an outbreak in non-native environments (Villacide and Corley, 2012), but levels of tree mortality up to >50% of stems are not necessarily considered remarkable in the native range when attributed to overstocking or a lack of effective silvicultural management and multiple mortality agents (Ayres et al., 2014).

Variable *S. noctilio* impacts are partially due to this species' unique niche: specialized venom gland secretions reduce the defense capability of attacked pines (Coutts, 1969; Spradbery, 1973), and the woodwasp is able to colonize weakened trees before they become available to other forest scavengers. With its preference for weakened and suppressed trees, *S. noctilio* likely shortens the life span of trees that might have lived longer in its absence, but its behavior at endemic levels does not resemble that of well-known aggressive forest pests such as *Dendroctonus ponderosae* (mountain pine beetle) in North America that use aggregation pheromones to mass attack large, healthy pines, or *Agrilus planipennis* (emerald ash borer), which kills most individuals of susceptible *Fraxinus* spp. in its invasive range generating substantial ecological and economic impacts (Klooster et al., 2018; Raffa and Berryman, 1983; Safranyik and Carroll, 2006; Tanis and McCullough, 2015).

With this project, we sought to better understand the ecological role of bottom-up effects (resource availability) in determining when *S. noctilio* serves as an aggressive forest pest that develops outbreaks as opposed to acting as a thinning agent that efficiently exploits available resources. We investigated stand-level drivers of *S. noctilio* impacts on diverse global forests.

We measured the magnitude of tree mortality and compared it across host tree species and locations, looking closely at how often *S. noctilio* kills vigorous trees. If availability of susceptible trees is a dominant factor driving *S. noctilio* population dynamics, we would expect levels of tree mortality to be clearly linked to stand and tree traits across a range of environmental and community contexts. In contrast, inconsistent mortality patterns might suggest that other factors, such as regional variation in top-down controls on woodwasp populations and environmental stressors, more strongly influence *S. noctilio* dynamics and impacts. We address these questions by comparing tree mortality associated with *S. noctilio* across sites on four continents that fell into three categories: (1) the woodwasp's native range; (2) the invaded Southern Hemisphere range where its planted pine hosts are also non-native; and (3) the recently invaded range in North America.

2. Materials and methods

2.1 Study areas

We surveyed pine stands in four regions that spanned a range of ecological contexts: native and non-native *S. noctilio* populations, a variety of native and non-native pine species, and differing management strategies reflecting variation in both the scale and regional economic importance of the pine forest product industry: the native range in Spain and the invaded ranges in North America, Argentina and South Africa (Table 1, Figure 1). Stands were selected to include the most abundant pine species in each region; these were sometimes native, sometimes non-native, and sometimes both. Every stand surveyed was within the confirmed range of *S. noctilio*. Mixed hardwood-pine stands rarely contained signs of *S. noctilio* and were not present in all regions so were excluded.

2.1.1 Spain

The native range of *S. noctilio* extends through most of Eurasia and northern Africa (Spradbery and Kirk, 1978). We surveyed stands in the autonomous region of Galicia in northwestern Spain (Figure 1b). Native forests in Galicia are predominantly hardwood, but is an important pine-growing region of southern Europe with > 277,000 hectares of planted forests in 2011 (IFN, 2011). For this project, we located stands of three pine species: the native European *P. pinaster* (maritime pine) which has been propagated in the region since at least the 19th century and is widely naturalized; *P. sylvestris* (scots pine) which while native to Europe, was rare in this region prior to being established in plantations mainly at high elevation sites; and the North American *P. radiata* (Monterey or radiata pine). Stands were surveyed during July-August 2013-2014.

2.1.2 Argentina

Study sites in Argentina were located in north-west Patagonia, in the provinces of Neuquén and Río Negro (Figure 1c). Approximately 100,000 hectares of exotic pines have been planted in this region, mainly for timber. Populations of *S. noctilio* have been present in pine plantations in Patagonia since at least 1993, and by 2004 occurred throughout our study area and the surrounding region (Lantschner et al., 2014). Between January and March in 2014 and 2015, we surveyed plantations of the two primary hosts in this area, both native to North America: *P. contorta* (lodgepole pine) and *P. ponderosa* (ponderosa pine) (Figure 1c, Table 1).

2.1.3 South Africa

South African study sites spanned a broad range of climatic conditions and elevational regions: the coastal Eastern Cape (year-round rainfall), mountainous Eastern Cape (summer rainfall), and multiple locations in KwaZulu-Natal and Mpumalanga (summer rainfall) (Figure 1d). Stand data were collected from October-December of 2013 (Mpumalanga), 2014 (Eastern Cape, coastal and mountainous), and from May-June 2018 (Mpumalanga and KZN). We focused on species that are commonly used for short-rotation pulp plantings (*P. patula* and *P. radiata*; Mexican weeping pine and Monterey pine), as these are the stands that typically experience high levels of mortality from *S. noctilio* during outbreaks (Hurley et al., 2012, 2007).

2.1.4 North America

Our study included stands in New York, Vermont, New Hampshire and Pennsylvania (Figure 1a). The woodwasp has been present in North America since detection in northern New York in 2004 (Hoebeke et al., 2005), and has spread northward into Ontario, Canada and southward and eastward into at least eight US states. The two primary pine hosts in the current U.S. range of *S. noctilio*, the native *Pinus resinosa* (red pine) and the introduced *P. sylvestris* (Scots pine), can be found in isolated stands throughout the Northeast. Stands of both species tend to be unmanaged and many mortality agents are present in addition to *S. noctilio* (Ayres et al., 2014). Even within the range of *S. noctilio*, attacked trees are rare and many pine patches are too small to assess stand characteristics in a meaningful way (e.g., trees planted in narrow strips along expressways). In this study, we included stands in some areas with previously known established *S. noctilio* populations, such as the Finger Lakes region in New York. We also worked to include as wide a range of new sites as possible: from 2013-2016, we surveyed small plots of pine in Vermont, New York and New Hampshire in an effort to locate new *S. noctilio* populations to better assess the range of their impacts throughout the region. We also visited sites near the southern and eastern edges of the known range, finding *S. noctilio* near Blacklick, PA (the southernmost reported site to date) in 2015, and in southern New Hampshire (the first report of the species in this state) in 2017. In localities where we identified new active *S. noctilio* populations, we surveyed suitable stands of hard pine nearby, even if those confirmatory signs of *S. noctilio* were found outside such stands.

2.2 Assessing presence of *S. noctilio*

We selected stands in areas with observed *S. noctilio* activity, determined by the presence of characteristic resin drippings, oviposition sites, and/or emergence holes (Krivak-Tetley et al., 2020). In the Northern Hemisphere, emergence holes alone were not sufficient to confirm *S. noctilio* due to the presence of native siricids with overlapping resource utilization and similar emergence hole morphology, so resin drippings and oviposition sites were used to confirm its presence. At Southern Hemisphere sites, emergence holes alone were considered sufficient to confirm *S. noctilio* in a tree because no other insects in these regions have emergence holes with similar morphology. When evaluating stands in new areas for possible surveys, confirmed *S. noctilio* presence in the area was a prerequisite for inclusion of a stand in our study. We recognize that tree mortality is a process that often has a number of factors involved and can be protracted (Manion, 1981). If an individual dead tree showed clear evidence of *S. noctilio* attack, we considered *S. noctilio* to be a contributing mortality factor. Hereafter, we refer to this as "*S. noctilio*-related tree mortality".

2.3.1 Tree and forest stand measurements

We established at least one 100-tree transect in each stand included in our study. The start tree for each transect was haphazardly located near an edge of the stand. We then used a random number generator to determine transect direction. In plantations with trees planted in rows, we adjusted the angle of the transect direction to follow the nearest row. We collected detailed measurements on a randomly selected subset of at least 30 individuals from the 100 trees: diameter at breast height (DBH), current health status (alive with no signs of attack, attacked, standing dead), and canopy status or crown class (suppressed, intermediate, codominant, dominant) as commonly defined in forestry (Helms, 1998) and simplified by DeYoung (2020). A detailed description of each crown class is included in the Supplementary Materials. Trees were included in the transect if they had DBH ≥ 5cm, which was our observed lower limit for *S. noctilio* attack and emergence. For eight randomly selected measurement trees, we also recorded basal area (BA) using a 10-BAF prism and the distance to the first and second nearest pine neighbors (≥ 5cm DBH). These measurements were used to calculate overall metrics for the stand.

For each dead, dying or *S. noctilio*- attacked tree in our 100-tree transect, we collected the variables listed above and estimated year of death based on level of decay in the standing stem, the visible weathering of *S. noctilio* oviposition sites and emergence holes, and presence and age of co-colonizers. Very recent mortality was assigned to year zero; these trees had new *S. noctilio* attacks or fresh emergence holes, and still retained brown needles. Normally, no other colonizing insects were present. Trees that had died the previous year had new or one-year old emergence holes and usually retained twigs and branches. Trees that had been dead for two years had visible weathering of both emergence holes and oviposition sites and their associated drippings. Trees dead for three or more years, if still standing, had extensive weathering of *S. noctilio* signs and bark loss or decay. Detailed descriptions of criteria for assigning year of death can be found in the Supplementary Materials. We recorded observations of all visible and identifiable mortality agents: *S. noctilio* attack and emergence as described above, other insect or pathogen attacks, lightning, tree structure anomalies such as bifurcation, and other structural damage. If we encountered fewer than five dead trees in the first 100-tree transect, we surveyed one or more additional 100-tree transects to improve mortality rate estimates.

We calculated the percentage of suppressed trees in each stand by dividing the number of trees recorded as suppressed or intermediate by the total number of trees sampled. To convert transect based measurements to a tree density metric, we calculated the number of trees per hectare (N) in each stand using mean basal area per hectare (BA) as estimated from prism measurements and quadratic mean diameter (QMD) from transect DBH measurements following Curtis and Marshall (2000):

$$N = \frac{BA}{k \cdot QMD^2} \text{ where } k=0.0000785.$$

2.3.2 *Sirex noctilio*-related mortality in vigorous trees

Our study was conducted in stands containing trees that had been established within a 1-3 year time period in all countries. For this reason, larger tree size consistently indicated co-dominant or dominant canopy status and, for healthy trees and in the absence of environmental stressors, high growth rates and vigor relative to neighbors. These trees were also the most economically valuable on a per-stem basis, as value increases with size (Dey et al., 2017; Moorhead et al., 2017). Stands with high levels of attack by pathogens (e.g., *Fusarium circinatum* (pitch canker) in some South African stands) had higher levels of overall mortality and reduced overall vigor, even in large trees. Environmental stressors can also periodically reduce vigor, but normally do so in a fairly consistent way across all trees in a stand. Ultimately, we chose to use tree diameter (relative to other trees in a stand) to define a group of “vigorous trees” in each stand, as it could serve as both a direct measure of relative economic value to a plantation manager as well as a reasonable proxy for relative vigor. For each stand, we calculated mortality in vigorous trees (MVT) as the estimated number of vigorous trees killed by *S. noctilio* (with vigorous trees defined as those with DBH > 0.9 • Average DBH for the stand). This metric was calculated in three steps: (1) We calculated the mean and variance of tree sizes for all trees in the stand and for standing dead trees killed by *S. noctilio* (Figure 2a). (2) We used these sample statistics as estimates of the parameters μ and σ, then scaled the resulting distributions with the percentage of dead trees to calculate the probability of mortality across the full range of tree sizes in each stand (Figure 2b). Finally, we (3) calculated the expected MVT for each stand as the area under the mortality curve for DBH > $0.9 \cdot \mu$.

2.4 Statistical Analysis

We used general linear models to test for effects of tree species and stand density metrics (basal area, stems ha^{-1}, proportion suppressed trees) on *S. noctilio*-related tree mortality and MVT. We did not combine multiple density metrics in the same model due to correlations among variables. To improve normality and reduce unequal variances, we performed square root transformations on mortality variables related to *S. noctilio* impacts: % of trees attacked by *S. noctilio*, *S. noctilio*-related mortality (stems ha^{-1}) and MVT (stems ha^{-1}). To test for different relationships among tree species, we compared individual regressions for each species with a pooled regression for the entire sample (after Neter et al., 1988). We used the same approach to compare relationships between stand density metrics and mortality for the same species across multiple countries. We used logistic regression to test for a change in the probability of tree mortality across a range of relative tree sizes.

To further examine mortality patterns in our stands, we visualized self-thinning patterns for groups of stands by plotting quadratic mean diameter (QMD) against trees per hectare on a log-log scale. We used quantile regression (90th percentile) to estimate self-thinning lines from these stand data (Cade and Noon, 2003; Zhang et al., 2005).

3. Results

We measured 6802 trees from 133 stands of eight tree species in four countries (Table 1, Figure 1). Across all countries and species, tree mortality due to *S. noctilio* ranged from 0-54% of standing stems (Supplemental Table I).

Across all species, trees killed by *S. noctilio* tended to be ~23% smaller than average-sized trees (Welch's test: $F_{1,889.3} = 384.18$, $P < 0.0001$) (Figure 3). For all trees of all species, the probability of being dead was > 40% for the smallest trees in our stands and decreased to about 5% in the largest trees ($\chi^2 = 183.54$, df = 1, n = 4948, $P < 0.0001$) (Figure 4). This relationship between relative tree size and probability of mortality varied among species (Supplemental Figure I), with *P. contorta* sustaining higher levels of mortality that decreased more slowly with increasing relative diameter ($z = 6.55$, $P < 0.0001$), and *P. sylvestris* experiencing a consistently lower probability of mortality ($z = -2.30$, $P = 0.02$).

Stand-level variables associated with tree density, tree size and spatial distribution, including basal area (m^2 ha^{-1}), stems ha^{-1}, proportion suppressed, DBH (cm), and distance to the first and second nearest neighbors, were related in expected ways (Supplemental Table II). *Sirex noctilio*-related tree mortality (*S. noctilio* trees ha^{-1}) increased with all of the following correlated variables: the proportion of suppressed trees in the stand, stems ha^{-1}, and basal area. Larger average tree size and greater nearest neighbor distances were associated with reduced tree mortality (Supplemental Table II).

To compare relationships between stand density and *S. noctilio*-related tree mortality, we assessed models using each variable associated with density (Supplemental Table II). Basal area was consistently the best predictor, so was used for all final analyses. The number of trees ha^{-1} killed by *S. noctilio* increased with basal area across all stands ($F_{1,130} = 62.4$, $P < 0.0001$). The slope of this relationship varied among tree species ($F_{6,118} = 16.84$, $P = 0.02$), but a significant relationship found for all except *P. resinosa* and *P. sylvestris* (Figure 5, Table 2). Mortality patterns were indistinguishable between *P. radiata* stands in Spain and South Africa (Figure 6; $F_{1,36} = 0.07$, $P = 0.79$).

Mortality in vigorous trees (MVT) was lower than total mortality across tree species and continents (Figure 7). MVT varied among species ($F_{6,118} = 18.8$, $P < 0.0001$), averaging under 20 trees ha^{-1} for all except *P. contorta* in Argentina. For all trees combined, MVT increased with basal area, and this relationship varied among species (Table 2; $F_{6,118} = 1.66$, $P = 0.01$), with the strongest being *P. contorta* in Argentina, where >100 vigorous trees ha^{-1} were killed in stands with the highest basal area (Figure 8; $F_{1,13} = 2.96$, $P = 0.01$). In both Spain and South Africa, lower overall levels of mortality in vigorous *P. radiata* increased moderately with basal area ($F_{1,38} = 2.89$, $P = 0.006$). For the remaining species we found no significant relationship between basal area and MVT (Table 2).

We used estimation of self-thinning lines from the data to examine tree mortality patterns and the relationship between tree size and stand density. We plotted quadratic mean diameter against trees ha^{-1} for all stands together and for each species alone. We then calculated self-thinning line estimates as 90th quantile regression lines for all species together and for each species in the study, yielding an overall slope of -0.25 and species-specific slopes ranging from -0.20 (for *P. contorta*) to -0.42 (for *P. ponderosa*) (Supplemental Figure II, Supplemental Table III).

4. Discussion

4.1 Mortality patterns across four continents

Our finding that *S. noctilio*-related tree mortality was strongly linked to metrics associated with stand density across both the native and invaded range supports observations that this woodwasp serves as a forest thinning agent throughout its range. Basal area was the best single predictor of mortality in our study and vigorous trees rarely died. This was consistent with regional studies from the native range of *S. noctilio* (Ayres et al., 2014) and the invaded range in North America (Dodds et al., 2010; Foelker et al., 2018; Haavik et al., 2016, 2017, 2018). Studies in the Southern Hemisphere have also highlighted the importance of stand condition and basal area in driving tree mortality rates (e.g., Slippers et al., 2015; Lantschner et al., 2019), but our study is the first to demonstrate that mortality patterns are often similar in the Northern and Southern Hemispheres.

Location did not change the susceptibility of individual pine species to *S. noctilio*. Stands of *P. radiata* in both Spain and South Africa had indistinguishable positive relationships between basal area and tree mortality. This was surprising given the apparent differences between these regions: in Spain, *S. noctilio* is so rare that it is difficult to find. In contrast, it is considered a major pest in pine plantations in South Africa and is readily located. It would be reasonable to expect higher levels of damage in South African stands. Nonetheless, in both places, similarly overstocked stands experienced similar mortality. Faster tree growth in Southern Hemisphere pine plantations has been cited as a possible cause of high susceptibility leading to high mortality. Trees with higher growth rates may allocate less resources to defense (Herms and Mattson, 1992), and *Pinus* spp. plantations established outside the native range of the genus may experience release from natural enemies in their new environment (Bossdorf et al., 2005; Colautti et al., 2004). Furthermore, selection for high growth rates in plant breeding programs (without attention to resistance) has been hypothesized to also select for reduced defenses, which could lead to differences in defenses among populations resulting from different breeding programs (Loehle and Namkoong, 1987). However, we found no evidence for differential susceptibility of *P. radiata* across regions which would have provided support for these growth rate difference hypotheses. Instead, our study suggests that a higher abundance of damaged stands in South Africa could be linked to an abundance of highly stocked stands on the landscape that would not be possible to maintain in the native range of *Pinus* spp., where a suite of pine species pests and pathogens more strongly limit stocking levels.

Mortality rarely extended into vigorous trees, even in stands with > 25% standing dead stems. Stands in southern Argentina were an exception to this pattern with high mortality seen in larger trees growing in stands that had experienced a large, ongoing *S. noctilio* drought-incited outbreak (total mortality up to 75% of stems) that peaked in 2007-2008 (Lantschner et al., 2019). At these sites as well as others in our study, our data set did not capture peak *S. noctilio* outbreak levels over the past 15 years. South African stands also experienced larger outbreaks prior to our study, including widespread tree mortality of up to > 35% in some stands in the Eastern Cape and Kwa-Zulu Natal around 2004-2006 (Hurley et al., 2007). The highest level of standing dead stems we recorded in South Africa was 26% (in a stand in the Eastern Cape; see Supplemental Table I) and stands with > 10% were found in most regions. It is also important to point out that unknown numbers of dead trees may have fallen prior to our surveys. Measured mortality (stems ha^{-1}) was not intended to represent overall stand loss, but rather to provide a useful metric that could be consistently recorded and compared. Most pulp stands that experienced severe outbreaks in South Africa in the mid-2000s have since been harvested and replaced. This was not true in southern Argentina, where we visited many stands that lost many trees 6-8 years before our surveys. In the case of those sites, it is impressive that even after experiencing a widespread and destructive outbreak that served as a major thinning event, sampled stands yielded some of our study's highest measures of basal area. This suggests the pre-outbreak density of standing stems must have been on the extreme end of overstocked, and that stocking levels in these stands remained among the highest in our study (Figure 5). The significant correlation between stand basal area and MVT generally supports the theory that overstocked conditions lead to the release of *S. noctilio* populations from endemic levels in which attacks are concentrated on small, suppressed trees to colonization of more healthy dominant trees during outbreaks (Aparicio et al., 2013; Westoby, 1984).

We estimated and visualized self-thinning lines from our stand data to explore whether observed tree mortality was similar to what might occur naturally in even-aged stands. Our findings support the hypothesis that *S. noctilio* attack can be one of a suite of factors acting to reduce the number of trees in a stand as tree sizes increase. Stands experiencing high tree mortality attributed to *S. noctilio* were clearly clustered around the estimated self-thinning limit at high tree density (Figure 9). Stand density management diagrams (SDMDs) for *P. radiata* in Spain and *P. resinosa* in North America show that the stands where we recorded high levels of *S. noctilio*-related mortality consistently occurred within the zone of imminent mortality, where self-thinning due to competition is expected (Castedo-Dorado et al., 2009; Smith and Woods, 1997). These are the stands that would be expected to have high mortality levels due to density-dependent mortality factors (Reineke, 1933), including colonization by pests and pathogens.

4.2 Host species identity and tree susceptibility

Host species identity can shape tree interactions with *S. noctilio* in a variety of ways. Tree host species differ in their attractiveness to *S. noctilio*, with impacts on host selection and oviposition behavior (Böröczky et al., 2012). But once a tree is selected for oviposition, species identity can influence tree susceptibility at both a stand scale and an individual scale. At the stand scale, variation among species in growth rates, the intensity of competition, and the timing of self-thinning might be expected to influence susceptibility to mortality. For example, *P. radiata* has been reported to show very early differentiation into crown classes (Jackson, 1955), leading to a distinct group of trees with suppressed canopies and reduced tree vigor—ideal hosts for *S. noctilio*. Our finding of consistent mortality patterns in *P. radiata* across a diverse range of sites may reflect this genetic similarity and the tendency for stands to produce a predictable number of susceptible trees. In contrast, *P. resinosa* has notoriously low genetic variation (Fowler and Morris, 1977) and even-aged stands tend to have less variation in the growth of individual trees, which could lead to less consistent formation of suppressed trees across stands and a looser link between basal area and mortality.

Drivers of susceptibility at the individual tree level include differences in tree chemistry and defenses, size relative to age, and growth rate (Bordeaux and Dean, 2012). The survival and growth of woodwasp larvae within trees is influenced both by tree defenses and the nutritional suitability of the wood for larvae and their symbiotic fungus, *Amylostereum areolatum* (Madden, 1981). The contrast we observed between high mortality, even in vigorous trees, for *P. contorta* in Argentina and very low mortality in neighboring *P. ponderosa* stands of equal or higher basal area levels (many > 75 m^2 ha^{-1}; Figure 5) shows that differences in tree traits can play a strong role in determining morality outcomes.

This mortality pattern has been previously attributed to very low resin production in *P. contorta* (Martinson et al., 2018), exacerbated by widespread drought that presumably further compromised tree defenses (Berner et al., 2017; Lantschner et al., 2019). Resin production is a tree's first line of defense against insect attack, and lowered *S. noctilio* reproductive success in oviposition sites flooded with resin has been reported in Spain (Lombardero et al., 2016). Both *P. ponderosa* and *P. contorta* are native to western North America and likely will face *S. noctilio* attack in their native ranges if the woodwasp becomes established there. These recent findings in Argentina suggest *P. contorta* could be particularly susceptible to *S. noctilio* outbreaks triggered by climatic conditions in its native range, particularly in the face of the hotter, drier future expected with changing climate in western North America (Allen et al., 2010; Fettig et al., 2013).

The continuing expansion of the *S. noctilio* range in North America will also bring this insect in contact with new host species closely related to *P. contorta*: the Contortae include *P. banksiana* (found in North-Central US and Southern Canada) and *P. virginiana* (found from southern New

York through western Tennessee and Alabama; Gernandt et al., 2005). Attacks on *P. banksiana* have been documented by Haavik et al. (2017), who reported low reproductive success in Ontario compared to *P. resinosa* and *P. sylvestris*. However, the tendency for *P. contorta* and *P. banksiana* to hybridize where their ranges overlap (Moss, 1949), and their shared susceptibility to pests like mountain pine beetle (*Dendroctonus ponderosae*) suggest the potential for higher impacts under conditions that stress trees. Meanwhile, *S. noctilio* is spreading southward into the range of *P. virginiana* in the mid-Atlantic states. The close phylogenetic relationship of *P. virginiana* with *P. contorta*, its tendency to produce overstocked stands (Snow, 1960), and bioassays with *S. noctilio* (Bookwalter et al., 2019) suggest that *P. virginiana* may provide a link for *S. noctilio* between the currently infested region and important pine production areas of the southeastern U.S. These include extensive stands of *P. taeda, P. echinata,* and *P. elliottii*, all of which have been observed in the southern hemisphere to be susceptible to *S. noctilio*- related mortality (Borchert et al., 2008; Iede et al., 2012).

4.3 Population dynamics of *S. noctilio*: top-down and bottom-up effects

Destructive outbreaks in pine plantations in Australasia during the mid 1900s drove the initial explosion of research on *S. noctilio* biology, ecology and biological control strategies. Subsequent outbreaks in South Africa, Chile, Argentina, Brazil and beyond have sustained this insect's reputation as a highly destructive and aggressive pest of pines. Our study did not capture mortality in Southern Hemisphere stands at their peak recorded outbreak levels or in North American stands during the initial establishment and spread of *S. noctilio* but stands with mortality levels of at least 5% of standing stems were sampled in each country.

Recent demographic models developed in Spain (Lombardero et al., 2016) and North America (Krivak-Tetley et al., 2020) have highlighted the dominant influence of host suitability on larval survival and potential *S. noctilio* population growth. Even in the presence of natural enemies, a change in host suitability or quality that resulted in near 100% larval success (aside from loss to parasitism) could theoretically increase population growth rates by 4 – 5X (Krivak-Tetley et al., 2020). This potential for large changes in population growth rate due to changes in host susceptibility could indicate that they are a key factor in outbreak initiation. Of course, variable top down effects also influence demography. Parasitism rates in both northern hemisphere countries averaged around 20% for parasitoid wasps (including *Ibalia spp.* and *Rhyssa spp.*) and 36% (Spain) to 63% (North America) for nematode parasitism. Unlike in Spain, where nematodes entered and sterilized eggs, North American nematodes have not been found to enter *S. noctilio* eggs so do not have direct demographic impacts. In part due to this lack of nematode sterilization, the calculated potential population growth rate for North American *S. noctilio* populations is over 2X that of native populations in Spain. Although demographic models are not available for Southern Hemisphere populations, traditional biological control has been an important component in *S. noctilio* management in many countries for decades (Cameron, 2012; Slippers et al., 2012b). Parasitoid wasp and nematode presence have varied widely in space and time but at high levels (e.g., >50% nematode parasitism in some South African stands; Hurley et al., 2012) have played an important role in limiting or preventing *S. noctilio* outbreaks.

Sirex noctilio is widely known for its pulse-like eruptive population dynamics, characterized by rapid increases in abundance that eventually decrease due to the presence of natural enemies or the depletion of resources (Corley and Villacide, 2012). This behavior might also be described by an alternate attractors model, where populations remain at endemic levels under normal circumstances, but when appropriately triggered, can sustain (for a period of time) at high, destructive levels (Martinson et al., 2013). Under this model, *S. noctilio* would be expected to experience positive density dependence upon reaching some threshold population level. A lack of density-limiting silvicultural management at the stand level and environmental factors like drought (Lantschner et al., 2019; Madden, 1988) can lead to a concentration of resources in stands with many suppressed trees. Additional spatial aggregation of woodwasps due to limited female dispersal (Corley et al., 2007), and a resulting increase in tree stress or oviposition success due to a high concentration of attacks that weaken previously vigorous trees might provide a strong mechanism for positive density dependence and could lead to sustained high population levels and mortality in trees not normally susceptible to *S. noctilio*. The positive relationship between MVT and stand basal area (Fig. 8) supports this concept.

The combined use of silvicultural strategies and biological control using parasitoid wasps and nematodes as described by Cameron (2012) has been widely utilized for the management of *S.*

noctilio. Future research directly comparing the role of top-down and bottom-up effects on *S. noctilio* population dynamics would be helpful to understand the relative importance, and the ideal timing, of these approaches. Yet the important role of host susceptibility in determining potential *S. noctilio* population growth rate, combined with our findings in this global study that tree mortality was strongly linked to stand-level factors suggest that the system is strongly regulated from below. High resource availability is likely a prerequisite for the development of outbreaks, both in the presence and absence of natural enemy populations.

5. Conclusion

The idea that *S. noctilio* plays an important role as a scavenger and thinning agent, even during moderate outbreaks, is not new (Cameron, 2012; Rawlings and Wilson, 1949). Lower stocking levels or pre-emptive thinning serve to reduce stand susceptibility to *S. noctilio* (Ayres et al., 2014; Dodds et al., 2014; Slippers et al., 2015, but see Lantschner et al., 2019), and this system has been highlighted as a model system for the potential to effectively control destructive forest pests through silvicultural approaches (Muzika, 2017). Long-term control of *S. noctilio* has been achieved in New Zealand, where catastrophic outbreaks first occurred, via a combination of adaptation of silvicultural practices to limit high concentrations of suppressed trees and naturalization of nematode and parasitoid wasp populations that were introduced as part of biological control programs (Bain et al., 2012). However, short-rotation pulp production stands in many regions present a unique challenge. The economic model upon which they rely does not permit substantial silvicultural intervention and pushes the harvest date to a point in time when a significant proportion of harvestable stems are experiencing heightened competition and are likely to have compromised vigor. In these stands, the variable nature of natural enemy levels presents a challenge in their primary use to control *S. noctilio* outbreaks, as the continuous presence of many susceptible host trees on the landscape represents constant risk for *S. noctilio* outbreak should the balance shift due to changes in natural enemy performance, environmental influences such as drought, or other factors. Furthermore, Southern Hemisphere yield expectations were likely established during a period when natural enemies were absent (enemy release is common when species are planted outside their native range and pests have not yet reached them), which may not be realistic in the face of the arrival and sustained presence of a suite of pests and pathogens, *S. noctilio* among them.

Future research that helps quantify the importance of the abundance, density and distribution of high-quality hosts on the landscape will help clarify the relationship between sustained resource availability, tree mortality patterns, and the development of *S. noctilio* outbreaks. A renewed awareness of controlling the stand- and landscape-level distribution of susceptible trees can both help manage *S. noctilio* in coming years, particularly in the face of a hotter, drier climate that is predicted to affect many pine-growing regions due to climate change (Anderegg et al., 2015).

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Table 1. Stands surveyed for this study contained eight pine species across four countries spanning the native and invaded range of *S. noctilio*. Table indicates number of stands and individual trees sampled and specifies whether each pine species is native in the indicated region.

Country	Species	Code	# stands	# trees	native
Spain	*P. pinaster*	PIPI	15	1043	yes
	P. radiata	PIRA	17	880	no
	P. sylvestris	PISY	5	303	yes
USA	*P. resinosa*	PIRE	11	984	yes
	P. sylvestris	PISY	2	88	no
South Africa	*P. patula*	PIPA	28	1140	no
	P. radiata	PIRA	23	796	no
	P. taeda	PITA	1	32	no
Argentina	*P. contorta*	PICO	15	895	no
	P. ponderosa	PIPO	16	641	no

Table 2. Species-specific regression statistics for relationships between *Pinus* spp. basal area and two measures of *S. noctilio*-related tree mortality: all mortality and mortality in vigorous trees (see Figure 5).

Species	Number of Stands	***S. noctilio*-related mortality (trees ha^{-1})**			
		All Trees		Vigorous trees[a]	
		slope ± SE	R^2	slope ± SE	R^2
P. contorta	15	0.35 ± 0.06***	0.74	0.17 ± 0.06*	0.40
P. patula	28	0.38 ± 0.08***	0.45	0.11 ± 0.07	0.09
P. pinaster	15	0.20 ± 0.08*	0.36	0.05 ± 0.03	0.19
P. ponderosa	16	0.13 ± 0.05*	0.31	0.06 ± 0.04	0.15
P. radiata	40	0.31 ± 0.05***	0.47	0.06 ± 0.02*	0.18
P. resinosa	11	0.11 ± 0.07	0.21	0.03 ± 0.04	0.06
P. sylvestris	7	0.13 ± 0.08	0.37	0.07 ± 0.03	0.50

[a] defined as DBH > 0.9 · Mean DBH; * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$

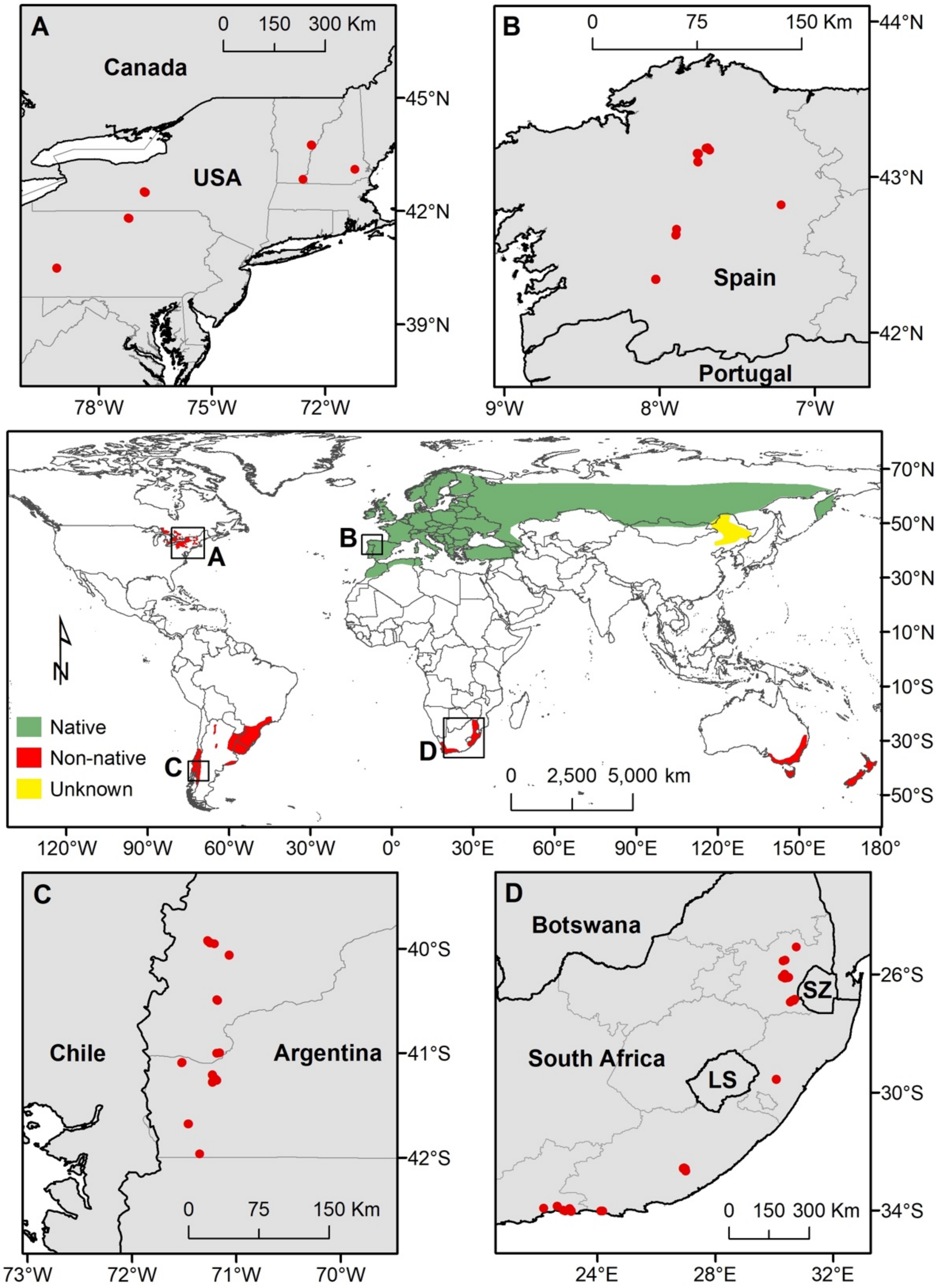


Figure 1. The native range of *S. noctilio* (shown in green) spans much of Eurasia and parts of Northern Africa. Non-native populations (shown in red) are found in Australasia, southern Africa, and South and North America. Field study locations for pine stand surveys were in four regions with established *S. noctilio* populations: (A) the recently invaded range in North America, (B) the native range in Spain, and the invaded range in (C) Argentina and (D) South Africa. Points show stand locations.

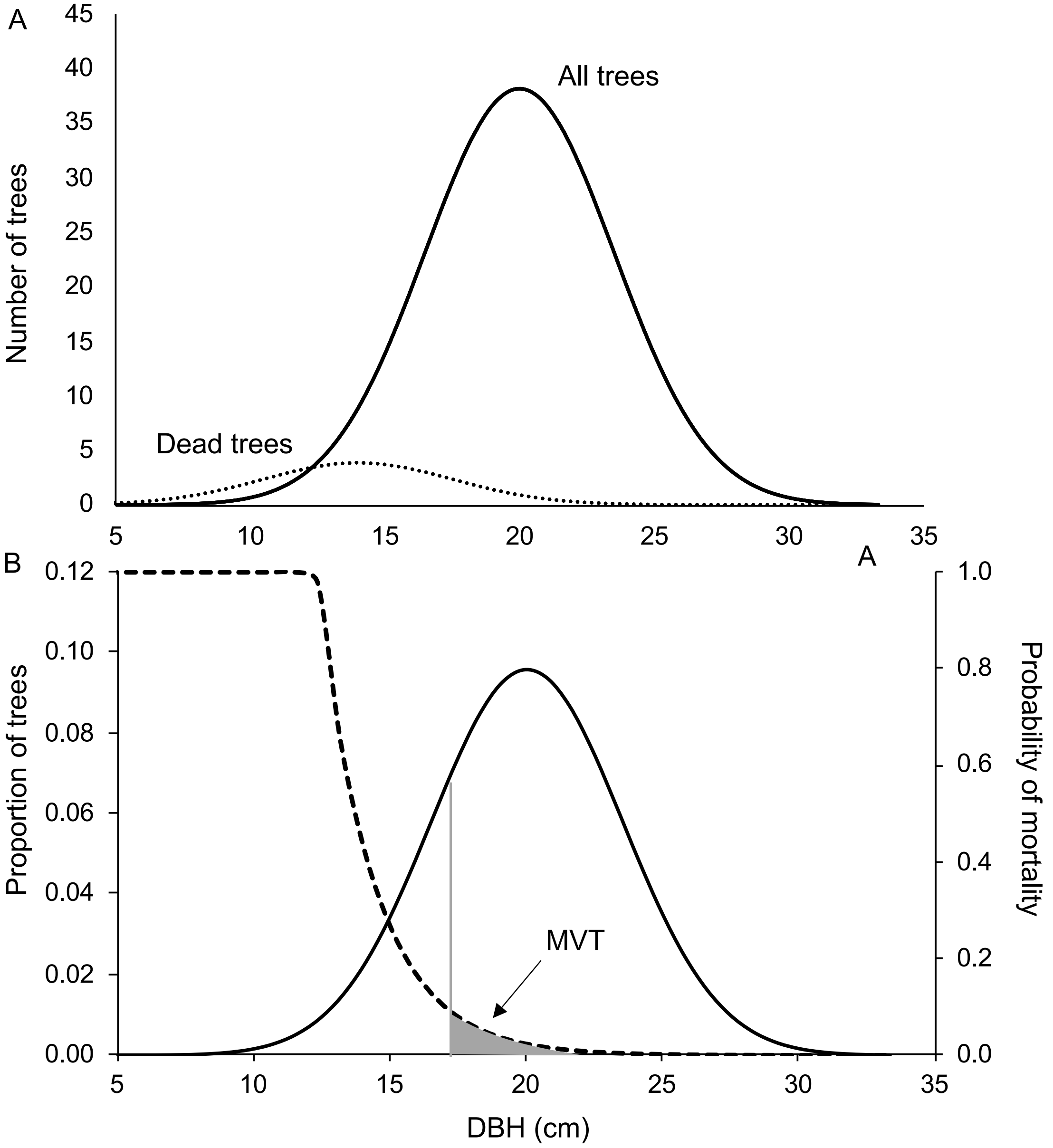


Figure 2. Mortality in vigorous trees (MVT) was calculated separately for each stand by (A) fitting separate normal distributions to the DBH data collected for standing dead trees in a stand (dotted line) and all trees in a stand (solid line) and (B) estimating the probability of mortality (dashed line) across the range of tree sizes (solid line) in that stand. MVT was then calculated as the number of trees per stand with DBH > (0.90 ・Mean DBH) expected to be dead. Data shown here are from a *P. resinosa* stand in the Finger Lakes National Forest, NY, USA, sampled in 2013.

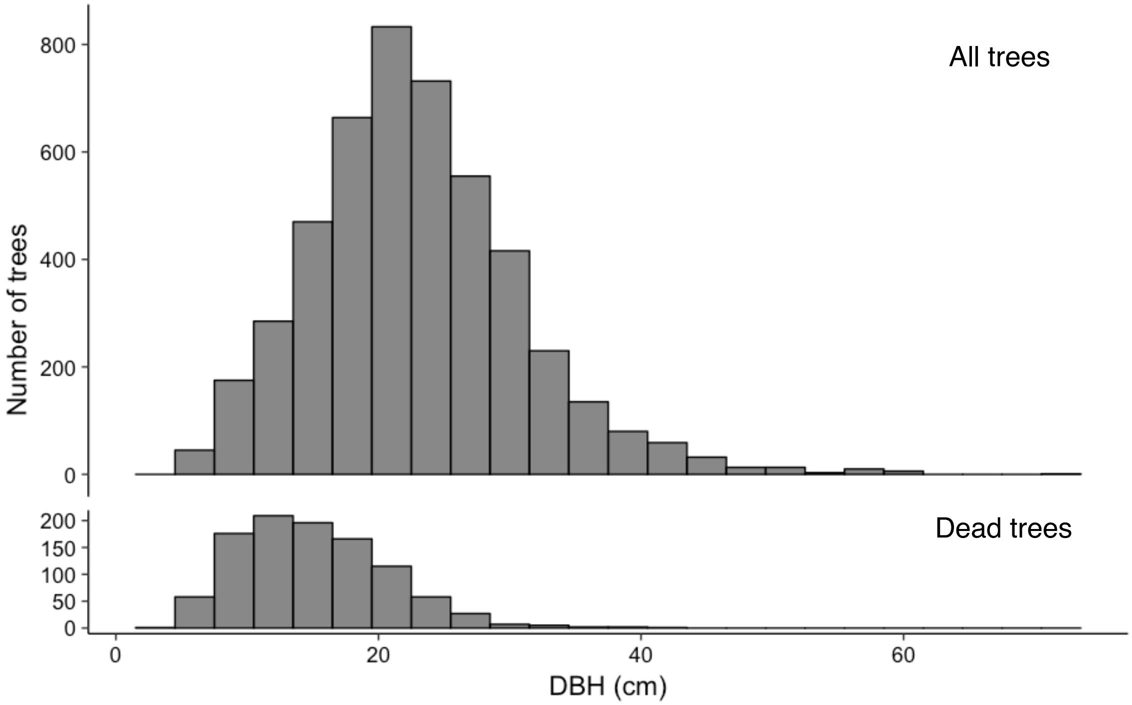


Figure 3. Trees killed by *S. noctilio* were smaller than average. Figures show aggregated distribution across all species and countries in the study.

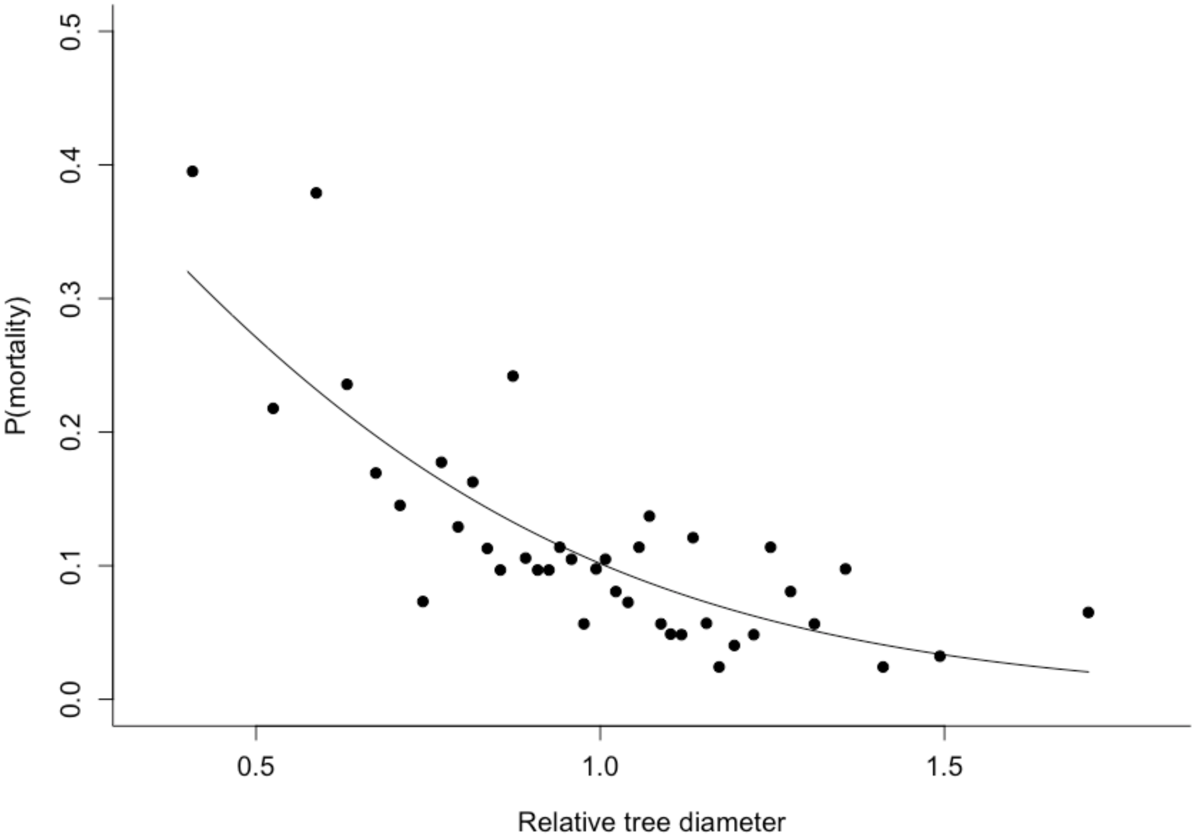


Figure 4. Probability of mortality was highest in trees that were small relative to the average tree in a stand. Plotted points are averages for binned data with groups of n=100, and include data from all stands, species and countries. Solid line shows the fitted logistic regression curve representing the probability of mortality across the range of relative tree sizes.

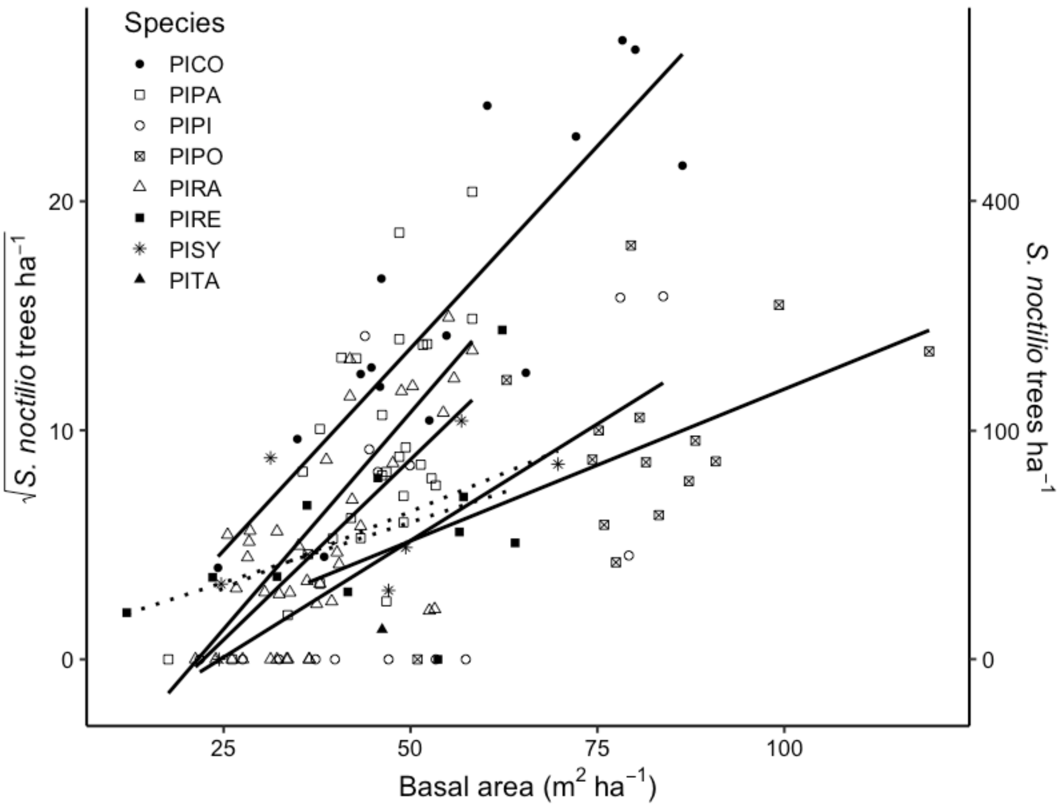


Figure 5. The number of *S. noctilio*-infested trees ha^{-1} increased with basal area but somewhat variably among species (Table 2). Lines are species-specific regressions (solid line indicated relationship was significant at $p < 0.05$, dashed line indicates not significant). Species shown are *P. contorta* (PICO), *P. patula* (PIPA), *P. pinaster* (PIPI), *P. ponderosa* (PIPO), *P. radiata* (PIRA), *P. resinosa* (PIRE), *P. sylvestris* (PISY) and *P. taeda* (PITA).

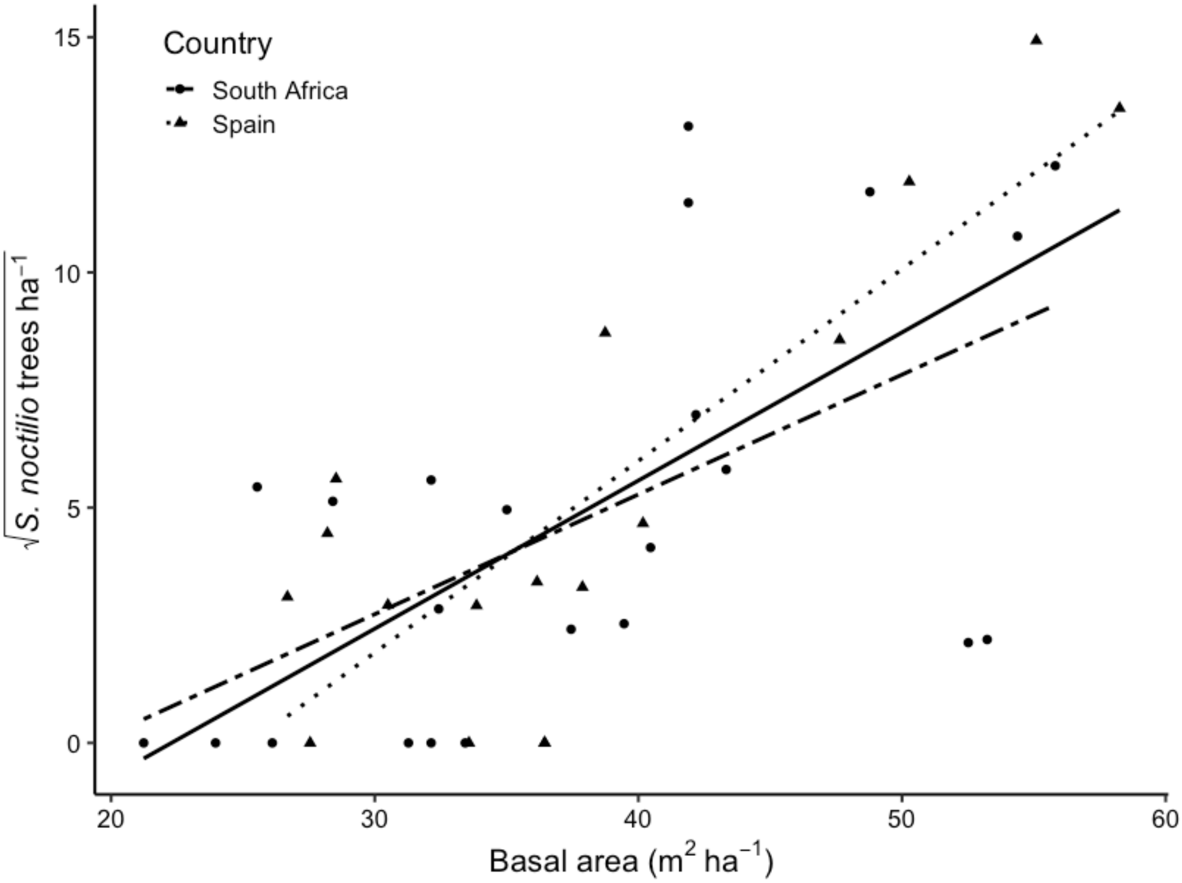


Figure 6. For *P. radiata*, which was well represented in both Spain and South Africa, there was no difference between countries in the relationship between *S. noctilio*-related tree mortality and basal area of host trees. Each point represents one stand. Solid line is aggregate regression, dotted lines are separate regressions for Spain (triangles, dotted line) and South Africa (circles, dashed line).

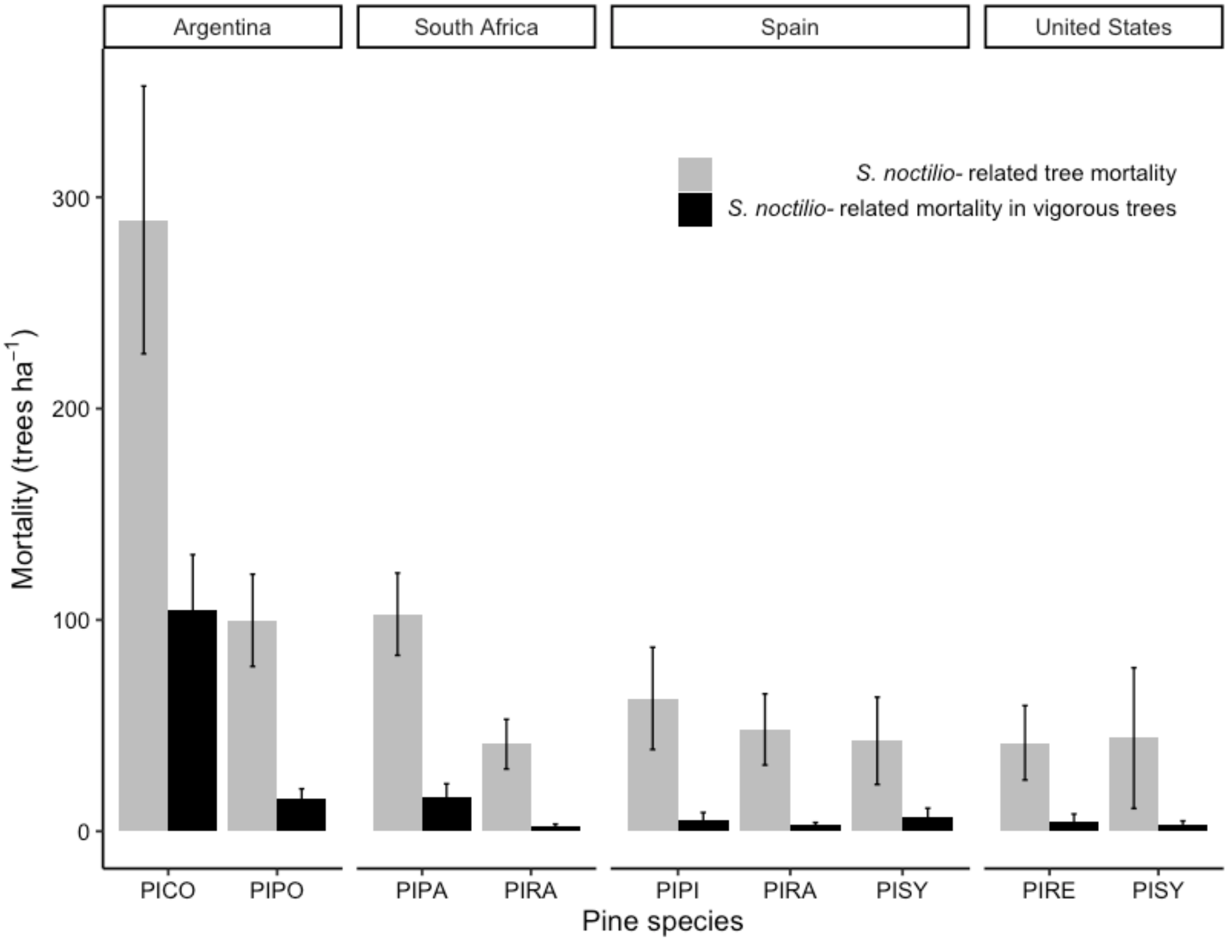


Figure 7. Mortality (mean ± SE) in vigorous trees (those with DBH > 0.9 *Average DBH in Stand; MVT) compared to all *S. noctilio*-related mortality. Number of stands for each pine species is listed in Table 1. In most cases, *S. noctilio* attacked and killed very few vigorous trees despite a range of mortality levels across stands and tree species. See Table 3 for tree species codes.

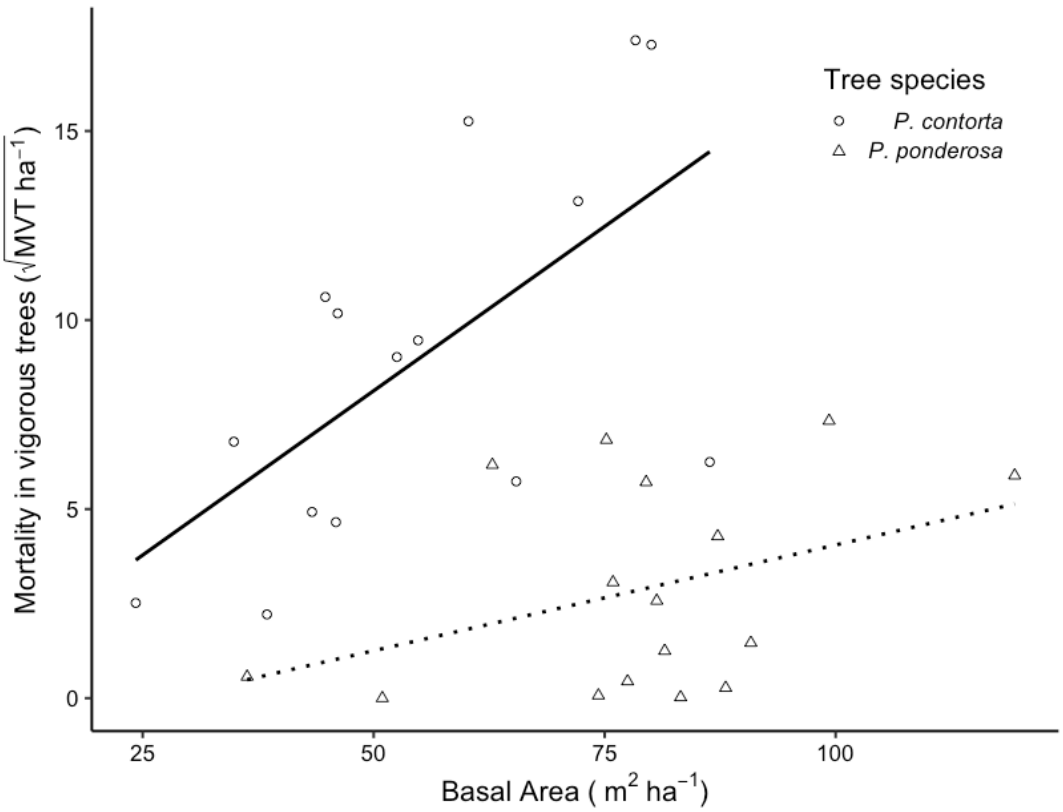


Figure 8. *Pinus contorta* (solid line) and *P. ponderosa* (dotted line) were growing in the same conditions in Argentina but showed very different patterns of *S. noctilio*-related mortality in vigorous trees (MVT).

Supplementary Materials

Field Methods

Canopy status/crown class was measured using standard forestry definitions (from DeYoung, 2020; Helms, 1998):

Dominant: Crowns that extend clearly above the general level of the canopy and receive full light from above and at least 2/3 of the sides. Our even aged stands had few dominant trees.

Codominant: Crowns that reach the level of the canopy and receive direct light from above but normally not from all sides (typically < 2/3).

Intermediate: Crowns that reach intermediate heights in the canopy. They receive light from above, but generally not from the sides. These trees are shorter than dominant and codominant trees and sometimes but not always taller than suppressed trees.

Suppressed: Crowns that reach low or intermediate heights in the canopy and are shaded from directly above as well as from the sides so do not receive direct light. When differentiating between suppressed and intermediate crowns, we checked for presence/absence of branches and foliage from neighboring trees directly above the growing tip of the tree.

Note: For many analyses (as noted in Methods and Results), codominant and dominant trees were grouped together and intermediate and suppressed trees were grouped together.

Year since tree death was estimated using a combination of factors including visual status of tree tissues (needles, bark, branches, phloem), apparent age of *S. noctilio* signs (including oviposition sites and emergence holes), and the presence and age of co-colonizers and their galleries. This was a rough estimate intended to allow for some assessment of the timing of attack in a given stand and to allow us to confirm whether *S. noctilio* was present in the stand in the current year. These data were not intended to provide firm time of death estimates for purposes of modeling spread or the timing of mortality.

Presence of co-colonizers varied substantially by location. Forests in native range *Pinus* range (Spain and North America) had higher diversity of co-colonizers. In South Africa and Argentina, the same two or three were often seen over and over. Climate, and thus weathering and decay rates varied substantially between sites, even within the same country. Time since death assessments were always made by comparing condition of dead trees in a stand to others in the same stand, and by conferring with local foresters and collaborators when possible. Trees that had been dead for longer than three years were often difficult to distinguish and often assigned a category of, e.g., “3+” to represent that uncertainty. These were coded for analysis by assigning the most recent possible year of death, e.g. in the case above “3”. The following is a general list of types of features we looked for when assigning year of death:

0: Very recent tree death, brown needles still attached to tree, sometimes fresh oviposition sites (current season) or new emergence holes. Some trees died in the first season of attack, while others died the following year when adults were emerging. Xylem at base of tree normally still resinous and wet, not fully dried out. These trees could be considered to undergoing the process of death but to have passed the “point of no return”.

1: Death during previous season. Browned needles often fallen, but branches have usually not lost all twigs and bark. Oviposition sites from previous season, and emergence holes may be fresh or from previous season. Phloem starting to dry, xylem no longer wet near base of tree. Commonly observed colonizers: *Pissodes nemorensis* galleries, bark beetles.

2: Trees that have been dead for two years have more weathering. Oviposition sites appear weathered, with drippings sometimes becoming difficult to see. Emergence holes generally appear weathered. Depending on site location and climate, tree may be starting to lose branches and bark, and wood is dry (in arid climates) or starting to decay (in wetter climates). Signs of Cerambicidae common at this stage.

3+: Oviposition sites and emergence holes weathered, oviposition sites often difficult to locate. Bark falling from tree, phloem dried/gone. Distinguishing 3 year old mortality from 4, 5, or more becomes quite difficult; trees with substantial decay often assigned 3+ unless other data were available to pinpoint year of death (e.g., stands in Spain with tagged trees that had previously been surveyed for *S. noctilio* attack and mortality). Sometimes stands contained trees that had clearly been dead longer than the primary 3-year old trees (e.g., substantial decay and moss growth, etc.) and these were assigned an older date. Beyond 3 years, many trees starting to fall.

Supplemental Table I. Select stand level variables collected and calculated in (a) Argentina, (b) South Africa, (c) Spain and (d) North America.

a.			**All Trees**				**Trees with Sirex**				
Country	Species	Transect	mean DBH	BA	stems ha^{-1}	Prop supp	mean DBH	% stems lost	MVT	% BA lost	stems ha^{-1}
Argentina	PICO	AR15AM011	23.80	65.43	1423.11	0.13	16.40	11.00	23.10	5.22	156.54
		AR15AM031	21.27	86.38	2323.71	0.20	13.75	20.00	16.79	8.36	464.74
		AR14BU020	19.64	60.26	1859.61	0.10	16.38	31.43	125.19	21.85	584.45
		AR15CS021	22.33	80.06	1968.35	0.40	19.45	36.00	151.73	27.32	708.61
		AR14EF010	23.17	34.87	761.94	0.10	20.16	12.14	60.39	9.20	92.52
		AR14EF030	21.53	45.91	1240.03	0.03	17.55	11.43	17.47	7.59	141.72
		AR14FO010	20.86	72.13	2022.52	0.12	17.38	25.77	85.43	17.88	521.14
		AR15PN011	18.55	46.10	1625.54	0.23	15.09	17.00	63.72	11.25	276.34
		AR14RO010	21.71	43.33	1143.51	0.08	17.65	13.57	21.21	8.97	155.19
		AR15SJ011	31.74	24.25	266.37	0.23	24.35	6.00	23.82	3.53	15.98
		AR15SP011	26.74	78.34	1352.81	0.47	23.49	54.00	223.80	41.68	730.52
		AR15SP021	22.07	54.81	1332.23	0.40	18.74	15.00	67.23	10.82	199.84
		AR15SP051	21.86	52.51	1360.88	0.33	21.79	8.00	59.83	7.95	108.87
		AR15SO031	26.35	38.45	668.85	0.17	17.87	3.00	7.34	1.38	20.07
		AR15TA021	18.45	44.77	1623.40	0.13	18.71	10.00	69.35	10.28	162.34
	PIPO	AR15AM021	26.80	83.22	1321.17	0.23	10.67	3.00	0.00	0.48	39.64
		AR15AM041	23.67	88.10	1823.59	0.37	10.80	5.00	0.04	1.04	91.18
		AR14BU1a0	25.84	36.30	632.16	0.17	16.13	3.33	0.51	1.30	21.07
		AR14BU1b0	23.51	90.82	1943.89	0.10	13.48	3.85	1.10	1.26	74.76
		AR15CS011	26.54	119.38	2009.02	0.27	18.78	9.00	17.26	4.50	180.81
		AR14EF020	30.42	50.94	681.90	0.03		0.00	0.00		0.00
		AR14FO020	22.42	74.32	1775.05	0.27	14.10	4.29	0.00	1.70	76.07
		AR14FO030	22.87	75.18	1747.67	0.10	20.15	5.71	26.71	4.44	99.87
		AR15PN021	19.82	62.84	1859.79	0.27	13.60	8.00	20.47	3.77	148.78
		AR15SJ021	20.60	79.49	2040.77	0.47	11.58	16.00	15.99	5.05	326.52
		AR15SP031	24.66	80.64	1592.33	0.20	16.96	7.00	4.17	3.31	111.46
		AR15SP041	26.26	99.29	1711.09	0.20	18.56	14.00	31.45	7.00	239.55
		AR15SP061	51.57	77.48	358.88	0.07	25.54	5.00	0.55	1.23	17.94
		AR15SO011	25.74	81.50	1481.36	0.13	12.44	5.00	1.06	1.17	74.07
		AR15SO021	22.74	87.24	2018.09	0.17	18.27	3.00	9.09	1.94	60.54
		AR15TA011	25.62	75.90	1379.52	0.13	17.26	2.50	6.81	1.13	34.49

b.			All Trees				Trees with Sirex				
Country	Species	Stand Code	mean DBH	BA	stems ha^{-1}	Prop supp	mean DBH	% stems lost	MVT	% BA lost	stems ha^{-1}
South Africa	PIPA	SA13HVC27	18.75	48.50	1663.18	0.07	11.72	11.75	2.00	4.60	195.42
		SA13HVE31	19.61	52.23	1612.68	0.13	11.78	11.75	1.68	4.24	189.49
		SA18HLA108	22.90	39.60	927.97	0.10	11.60	3.00	0.00	0.77	27.84
		SA18HLA14a	19.44	43.33	1399.64	0.13	8.94	2.00	0.00	0.42	27.99
		SA18HLA75	21.13	53.37	1442.01	0.10	12.93	4.00	0.06	1.50	57.68
		SA18HLB31a	22.39	49.07	1191.72	0.20	12.80	3.00	0.02	0.98	35.75
		SA18HLH35	22.13	51.37	1204.31	0.23	8.55	6.00	0.01	0.90	72.26
		SA14HBV12a	26.28	48.50	869.70	0.20	18.80	9.00	8.31	4.60	78.27
		SA14HBV1b	24.09	42.76	908.72	0.27	19.42	19.00	45.83	12.35	172.66
		SA14HBW10a	22.10	49.36	1223.05	0.23	13.07	7.00	0.26	2.45	85.61
		SA14HBW12b	20.25	42.04	1269.09	0.23	14.83	3.00	7.79	1.61	38.07
		SA14HBW23b	24.44	33.57	690.44	0.07	15.13	0.54	0.73	0.21	3.73
		SA14HBW24a	20.67	37.88	1089.17	0.17	7.20	1.00	0.00	0.12	10.89
		SA14HBW26c	21.74	35.58	928.69	0.17	12.39	7.23	0.38	2.35	67.18
		SA14HBW28	21.41	49.07	1272.37	0.33	11.23	4.00	0.04	1.10	50.89
		SA14HBX23a	20.75	26.11	755.20	0.13		0.00	0.00		0.00
		SA14HBX28a	23.46	37.88	842.81	0.17	16.25	12.00	21.37	5.76	101.14
		SA18LWB005a	19.87	58.25	1700.60	0.33	10.24	13.00	1.97	3.45	221.08
		SA18LWC14	19.27	51.65	1570.93	0.27	13.93	12.00	31.56	6.26	188.51
		SA18RHA5a	19.20	58.25	1894.31	0.13	14.66	22.00	57.22	12.83	416.75
		SA18RHB15	18.51	46.20	1614.80	0.20	10.85	4.00	0.52	1.37	64.59
		SA18RHC3	20.15	40.75	1239.38	0.13	14.37	14.00	21.56	7.12	173.51
		SA18RHE36	20.44	48.50	1335.04	0.30	16.46	26.00	107.12	16.86	347.11
		SA18RHF12b	22.63	46.77	1116.22	0.10	14.88	6.00	3.58	2.60	66.97
		SA18RHF22b	20.95	46.20	1264.66	0.13	14.63	9.00	20.62	4.39	113.82
		SA18RHR22	18.82	52.80	1785.62	0.20	11.89	3.50	2.07	1.40	62.50
		SA18RHR27b	21.30	46.77	1283.49	0.03	7.51	0.50	0.00	0.06	6.42
		SA13SP16a	32.56	17.60	207.18	0.00		0.00	0.00		0.00

b. continued			All Trees				Trees with Sirex				
Country	Species	Transect	mean DBH	BA	stems ha^{-1}	Prop supp	mean DBH	% stems lost	MVT	% BA lost	stems ha^{-1}
South Africa	PIRA	SA14BEL13a	27.06	39.46	641.73	0.27	15.00	1.00	0.08	0.31	6.42
		SA14BEL14	22.28	42.18	973.30	0.33	11.42	5.00	3.18	1.31	48.67
		SA14BEL24	23.61	40.46	862.08	0.30	10.50	2.00	0.00	0.40	17.24
		SA14BRS5	32.73	33.43	383.69	0.20		0.00	0.00		0.00
		SA14BUL15a	21.97	32.43	810.82	0.27	18.20	1.00	3.43	0.69	8.11
		SA14HBT54	37.23	52.51	454.35	0.33	18.50	1.00	0.00	0.25	4.54
		SA14HBV13a	36.56	53.23	482.69	0.17	16.80	1.00	0.00	0.21	4.83
		SA14HBV1a	21.71	41.90	1073.57	0.20	14.20	16.00	16.51	6.85	171.77
		SA14HBW14d	21.88	32.14	780.34	0.43	11.98	4.00	0.32	1.20	31.21
		SA14HBW21a	22.76	35.01	818.95	0.17	11.93	3.00	0.00	0.83	24.57
		SA14HBW21b	24.68	43.33	843.87	0.23	14.03	4.00	0.34	1.29	33.75
		SA14HBW27a	18.44	55.81	1880.74	0.33	10.96	8.00	7.26	2.83	150.46
		SA14HBW30b	21.67	48.78	1247.12	0.13	11.17	11.00	0.01	2.92	137.18
		SA14HBX23b	22.44	32.14	774.17	0.20		0.00	0.00		0.00
		SA14JOJ10a	28.18	37.45	583.53	0.03	8.40	1.00	0.00	0.09	5.84
		SA14JOJ10c	24.16	23.96	497.13	0.10		0.00	0.00		0.00
		SA14KEM14	15.80	28.41	1318.14	0.30	5.30	2.00	0.00	0.22	26.36
		SA14KRF11a	24.96	25.54	493.28	0.20	16.67	6.00	12.10	2.67	29.60
		SA14KRF15a	30.53	31.28	409.32	0.13		0.00	0.00		0.00
		SA14RUH7	20.92	21.24	589.04	0.23		0.00	0.00		0.00
		SA14RUM13	21.78	26.11	673.78	0.20		0.00	0.00		0.00
		SA14WIC27a	22.60	41.90	941.71	0.53	14.21	14.00	8.76	5.54	131.84
		SA14WIC69a	28.11	54.38	724.64	0.37	13.10	16.00	3.86	3.47	115.94
	PITA	SA14HBT55a	40.89	46.20	338.96	0.03	42.00	0.50	4.46	0.53	1.69

c.			All Trees				Trees with Sirex				
Country	Species	Transect	mean DBH	BA	stems ha^{-1}	Prop supp	mean DBH	% stems lost	MVT	% BA lost	stems ha^{-1}
Spain	PIPI	SP14CS010	20.30	43.90	1268.12	0.43	14.65	15.71	36.49	8.19	199.28
		SP14PP020	25.96	27.55	493.56	0.13		0.00	0.00		0.00
		SP14PP030	17.96	21.81	781.72	0.37		0.00	0.00		0.00
		SP13OUpx1	14.64	79.20	4297.76	0.30	6.50	0.48	0.24	0.09	20.56
		SP13OUpx11	24.60	39.89	827.02	0.00		0.00	0.00		0.00
		SP13OUpx10	23.03	37.30	881.56	0.00		0.00	0.00		0.00
		SP13OUpx12	15.09	78.05	3933.46	0.27	8.84	6.34	1.35	2.18	249.44
		SP14OUpx2	18.28	57.39	2131.89	0.11		0.00	0.00		0.00
		SP14OUpx3	18.93	47.06	1601.87	0.18		0.00	0.00		0.00
		SP13OUpx4	22.77	32.43	781.89	0.00		0.00	0.00		0.00
		SP14OUpx5	15.65	44.48	1951.02	0.55	8.06	4.31	0.00	1.14	84.10
		SP14OUpx6	22.94	53.37	1252.72	0.05		0.00	0.00		0.00
		SP14OUpx7	16.94	49.93	1953.54	0.39	8.50	3.67	0.01	0.92	71.69
		SP13OUpx8	14.93	83.79	4438.51	0.27	9.80	5.66	6.39	2.44	251.24
		SP14OUpx9	15.59	45.63	2024.98	0.55	7.38	3.31	0.00	0.74	66.94
	PIRA	SP14BE030	22.86	36.16	820.34	0.40	9.55	1.43	0.03	0.25	11.72
		SP13BE020	21.61	33.86	852.63	0.17	13.41	1.00	0.13	0.39	8.53
		SP13BE010	16.67	38.74	1599.38	0.23	10.46	4.75	5.89	1.87	75.97
		SP14CS020	31.28	36.44	460.98	0.03		0.00	0.00		0.00
		SP13BEnz1	33.42	33.57	373.82	0.00		0.00	0.00		0.00
		SP13BEnz10	18.44	50.28	1487.46	0.63	10.67	9.57	11.16	3.20	142.28
		SP13BEnz11	30.94	36.44	465.80	0.00		0.00	0.00		0.00
		SP13BEnz12	19.30	58.25	1819.76	0.30	10.55	10.00	2.15	2.99	181.98
		SP13BEnz2	18.17	55.10	1857.26	0.49	10.62	12.00	6.23	4.10	222.87
		SP14BEnz3	27.63	26.69	404.39	0.26	17.00	2.38	0.83	0.90	9.63
		SP14BEnz4	26.87	28.20	446.62	0.38	15.43	4.44	3.95	1.46	19.85
		SP14BEnz5	25.55	28.53	472.61	0.36	12.23	6.67	0.00	1.53	31.51
		SP13BEnz6	31.22	27.55	351.45	0.00		0.00	0.00		0.00
		SP14BEnz7	30.03	30.50	412.12	0.13	22.10	2.08	1.76	1.13	8.59
		SP14BEnz8	27.68	40.17	631.61	0.24	17.40	3.45	0.10	1.36	21.78
		SP14BEnz9	27.90	37.88	569.86	0.38	23.80	1.92	8.59	1.40	10.96
		SP14PP010	21.19	47.64	1284.16	0.17	13.70	5.71	0.00	2.39	73.38
	PISY	SP13BC010	28.25	47.06	723.90	0.00	19.00	1.25	1.97	0.57	9.05
		SP14BC020	22.04	69.73	1695.67	0.37	16.13	4.29	13.99	2.30	72.67
		SP13FA010	19.09	56.82	1885.70	0.10	11.67	5.75	3.67	2.15	108.43
		SP14FA020	17.77	24.39	909.46	0.33		0.00	0.00		0.00
		SP14FA030	18.98	49.36	1669.04	0.13	5.70	1.43	0.01	0.13	23.84

d.			All Trees				Trees with Sirex				
Country	Species	Transect	mean DBH	BA	stems ha^{-1}	Prop supp	mean DBH	% stems lost	MVT	% BA lost	stems ha^{-1}
United States	PIRE	US15BL010	14.54	23.53	1282.03	0.43	9.50	1.00	2.14	0.43	12.82
		US17BR010	30.08	32.14	435.65	0.07	12.97	3.00	0.00	0.56	13.07
		US15FL030	21.87	62.27	1590.83	0.20	16.42	13.00	24.86	7.33	206.81
		US14FL010	19.51	57.08	1845.48	0.22	13.71	2.73	2.65	1.35	50.30
		US15HC010	24.89	63.99	1292.83	0.03	10.55	2.00	0.00	0.36	25.86
		US15HC020	21.20	56.53	1547.22	0.03	9.90	2.00	0.00	0.44	30.94
		US16NW010	32.78	12.05	138.69	0.03	18.73	3.00	3.14	0.98	4.16
		US16NW020	24.06	36.16	753.73	0.10	15.67	6.00	4.25	2.54	45.22
		US16NW030	26.79	45.63	784.53	0.00	17.28	8.00	0.36	3.33	62.76
		US16NW040	28.25	53.66	819.19	0.07		0.00	0.00		0.00
		US17PW010	34.27	41.61	434.10	0.13	24.45	2.00	0.00	1.02	8.68
	PISY	US15BL020	16.47	24.68	1081.59	0.10	9.70	1.00	0.98	0.35	10.82
		US15FL020	24.17	31.28	644.73	0.27	15.60	12.00	7.57	5.00	77.37

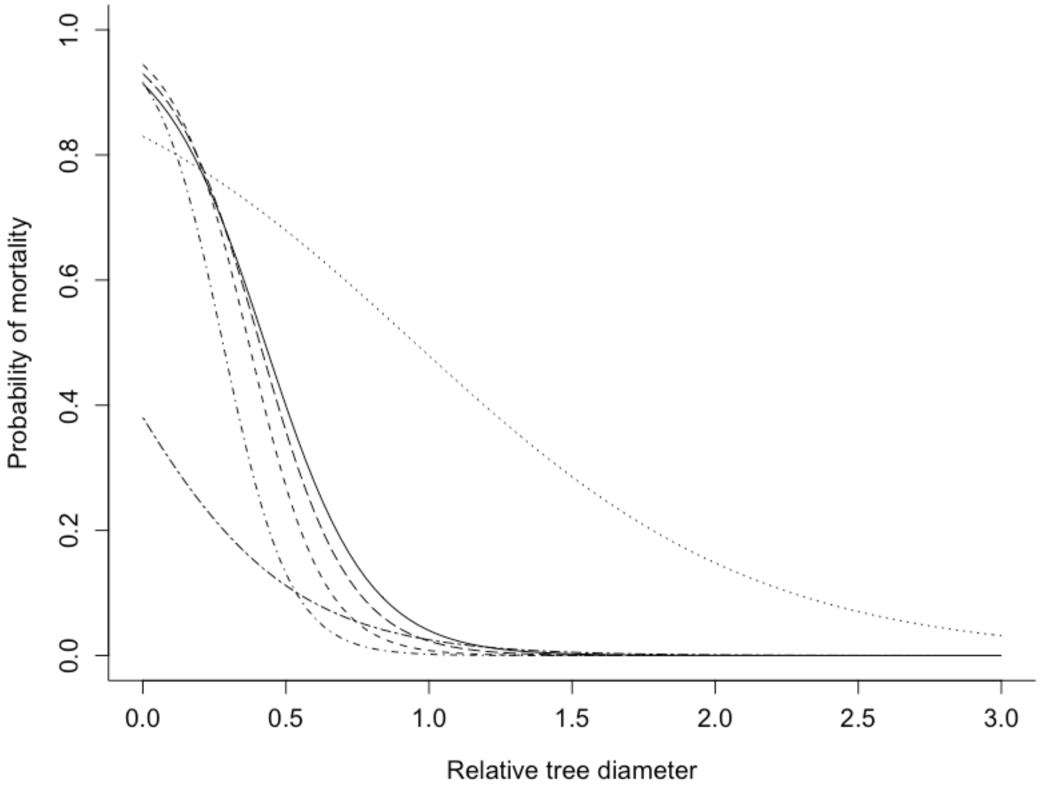
Supplemental Table II. Correlation matrix of stand-level attributes (1-7) and damage from *S. noctilio* (8-12)[i]. Bold indicates significant at 0.05 level.

	DBH	QMD	Basal area	Trees ha^{-1}	Proportion suppressed	NN1	NN2	*S. noctilio* DBH	% trees with *S. noctilio*	*S. noctilio* trees ha^{-1}	Basal area lost
1. DBH											
2. QMD	**1**[ii]										
3. Basal area	-0.07	-0.07									
4. Trees ha^{-1}	**-0.64**	**-0.64**	**0.68**								
5. Proportion suppressed	**-0.35**	**-0.3**	0.13	**0.27**							
6. NN1	**0.67**	**0.67**	**-0.49**	**-0.71**	**-0.31**						
7. NN2	**0.75**	**0.75**	**-0.54**	**-0.77**	**-0.29**	**0.92**					
8. *S. noctilio* DBH	**0.67**	**0.66**	0.03	**-0.4**	**-0.21**	**0.4**	**0.44**				
9. % trees with *S. noctilio*	**-0.23**	**-0.21**	**0.43**	**0.34**	**0.35**	**-0.36**	**-0.39**	0.18			
10. *S. noctilio* trees ha^{-1}	**-0.37**	**-0.35**	**0.57**	**0.56**	**0.35**	**-0.49**	**-0.54**	0.02	**0.95**		
11. Basal area lost	-0.09	-0.1	**0.25**	0.15	0.15	-0.19	**-0.21**	**0.31**	**0.87**	**0.81**	
12. MVT	-0.09	-0.1	**0.26**	**0.17**	**0.19**	**-0.2**	**-0.21**	**0.34**	**0.7**	**0.69**	**0.97**

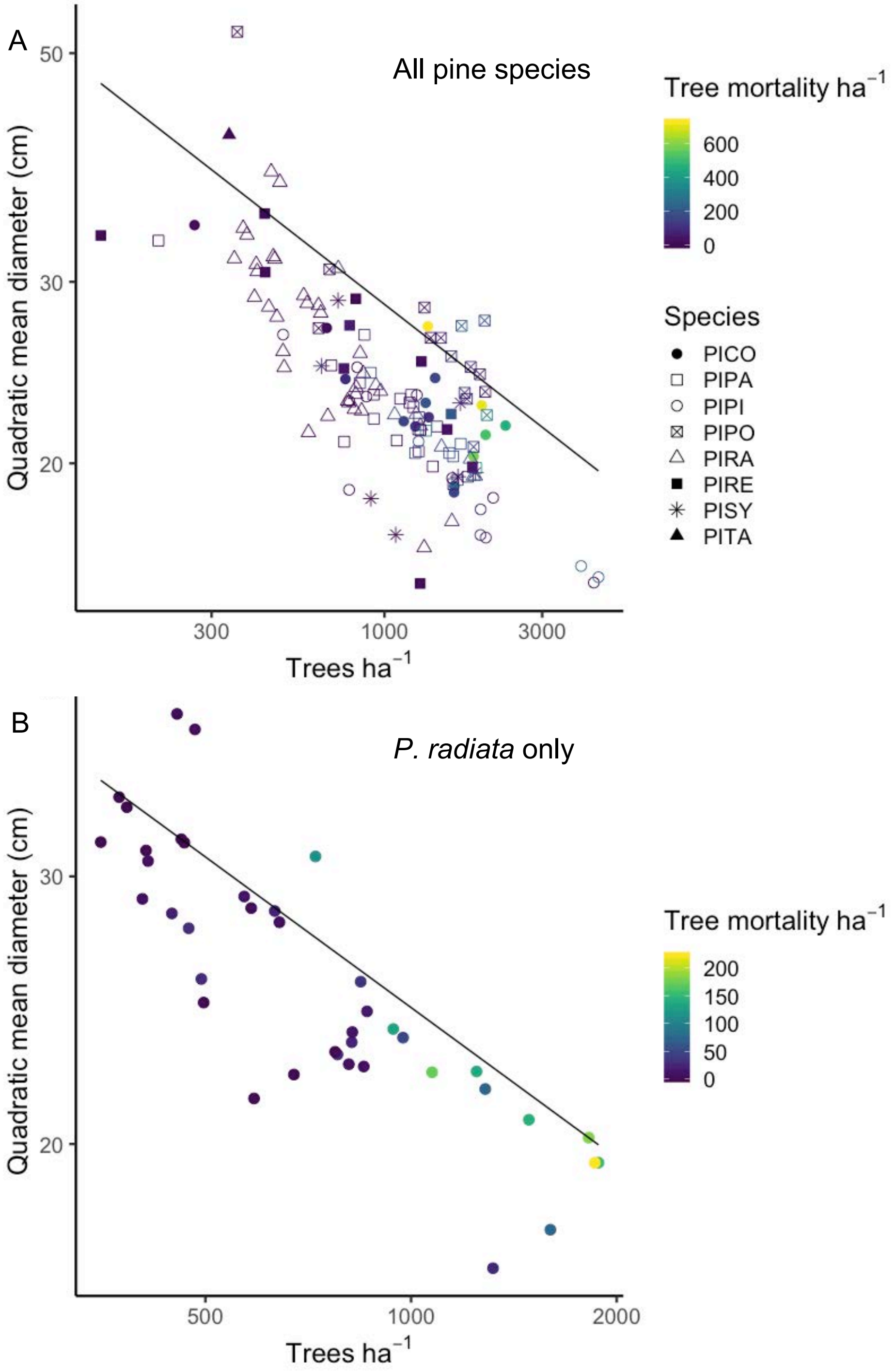
[i] Detailed variable descriptions: 1. DBH: diameter at breast height (arithmetic mean); 2. QMD: quadratic mean diameter, $\sqrt{\frac{\sum D_i^2}{n}}$, where D_i= DBH of *i*th tree, *n* = number of trees in stand; 3. Basal area: (m2 ha^{-1}) measured with 10-BAF prism; 4. Trees ha^{-1}: number of stems per hectare; 5. Proportion suppressed: proportion of trees in the stand with suppressed crowns; 6. NN1: distance (m) to the closest neighboring tree ≥ 5 cm DBH; 7. NN2: distance (m) to the second closest neighboring tree ≥ 5 cm DBH; 8. *S. noctilio* DBH: diameter at breast height of trees attacked by *S. noctilio* (arithmetic mean); 9. % trees with *S. noctilio*: square root of the percentage of trees in stand with signs of *S. noctilio* attack; 10. *S. noctilio* trees ha^{-1}: square root of the number of trees per hectare with signs of *S. noctilio* attack; 11. Basal area lost: percent of total stand basal area lost due to *S. noctilio*- associated tree mortality; 12. MVT: estimated number of vigorous trees ha^{-1} (defined as those with DBH > 0.9 • Average DBH for the stand) lost due to *S. noctilio*. [ii] Unrounded correlation= 0.9969.

Supplemental Table III. Estimated slopes and intercepts from 90th quantile regression (where x = log (trees ha^{-1}) and y = log (quadratic mean diameter). Estimates computed for all stands combined and for all stands of each pine species separately (see Figures 9a-b).

Species	Code	Slope	Intercept
All		-0.25	5.08
P. radiata	PIRA	-0.33	5.48
P. contorta	PICO	-0.20	4.65
P. ponderosa	PIPO	-0.42	6.43
P. patula	PIPA	-0.26	4.96
P. pinaster	PIPI	-0.28	5.09
P. resinosa	PIRE	-0.30	5.39
P. sylvestris	PISY	-0.27	5.13



Supplemental Figure I. For all tree species, probability of mortality was highest for the smallest trees in a stand and decreased with increasing relative tree diameter. Combined logistic regression shown in Figure 4. This figure shows separate logistic regression curves for each of the following tree species, from left to right: *P. sylvestris*, *P. pinaster*, *P. radiata*, *P. resinosa*, *P. patula*, *P. contorta*.



Supplemental Figure II. Approximate self-thinning boundaries as estimated by 90th quantile regressions of quadratic mean diameter vs. trees ha^{-1} (both log-transformed). Upper panel includes all pine species in the study. Lower panel is *P. radiata* alone. See Table 3 for regression coefficients, including separate estimates for each species.

Author Contributions

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