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RESPONDING TO AN EMERGENT PLANT PEST-PATHOGEN COMPLEX ACROSS SOCIAL-ECOLOGICAL SCALES

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by

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Abstract

RESPONDING TO AN EMERGENT PLANT PEST-PATHOGEN COMPLEX ACROSS SOCIAL-ECOLOGICAL SCALES

by

SHANNON COLLEEN LYNCH

Responding effectively to accidental introductions of plant pests (e.g., fungi, bacteria, viruses, animals, plants) is complicated because timely and costly decisions must be made across social and ecological scales with limited information. In this dissertation, I provide an interdisciplinary framework that allows responsible institutions to respond quickly and effectively to an emerging, introduced, multi-host pest-pathogen complex using even minimal knowledge available about pest attributes. First, I take an evolutionary ecology approach and examine how the phylogenetic structure of host ranges of different pest-pathogen combinations can be used to predict likelihoods of establishment, spread, and impacts of Fusarium dieback - invasive shot hole borers (FD–ISHB) in the urban-wildland forests and avocado growing regions of Southern California, where the pest-pathogen complex has established after its introduction from Southeast Asia. Phylogenetic dispersion analysis on a comprehensive FD–ISHB host-range data set shows that the strength of the phylogenetic signal is progressively more pronounced for more severely affected host species. As a basis for risk analysis, this understanding helps plant health first responders assess how any polyphagous pest complex might behave when introduced

to novel environments with a new set of possible hosts, which in turn informs more efficient and cost-effective phytosanitary surveillance priorities.

Second, I conduct a multivariate analysis of fungi and bacteria cultured from wood in a phylogenetically diverse set of live tree hosts to determine if the structure and composition of tree microbiomes is predictive of the likelihood or outcome of attack by FD–ISHB. I further explore interactions within the microbiome between endophytic microbes and the pathogen to identify potential opportunities and mechanisms to shape disease establishment and spread, and evaluate whether endogenous microbes could be manipulated for sustainable integrated pest management. I found consistent differences in wood-inhabiting microbial communities between avocado, which grows in an agricultural setting, and three wildland tree species (willow, sycamore, and oak), but there were no strong, consistent differences among microbial communities based on host attack status. However, enough differences were detected to suggest that inconsistencies most likely reflect undersampling in the community – a common problem with culture-based studies – which sets the stage for future culture-independent studies that integrate a richer data set into the analysis. Furthermore, 15 fungal species and 11 species of bacteria exhibited clear *in vitro* antagonism against the pathogen, indicating their potential to confer a protective benefit to tree hosts as biological control agents.

Finally, I analyze participant-observation and public-document data to assess the effectiveness of governance processes that influence management decisions in a

statewide deliberative and consensus-directed process to control FD–ISHB spread and impacts. I found that the comprehensive set of collaborative actions that emerged from this process were due to conditions identified in theoretical frameworks for collaborative governance and could not have been attained by any organization acting alone. These actions were enhanced by the structure and quality of principled-engagement process elements, which benefited from prior histories of cooperation and conflict. Collectively, this dissertation provides valuable technical and collaborative tools to improve integrated pest management and respond to the large-scale socio-ecological disturbances that accompany invasive, introduced pests.

DEDICATION

I dedicate this dissertation to my husband, colleague, and hayatım:

Akif Eskalen

for his unconditional love and support.

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Chapter 1

Introduction

In this final year of my graduate career, the global and unpredictable phenomenon of coronavirus disease 2019 (COVID-19) that has changed how we work, learn, and interact has no doubt raised awareness and demonstrated to the general public that pathogens play an important role in the world and can have devastating impacts. Pests more broadly (e.g., fungi, bacteria, viruses, animals, plants) evolve in particular places, and their impacts can be especially severe when introduced to new locations and new hosts. As the COVID-19 pandemic illustrates, responding effectively to accidental introductions of pests is complicated because timely and costly decisions must be made across social and ecological scales. Such decisions are usually based on very little information about the pest's natural history and origins, what it can attack, and where it is likely to spread and cause the most damage. Therefore, these destructive, living threats require a framework that allows responsible institutions to respond quickly and effectively using whatever minimal knowledge is available about pest attributes. In this dissertation, I address how we can respond in real time to an emerging pest-pathogen complex that has been introduced from Southeast Asia to Southern California, where it now affects trees in urban-wildland forests and avocado groves. I explore how an understanding of host range and host-microbial communities can potentially explain patterns of disease

establishment and spread, and assess the effectiveness of governance processes that influence management decisions. This dissertation centers on three distinct but interrelated topics: (1) evolutionary ecology of plant disease, (2) phytobiomes and forest health, (3) collaborative governance.

This dissertation represents my leadership role in a multi-campus and multi-agency collaborative research effort towards the control and management of the emergent pest-pathogen complex Fusarium dieback - invasive shot hole borers (FD–ISHB) in California. The *Fusarium* pathogens (*Fusarium euwallaceae* and *F. kuroshium*) and ambrosia beetle vectors (*Euwallacea fornicatus* and *E. kuroshio*) that cause FD–ISHB are able to attack a broad range of host species, causing ecological and economic damage to urban-wildland forests, and the avocado growing regions of the state. The ecological complexity of the problem also broadens the social context to involve a wider variety of people who have a stake in the outcomes of management decisions. As with most cases concerning invasive species, it is beyond the ability of any single organization to address the full scope of devastating impacts FD–ISHB has on the environment, public health, and economic vitality of diverse social-ecological systems. For action to be effective on a large-scale problem such as FD–ISHB, interactive decision-making across scales is essential. In practice, my research questions are the product of my collaborations with diverse stakeholders in response to their short- and long-term management needs to control emerging plant pathogen threats. At the same time, my research questions reflect my commitment to advancing our knowledge of plant diseases within an ecological framework to expand the

theoretical impact of my applied plant pathology research. As such, this dissertation research is inherently interdisciplinary and has regional, national, and international impacts.

Overall, this dissertation consists of two ecologically focused chapters and one chapter concentrating on social considerations, each centered around responses to the FD–ISHB epidemic. In Chapter 2, I examine the phylogenetic effects of the FD–ISHB host range to assess host impacts in Southern California and predict host range and impacts in South Africa, where the complex has recently established. The research builds on previous work that demonstrated a phylogenetic signal in host range (i.e., closely related plants are more likely to share pests and pathogens) (Gilbert & Webb 2007), and applies it towards FD–ISHB, which involves a more complex interaction; namely a plant-insect-pathogen interaction. Phylogenetic dispersion analysis on a comprehensive FD–ISHB host-range data set (Eskalen *et al.* 2013) shows that the strength of the phylogenetic signal is progressively more pronounced for more severely affected host species. As a basis for risk analysis, this understanding helps plant health first responders assess how any polyphagous pest complex might behave when introduced to novel environments with a new set of possible hosts, which in turn informs more efficient and cost-effective phytosanitary surveillance priorities. This chapter also informs my future research, which will evaluate how well microclimate and abundance-weighted phylogenetic structure of local host communities predict disease establishment. The chapter has been accepted

for publication in the peer-reviewed journal *Evolutionary Applications* and is formatted with my co-authors Gregory Gilbert and Akif Eskalen.

In Chapter 3, I investigate whether the structure and composition of tree microbiomes is predictive of the likelihood or outcome of attack by FD–ISHB of a phylogenetically diverse set of tree hosts. I further explore interactions within the microbiome between endophytic microbes and the pathogen to identify potential mechanisms for shaping disease establishment and spread, and evaluate whether endogenous microbes could be utilized for sustainable integrated pest management. In this study of bacteria and fungi from the tree microbiome that could be cultured in the laboratory, I found consistent differences in wood-inhabiting microbial communities between *Persea* (avocado), which grows in an agricultural setting, and three genera of wildland host species [*Salix* (willow), *Platanus* (sycamore), and *Quercus* (oak)], but there were no strong, consistent differences among microbial communities based on attack status of the hosts. However, our analysis did detect enough differences among microbes that the inconsistencies most likely reflect undersampling in the community – a common problem with culture-based studies – which sets the stage for future studies that integrate a richer data set into the analysis of these communities using a culture-independent approach. All the preparatory work for such a culture-independent approach using high-throughput DNA sequencing has been completed, but the actual sequencing work has been interrupted by COVID-19 research efforts, which froze non-essential processing. The results from that sequencing work will be combined with these culture-based results for later

submission for publication. Furthermore, we identified 15 fungal species and 11 species of bacteria exhibiting clear *in vitro* antagonism against the pathogen, indicating their potential to confer a protective benefit to tree hosts as biological control agents. For land managers seeking more sustainable preventative measures, these findings provide the rationale to pursue greenhouse and field experiments testing the efficacy of these endophytes to control pest-pathogen establishment. This research provides an empirical foundation to help stakeholders evaluate the relative importance of biotic and abiotic factors that influence pest-pathogen spread and guide more strategic management decisions.

Chapter 3 is primarily my work in conceiving and coordinating the fieldwork and sample processing, and I did all the writing and analysis as part of my dissertation. It will be submitted for publication with five additional co-authors. Gregory Gilbert, my major advisor, significantly contributed to the design, analysis, and writing of this study. My colleague Akif Eskalen provided key guidance for the microbial interaction experiments. Three additional co-authors, Edeli Reyes-Gonzalez, Emily Bossard, Karen S. Alarcon, significantly contributed to the collection of data and sample processing under my supervision.

Finally, in Chapter 4, I study collaborative governance in action using a collective action effort to control FD–ISHB in California. I use qualitative research methods to explore how the conditions in cooperative decision-making led to a consensus on statewide response priorities. This collective decision-making process involved diverse sets of actors who share an interest or stake in the management of

FD–ISHB. As co-chair of one of the subcommittees in this process, and with the added responsibility of synthesizing the outcomes of all sub-committees in a final report, I was in a unique position to study collaborative governance processes in real time. The limited number of studies that have explored governance with respect to invasive species management have focused on the influence of collaborative network structures on decision making (McAllister *et al.* 2015; Lubell *et al.* 2017; Nourani *et al.* 2018). By using participant observation methods that allowed me to focus on interactions among individuals representing different entities, this chapter goes beyond the network structure and delves more deeply into the influence of collaborative dynamics within the social context. Given the number and intensity of conflicts over transboundary challenges associated with environmental management, understanding the conditions that promoted successful outcomes in this case can help to mitigate such conflicts in other cases concerning pest management.

Collective contributions

Together, these chapters provide valuable technical and collaborative tools to improve integrated pest management (IPM) and best respond to the large-scale socio-ecological disturbances that accompany invasive, introduced pests. Essential components to any IPM program include (1) early detection and monitoring to facilitate rapid response efforts; (2) risk assessments to identify which habitats are most vulnerable to novel pests and which pathways are most important in their spread; (3) evaluation of preventive and curative biological, mechanical, and

chemical control options appropriate for different habitat types. My work in chapters 2 and 3 jointly and individually enhance these technical aspects of an IPM program. The phylogenetically informed analysis of pest host range enhances the first two IPM components by offering an innovative and cost-effective approach to pest surveillance and helping stakeholders begin to identify likely disease outcomes across multiple host-pest combinations. This is complemented by work to characterize resident host microbial communities and their interactions with a plant pathogen to provide an understanding of factors that shape disease outcomes beyond simple lists of which hosts are susceptible to a pest. Additionally, microbiome work in Chapter 3 represents the first step to evaluating more sustainable biological control options that reduce the environmental and health impacts of pesticides, which strengthens the third key element of an IPM program. However, as I describe in Chapter 4, my analysis of the FD–ISHB collaborative governance process illustrates how technical advances do not themselves ensure that effective solutions will be enacted. One of the biggest themes that emerged from my analysis was the importance of a clear commitment to measures that accommodate the needs of stakeholders. In other words, the adoption of any particular management approach was contingent on supportive relationships among stakeholders, no matter how well the technical measure could potentially mitigate pest spread. My approach to finding technical solutions through my work in phylogenetic and microbiome ecology emulates this theme because that work was the outcome of time and energy spent in a co-creation process with diverse groups focused on their needs and interests. Collectively, the complementary chapters of my

dissertation show that an effective IPM framework must integrate a collaborative decision-making process involving many different perspectives and good working relationships to ensure sound management.

Making quick decisions in the face of an unexpected pest arrival with uncertain social and ecological ramifications is an unfortunate reality of our time. Accidental introductions of pests from their home range into new environments have escalated in the 21st century due to much more permeable international borders commensurate with the rapid increase in agricultural trade and human mobility (Venette & Carey 1998; Gottwald *et al.* 2001). The sheer volume of incoming cargo makes it impossible to detect all introductions at international entry ports (Fletcher *et al.* 2010). In addition to my work with FD–ISHB, I have conducted research and outreach extension activities over the last 18 years to address several other emergent and invasive pest and pathogen problems caused by introductions that have had devastating impacts on ecological and social systems. Examples include the goldspotted oak borer (GSOB, *Agrilus auroguttatus*), the pathogen *Phytophthora ramorum* (the cause of sudden oak death, or SOD), and *Botryosphaeria corticola* (the cause of Bot canker), all of which have contributed to widespread oak decline in California (Rizzo *et al.* 2002; Lynch *et al.* 2010, 2013, 2014; Coleman *et al.* 2011; Dreaden *et al.* 2011). Through these experiences, I have learned that effective responses require an interdisciplinary approach to create the tools needed to help make governance decisions for short- and long-term responses. That understanding motivated this dissertation research.

This dissertation provides a template to help decision-makers prepare for "the next big thing." It is a set of holistic principles that users can apply in response to many different kinds of multi-host pest invasions. This research equips Extension Specialists responsible for transferring their scientific discoveries from the laboratory to the public with a new kind of quick decision tool and an approach to finding long-term sustainable biocontrol measures. More importantly, it provides them with a framework on the best ways to leverage the right institutional arrangements and communication approaches to ensure these cutting-edge control strategies are implemented. The dissertation provides state and federal regulatory agencies responsible for plant health emergency decisions with ways to leverage unique control strategies while adopting a bottom-up approach to ensure public buy-in and implement the best technical solutions available. For the "boots-on-the-ground" land managers, my work shows how appropriate, collaborative governance structures provide a pathway to receive the most up to date information from researchers on pest distribution and treatment options, to apply that information, and then communicate feedback to researchers that stimulates further research on control strategies accommodating realized constraints and better meet their specific needs. In sum, this body of work represents a model framework to help all stakeholders with a vested interest in invasive pest management outcomes to respond effectively to emergent pest problems in the short term, while working towards long-term sustainable solutions.

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Chapter 2

Host Evolutionary Relationships Explain Tree Mortality Caused by a Generalist Pest–Pathogen Complex

Abstract

The phylogenetic signal of transmissibility (competence) and attack severity among hosts of generalist pests is poorly understood. In this study, we examined the phylogenetic effects on hosts differentially affected by an emergent generalist beetle-pathogen complex in California and South Africa. Host types (non-competent, competent, and killed-competent) are based on nested types of outcomes of interactions between host plants, the beetles, and the fungal pathogens. Phylogenetic dispersion analysis of each host type revealed that the phylogenetic preferences of beetle attack and fungal growth were a non-random subset of all available tree and shrub species. Competent hosts were phylogenetically narrower by 62 Myr than the set of all potential hosts, and those with devastating impacts were the most constrained by 107 Myr. Our results show a strong phylogenetic signal in the relative effects of a generalist pest-pathogen complex on host species, demonstrating that the strength of multi-host pest impacts in plants can be predicted by host evolutionary

relationships. This study presents a unifying theoretical approach to identifying likely disease outcomes across multiple host-pest combinations.

Introduction

Accidental introductions of plant pests (e.g., fungi, bacteria, viruses, animals, plants) into areas outside their place of origin have resulted in novel species interactions that pose ecological and economic threats to agricultural, urban, and wildland landscapes (Donatelli et al., 2017; Goodell et al., 2000; Parker & Hay, 2005; Pimentel et al., 2000; Young et al., 2017). To respond appropriately to such threats and optimize the use of limited resources for management, decision-makers require robust analytical tools that help determine in which plant communities emergent pests are most likely to establish and cause damage during critical early stages of invasions. As a necessary first step to developing predictive models of pest spread in novel habitats, we take an evolutionary ecology approach and examine how the host range structure of different pest-pathogen combinations can be used to better understand mechanisms of their establishment, spread, and impacts.

Evolutionary tools show promise as a way to understand invasions and predict host range of pests in novel locations (Briese, 2003; Fountain-Jones et al., 2018; Gilbert et al., 2012). For plants and their pathogens, evolutionary constraints in physiological, morphological, and chemical traits that confer host susceptibility or pathogen virulence produce a phylogenetic signal for host range; hence, closely

related plants are more likely to share pests and pathogens (Gilbert & Webb, 2007; Young et al., 2017). Phylogenetic signal in host range has been used to predict the likely host range of generalist plant pests in local communities not yet invaded by such pests (Parker et al., 2015; Gilbert & Parker, 2016). Patterns of phylogenetic signal in host range have been well documented for plant–pest relationships involving a single pest interacting with their host plants (e.g., plant–pathogen, plant–insect), but not for those exhibiting multiple interactions (e.g., pest–pathogen complexes) where the traits shaping the relationships may differ among the multiple partners and their interactions. As such, the patterns and strength of the signal as a basis for risk analysis for more complex plant–pest problems are less well understood. Here, we use an emergent invasive pest–pathogen complex affecting a diversity of tree hosts in Southern California to test the utility of this phylogenetic tool in evaluating host range for novel plant–insect–pathogen interactions. Further, we assess whether we can use information on the phylogenetic structure of the pest-pathogen host range in California, where the complex has been intensively studied, to guide an understanding of likely patterns in South Africa and inform priorities for phytosanitary surveillance, where the invaders have only recently established.

Fusarium dieback–invasive shot-hole borers (FD–ISHB) is a pest–pathogen complex with a broad host range that involves two cryptic ambrosia beetles (PSHB & KSHB, Table I) in the *Euwallacea* species complex (Coleoptera: Curculionidae: Scolytinae) (Gomez et al., 2018; Smith et al., 2019; Stouthamer et al., 2017) and the specific symbiotic fungal pathogens each beetle species carries (Tables I & SI)

(Freeman et al., 2013; Lynch et al., 2016; Na et al., 2018). The beetles were introduced to California from Southeast Asia (Eskalen et al., 2012; Stouthamer et al., 2017), presumably on packing material. Since the appearance of ISHB in California in 2012, the combined effects of ISHB and their fusaria symbionts have killed or caused dieback on 77 tree species on which the beetles can reproduce, but the beetles make attempted attacks on an additional 247 tree species (Fig. 1, Table SI) (Eskalen et al., 2013). The two pest-pathogen complexes that form FD-ISHB have indistinguishable host ranges. Critically, the recent introduction of one of those complexes to South Africa, the polyphagous shot hole borer (PSHB, Table I) (Paap et al., 2018) has been cause for concern given the severe damage these invasive species have caused in California. The known host range in California and South Africa continues to grow, pointing to the need for a sound scientific understanding of the complexity of the FD–ISHB host range to inform risk assessments and focus phytosanitary actions in areas where the beetles have established, and in non-invaded locations worldwide that have favorable conditions for their establishment.

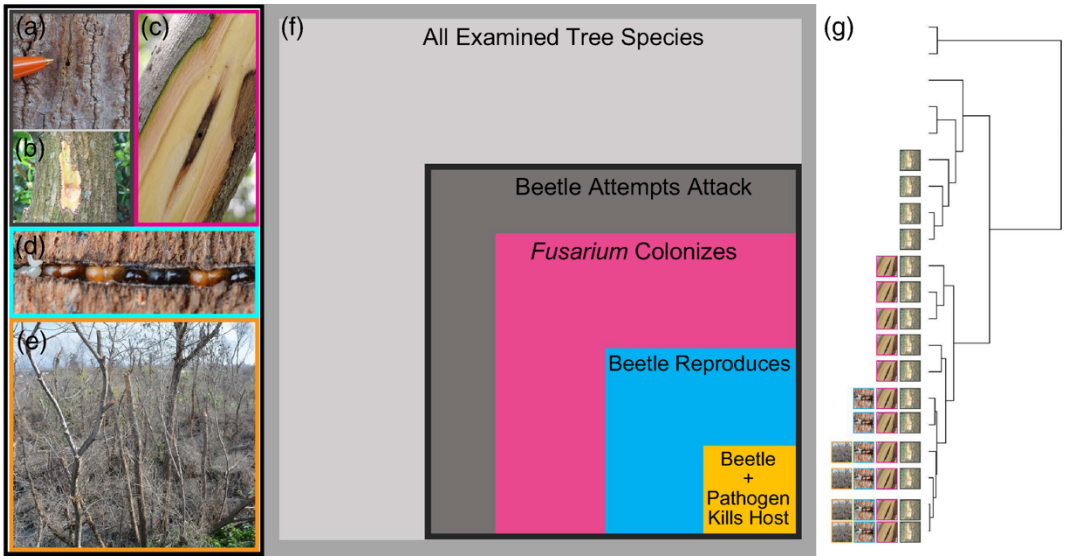

Figure 1. Representation of the expected phylogenetic effects on different host types impacted by Fusarium dieback-invasive shot hole borers. The left panel (a-e) depicts examples of nested types of outcomes of interactions between host plants, the beetles, and the fungi. **Non-competent hosts** (a-c) represent tree species that do not support beetle reproduction or fungal transmission. For host types on which the beetle **attempts an attack** (a-b), entry holes are observed but removal of the bark reveals healthy tissue and no signs of a gallery. Removal of the outer bark on hosts susceptible to ***Fusarium* colonization** (c) reveals necrotic tissue caused by the pathogen, but no signs of a gallery. On **competent hosts** (d), the beetle is able to establish a natal gallery and produce offspring and on some of these (e), the beetle and pathogen can kill the host (i.e., **killed-competent**). Successfully established breeding galleries in competent hosts contain a "fungal garden" and beetles at all life stages (eggs, developing larvae, adults), demonstrating the beetles' ability to cultivate their nutritional symbiotic fungi and complete their life cycle. Colors around each image correspond to the host type represented by the nested boxes in the middle panel (f), the sizes of each which correspond to the relative proportion of tree species for each host type. The phylogenetic tree in the right panel (g) depicts our hypothesis that hosts are a non-random, closely related, subset of all available tree species and that this phylogenetic signal is more pronounced for each of the nested interaction outcomes. The icons represent the examples of the nested types of interaction outcomes from most inclusive to least inclusive.

While a large body of work has established there is a phylogenetic signal in overall host ranges of pests and pathogens (Gilbert & Parker, 2016), the phylogenetic signal of competence and severity among hosts is much less well understood (Gilbert et al. 2015). In addition to distinguishing between hosts that do not support reproduction of the beetle-pathogen (non-competent) and those that do (competent),

phylogenetic relatedness may also predict those hosts that are killed by the beetle-pathogen (killed-competent) (Fig. 1). For FD–ISHB, different host types (non-competent, competent, and killed-competent) are based on nested types of outcomes of interactions between host plants, the beetles, and the fungi (Fig. 1). Hosts that are competent for pest reproduction are the most important in driving the spread of invasive enemies, and the lethality to different hosts is the most important for ecological impact. Thus, assessing the phylogenetic signal of host competency is key to evaluating the potential for establishment, spread, and damage from novel pests and pathogens.

The apparent damage caused by complex novel pest invasions such as FD–ISHB highlights the need to strategically apply, in early response efforts, an understanding of the phylogenetic signal in competence and severity among their hosts. The 77 currently recognized competent host species occur across varied and complex landscapes, with important implications for the ecological and economic vitality of a variety of systems. For example, the California avocado industry, which produces 90% of the United States domestic crop, has spent over $2.5 million to combat the problem. For urban forests, initial estimates suggest that FD–ISHB has the potential to kill roughly 27 million trees (38%) in Southern California's 10,992-square kilometer urban region (McPherson, 2016). In Orange County, California, the removal of 1,524 infested trees and treatment of 2,228 trees cost the county approximately $3 million between 2013–2017 (Parks, 2017). Costly large-scale tree removal efforts to manage the problem could have unintended consequences for the

environment and public health, given that urban forest trees in California remove 567,748 t CO_2 annually, equivalent to the annual output of 120,000 cars (McPherson et al., 2015). FD–ISHB has also resulted in the loss of hundreds of thousands of trees in riparian ecosystems of Southern California (Boland, 2016; Parks, 2017), habitat critical for breeding by endangered bird species and highly vulnerable to encroachment of damaging invasive plant species.

In South Africa, the PSHB infestation is currently in a stage similar to the situation in California in 2012. At that time, the beetle was discovered in the Los Angeles basin on a backyard avocado tree but had not yet established in commercial groves, and the damage it caused was restricted to urban forests and botanical gardens (Eskalen et al., 2012; van den Berg et al., 2019). A rapid monitoring response uncovered the broad host range of the pest-pathogen complex (Eskalen et al., 2013), but its ability to establish in native vegetation was only gradually recognized. Similarly, in South Africa today the most visible impact of the PSHB invasion is in urban forests, and the beetle has not yet been detected in commercial avocado groves (https://www.fabinet.up.ac.za/pshb). Given that wildland habitats differ in vegetation composition in California and South Africa, the impact of the invasion on South African native forests is unclear. Reports of the beetle occurring in eight of the nine provinces in South Africa and spreading from urban areas into native forests suggests those habitats are invadable (https://www.fabinet.up.ac.za/pshb). However, which species will be affected, and to what extent, is unknown. Understanding the influence

of host range on FD–ISHB impacts during this key phase of the infestation in South Africa is therefore imperative.

In this study, we tested the hypothesis that hosts supporting ISHB-*Fusarium* reproduction are more strongly phylogenetically constrained than non-competent hosts. As such, we expect that the probability of finding ISHB on two host species declines with phylogenetic distance between the hosts, and this decline is steeper for competent hosts. Moreover, we expect that phylogenetic signal in host range is stronger on competent hosts that are killed when attacked.

Methods

Host Range Assessment

The FD–ISHB host range comprises 77 host species that support beetle reproduction (competent hosts), 18 of which are killed when attacked **(**Fig. 1, Table SI**)**. The adult beetles make attempted attacks on another 247 species in 61 families that do not support their reproduction (non-competent hosts), although the fungi can colonize and cause necrosis on 137 of these non-competent hosts (Fig. 1, Table SI) (Eskalen et al., 2013). These non-competent hosts are never killed when attacked. The specific definitions and details for each of these categories are provided in Figure 1. The host range in California was determined in a previous study of heavily infested botanical gardens at the epicenter of the infestation in Los Angeles County (Eskalen et al., 2013), and subsequent systematic surveys of 23,588 trees from 2012-2019 in a variety of habitats throughout San Diego, Orange, Los Angeles, San Bernardino,

Ventura, Santa Barbara, Riverside and San Luis Obispo Counties (Lynch *in prep*; https://ucanr.edu/sites/pshb/Map). The botanical gardens harbor a wide range of plant species that represent unique and common ecosystems worldwide and contain all the host species that occur throughout urban and wildland forests in Southern California. Seven competent and 25 non-competent hosts were similarly identified in a separate survey of the national botanical gardens of South Africa through the International Plant Sentinel Network tree health monitoring program (Paap et al., 2018; Paap et al., 2018b) and preliminary surveys of national nature reserves and urban forests throughout all nine provinces in 2017-2019 (Wilhelm de Beer, *personal communication*; https://www.fabinet.up.ac.za/pshb) (Table SI). In California, surveys were conducted by trained experts representing the University of California (UC) Riverside, Santa Cruz, and Davis; UC Cooperative Extension; Orange, San Diego, Los Angeles, and Ventura County Agriculture; USDA Forest Service, Forest Health Protection; California Department of Forestry and Fire Protection; Disney; the Huntington Library Art Collections and Botanical Gardens; and the Los Angeles County Arboretum and Botanic Gardens. Experts conducting surveys in South Africa represent the Forestry and Agricultural Biotechnology Institute (FABI) at the University of Pretoria; Stellenbosch University; Rhodes University; South African National Biodiversity Institute; and the City of Johannesburg Metropolitan Municipality.

For each individual tree, surveyors recorded at minimum the tree location, species, and the presence or absence of FD–ISHB based on the unique symptoms

caused by the beetles and fungi as described in Eskalen et al. (2013). Tree species not exhibiting FD–ISHB symptoms, but in areas with active infestations, were classified as apparent non-hosts. In all cases of new tree species exhibiting symptoms characteristic of FD–ISHB, fungal and beetle identities were confirmed using morphological and molecular identification techniques described in Eskalen et al. (2013). Suitability for reproduction was confirmed by the presence of eggs, larvae, pupae, or teneral females, or by the presence of males in the galleries of infested trees.

Analyses

To estimate the time of independent evolution between plant species (phylogenetic distance), we first created a hypothesis for the phylogenetic relationships among tree and shrub species in California and South Africa using the R2G2_20140601 supertree of Parker et al. (2015) (see Supplemental Data for newick file). This tree includes dated nodes for all angiosperm families given by the Angiosperm Phylogeny Group classification III (APG III) (Bremer et al., 2009) as well as gymnosperm and monilophyte families; the tree was dated using Wikström ages (Davies et al., 2004; Wikström et al., 2001) and additional consensus dates from the literature, with all nodes in the tree given stable dates (Parker et al., 2015). We used this tree rather than basing our phylogenetic tree on APG IV (Byng et al., 2016) to be consistent with and comparable to the validated work on phylogenetic signal in host ranges in the previous studies. All 2,717 taxa for which the beetles could

encounter in California or South Africa include native and non-native trees and shrubs found across agricultural, urban, and wildland landscapes, and were compiled using the CalFlora, West Coast Arborists, The Plant List, and Dendrological Society of South Africa curated databases (Supplemental Data). We used Phylomatic version included in Phylocom v4.2 (Webb et al., 2008) to create a pruned ultrametric tree of all genera in the database, with branch lengths that reflected the estimated time between branching events (Supplementary Data).

In the absence of information about intrafamilial phylogenetic resolution, relationships from the R2G2_20140601 supertree are modeled as polytomies. To improve estimates of phylogenetic signal between hosts exhibiting different levels of attack, we reviewed the literature to resolve polytomies across taxa that interacted with the beetle and/or the *Fusarium* pathogens. Taxa comprised genera in the Fabaceae including *Acacia* (Gómez-Acevedo et al., 2010; Kyalangalilwa et al., 2013; Miller et al., 2011; Miller & Seigler, 2012), *Senegalia* (Kyalangalilwa et al., 2013), *Vachellia* (Kyalangalilwa et al., 2013), *Prosopis* (Catalano et al., 2008), *Erythrina* (Bruneau, 1996; De Luca et al., 2018), and *Bauhinia* (Hao et al., 2003; Meng et al., 2014; Sinou et al., 2009); genera in the Lauraceae including *Cinnamomum*, *Cryptocarya* (Chanderbali et al., 2001); and genera in the Salicaceae, including *Salix* and *Populus* (Hamzeh & Dayanandan, 2004; Lauron-Moreau et al., 2015; Liu et al., 2016; Wang et al., 2014; Zhang et al., 2018; Zhou et al., 2018). Topologies for *Acer* (Grimm et al., 2007; Harris et al., 2017; Li et al., 2006, 2019; Suh et al., 2000; Tian et al., 2002), *Platanus* (Feng et al., 2005; Grimm & Denk, 2008) and *Quercus*

(Cavender-Bares & González-Rodríguez, 2015; Hipp et al., 2014, 2018; Manos et al., 1999, 2001) were additionally resolved. Finer scale node ages were then estimated by interpolation using the Phylocom bladj function in Phylomatic v4.2 (Webb et al., 2008). From this finer resolution tree, we used the phydist function in the R package Picante v. 1.2-0 (Kembel et al., 2010) to calculate pairwise phylogenetic distances for each pair of plant species, which is twice the time to the most recent common ancestor in My. The case of zero phylogenetic distance (distance from a known host species to itself) was included in the analysis.

We performed a phylogenetic dispersion analysis of phylogenetic distances for all examined tree species, confirmed non-hosts, non-competent hosts (attempted host attack only and attacked hosts suitable for fungal colonization), and all competent host species and their subsets of those that are killed or not killed when attacked. We followed approaches used in previous publications and inspected the cumulative distribution of phylogenetic distances between species pairs (CDPD), which provides useful information on the depth of trait conservatism in plant-pathogen interactions (Gilbert & Parker, 2016; Parker et al., 2015). Overlap of CDPD curves between all examined tree species and host tree species indicates that hosts are a random subset of all available tree species (no phylogenetic signal). A downward shift in the host CDPD curve indicates that host species are a more closely related subset of all available tree species than expected at random, because the removal of more distantly related clades retains shorter distances (phylogenetic signal). We expect these downward shifts to be more dramatic with hosts that are increasingly

more severely impacted by the beetle-fungal interactions. Measures of mean phylogenetic distance in pest host ranges across broad plant phylogenies tend to be dominated by the influence of many long phylogenetic distance pairings (Gilbert & Parker, 2016). Additionally, nearest phylogenetic distance measures can be unstable because they do not reflect the plant community as a whole. In addition to examining the overall CDPD, we follow Parker et al. (2015) and compare distances at the 10^{th} quantile, which were found to be more informative than mean distances for plant-fungal interactions because it reduces the structural swamping effect of many distantly related pairs in phylogenies.

In addition to phylogenetic dispersion analysis, we measured the strength of the phylogenetic signal (*D*) for binary traits using the phylo.d function in the R package caper v.1.0.1. This measure developed by Fritz and Purvis (2010) is computed by scaling the observed sum of sister-clade differences in a given phylogeny with the mean values of simulated expected distributions under Brownian motion and a random phylogenetic pattern. The given *D* statistic is scaled between 0-1, where a value of 1 indicates phylogenetic randomness. All analyses were performed using R statistical framework, with functions from the Picante v. 1.2-0, Vegan v. 1.17-8, Hmisc v. 4.3.0, phytools v. 0.6, phangorn v. 2.5.5, Geiger v. 2.0.6.2, caper v. 1.0.1, and Stats v. 2.12.2 packages (http://cran.r-project.org/).

Results

Phylogenetic patterns of host-pest interactions

The distribution of non-competent and competent hosts exhibited a nested pattern across the phylogeny of potential host species in California and South Africa. Species that were attacked by the beetles clustered within 62 families and 170 genera within our geographic ranges (Fig. 2). These taxa cover the range of angiosperm and some gymnosperm tree species. For gymnosperms, beetle attack attempts occurred on species within the "crown conifer" clade (Cupressaceae, Podocarpaceae, Pinaceae) but not species within other more distantly related groups (e.g., Ginkgoaceae or Cycadales) (Fig. 2). Other groups containing species free from beetle attack included families within the Caryophyllales (with the exception of Tamaricaceae), Malpighiales (with the exception of Phyllanthaceae, Salicaceae, and Euphorbiaceae), and families within groups containing Huertales (Gerrardinaceae), Brassicales, and Malvales (with the exception of Malvaceae) (Fig. 2). The beetles' fusaria symbionts could colonize on a subset of 50 families and 122 genera of beetle-attacked species across the phylogeny, including species within Cupressaceae and Podocarpaceae (Fig. 2). The 77 competent host species clumped within 24 families and 48 genera of all attacked species. These species were nested within angiosperm lineages ranging from the most basal Magnoliids that diversified ~150 Mya to lineages that originated as recently as ~35 Mya (e.g., Malvaceae). Notably, 59 of the 77 competent host species (77%) and 14 of the 18 killed-competent host species (78%) clustered within the

Rosids clade (Fig. 2). Within the Rosids, 43 competent (56%) and ten killed-competent (55%) host species grouped within the Fabids; half of the competent host species were further clustered within the Eurosid II clade (Fig. 2). Only killed-competent hosts exhibited a significant phylogenetic signal measured by the *D* statistic ($D = 0.299$) and the strength of the signal indicated a clumped phylogenetic pattern consistent with Brownian motion (Table II).

Phylogenetic dispersion analysis

The phylogenetic distances for all pairs of the 2,717 observed tree species and confirmed non-hosts from California and South Africa ranged between 1.4 – 806 Myr (Fig. S1). This range decreased notably with increasingly severe nested types of outcomes of interactions between host plants, the beetles, and the fungus (Fig. S1). We ranked the phylogenetic distances for all species pairs and their respective subsets (Fig. 3a; Figs. S2-S3). Consistent with results in Parker et al. (2015), inspection of the full cumulative distribution of phylogenetic distance curves (CDPDs) indicated that affected phylogenetic distances tend to be much shorter than the overall median because of the swamping effect of many distantly related pairs (Fig. S2). As such, we focused our analysis at the scale of the 10^{th} quantile of pairwise phylogenetic distances between species, where the depth of conservatism of important traits that confer host susceptibility is most informative (Fig. 3b). As phylogenetic distance

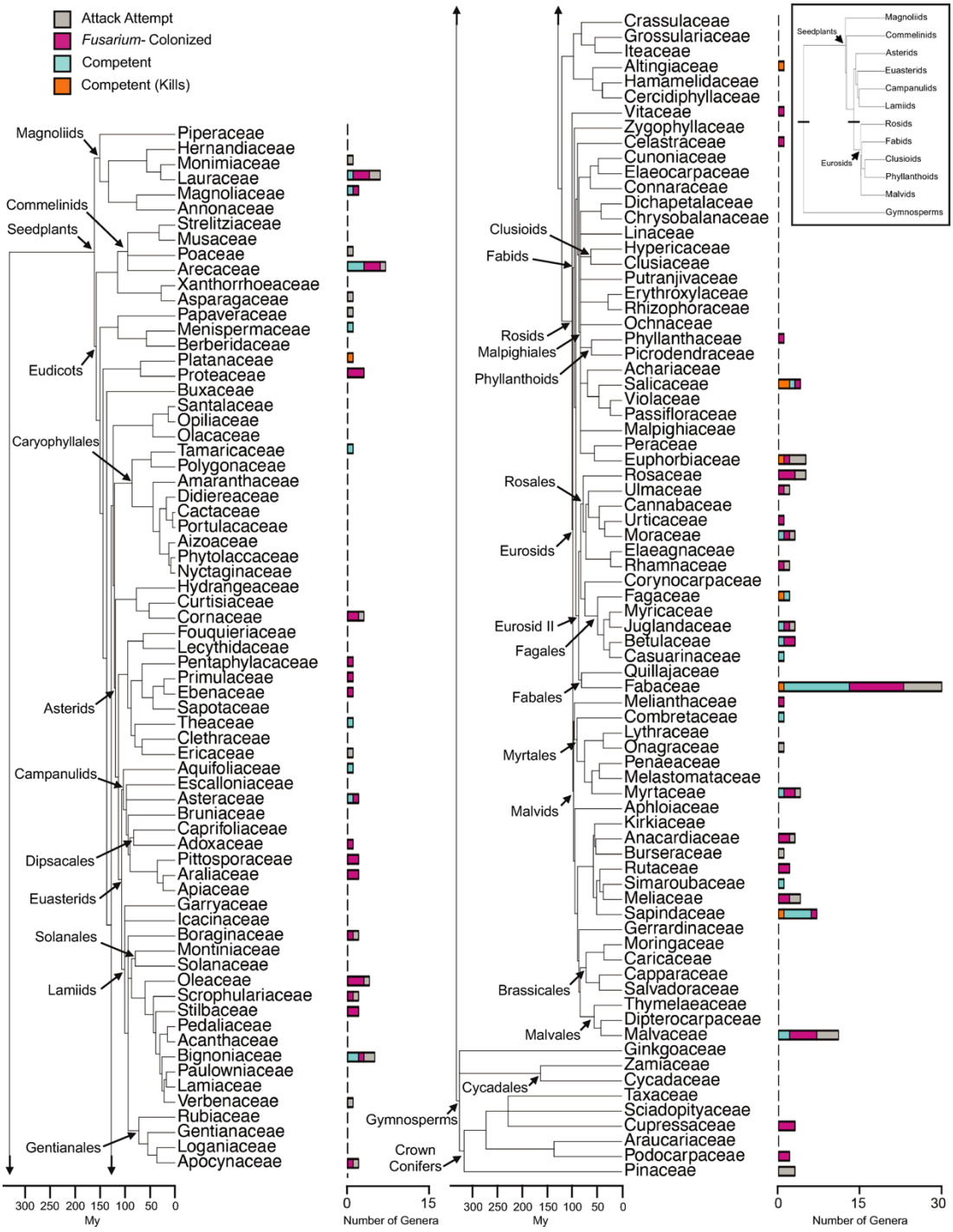

Figure 2. Phylogenetic tree of families representing all examined tree species in the present study. Stacked columns at the tree tips depict the nested types of outcomes of interactions between host plants, beetles, and fungi for genera within each family. Segments within each column represent the number of attacked genera with tree species that are *Fusarium*-colonized, competent, and killed-competent hosts within each family.

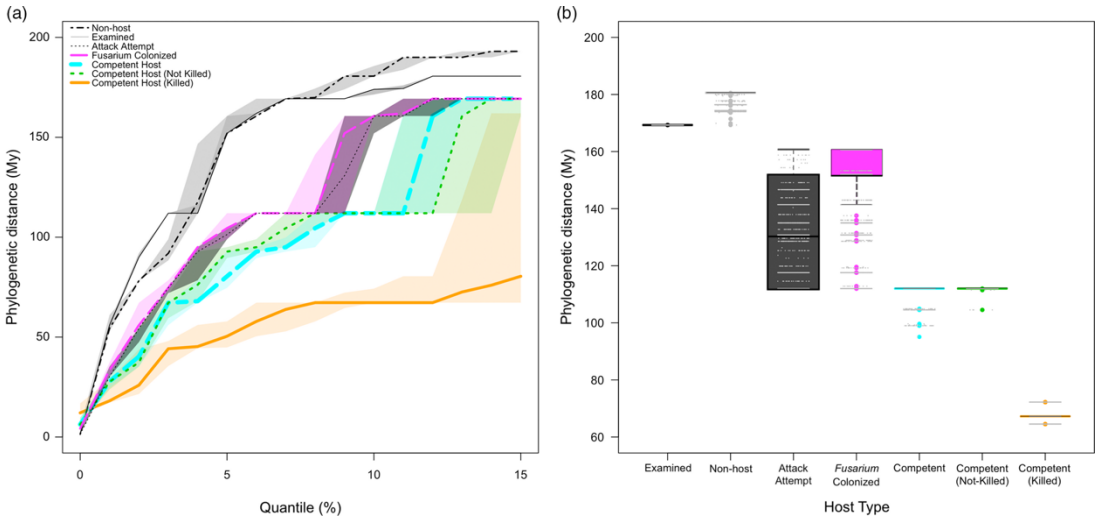

Figure 3. Phylogenetic distances for all species pairs of each host type (a-b). Intervals represent the 95% confidence interval envelope generated from 10,000 bootstrap simulations on a random sample of 90% of the species within each host type. **a**, Cumulative distribution of phylogenetic distances (CDPD) from quantiles 1% to 15%. **b**, Boxplots of phylogenetic distances at the 10th quantile. Gray dots represent actual data from the simulations.

represents time of independent evolution (Myr), shorter distances indicate species are more closely related to one another.

Species that were attacked by beetles were a non-random subset of all the available hosts as indicated by a downward shift in their CDPD curve; the phylogenetic distances among the attacked hosts are consistently much shorter than those among all available species (Fig. 3b). Shorter distances indicate a selectivity where if one species of tree is attacked, close relatives are also more likely to be attacked. The CDPD curves for beetle-attacked and *Fusarium*-colonized hosts overlapped, suggesting that the phylogenetic preferences for beetle attack and fungal growth are very similar. Notably, within those attacked hosts, an even more phylogenetically restricted subset of hosts was able to serve as competent hosts for

beetle reproduction. A very striking phylogenetic effect was seen on the most severely affected competent hosts. Competent host species that were killed by beetle/fungal attack fell into phylogenetic clusters that produced a much flatter CDPD. Consistent with entire clades being lost from the host range with increasingly more severe interactions, these hosts for which attack was lethal had a decile phylogenetic distance of only 60 My, compared with 160 Myr for all the hosts attacked by the beetles (i.e., killed host species are much more closely related to each other than are all the species attacked by the beetles). Removal of gymnosperms from the host data revealed a shift in the CDPD for non-competent hosts, but distances were still longer than competent hosts (Fig. S3). Patterns were not different when South African trees were removed from the analysis (Fig. S3).

Discussion

In this study, we quantified the degree of phylogenetic signal in the host range of a new invasive generalist pest and pathogen complex from southeast Asia that elicits different effects across different host tree species. As we expected, the 327 tree species attacked by Fusarium dieback-invasive shot hole borers (FD-ISHB) in California and South Africa were phylogenetically constrained compared to all examined tree and shrub species. Additionally, competent hosts (those that support beetle reproduction) were more phylogenetically constrained than non-competent hosts. Finally, those competent hosts that are killed when attacked exhibited the strongest phylogenetic signal. Phylogenetic dispersion analysis of each host type from

the most inclusive (beetle attempts an attack) to most restrictive (beetle and pathogen kill their host) revealed that the phylogenetic preferences of beetle attack and fungal growth were the same, non-random subset of all available tree and shrub species. Competent host range was phylogenetically narrower than attacked hosts by 62 My, and those with devastating impacts were the most constrained, narrower by 107 My. As such, our results show a strong phylogenetic signal in the relative effects of FD-ISHB on host species, demonstrating that the strength of multi-host pest impacts in plants can be predicted by host evolutionary relationships. These findings form the basis for developing predictive models of multi-host pest spread in novel habitats using tools in phylogenetic ecology.

Estimations of phylogenetic signal

Both phylogenetic dispersion analysis and the *D* statistical measure of phylogenetic signal (Fritz & Purvis, 2010) detected a phylogenetic effect on the most severely affected competent hosts. Phylogenetic dispersion analysis was potentially more sensitive in detecting a signal for non-competent and all competent hosts than *D* because while there are "jumps" in the signal (i.e., roughly 25% of competent hosts occur outside the Rosids), we see high clustering within groups containing competent host species. Within the Rosids, there is another jump in the signal between the Fabids and Malvids, but a high degree of clustering occurs within those two groups, particularly in the Fabids (i.e., Salicaceae, Fagaceae, and Fabaceae) and the Malvids (i.e., Sapindaceae). The *D* measure in phylogenetic signal is based on an underlying

threshold model, which assumes that patterns of a binary trait across the phylogeny are based on one or more evolved, continuous traits (Fritz & Purvis, 2010). However, although many traits important in plant-enemy interactions show a phylogenetic signal (Agrawal, 2007; Boller & Felix, 2009; Gilbert & Parker, 2016; Pearse & Hipp, 2009), there are exceptions (Becerra, 1997; Pichersky & Lewinsohn, 2011; Wink, 2003). Thus, our results suggest there are many ways for hosts to be susceptible. Those ways are moderately constrained phylogenetically, but susceptibility clusters within phylogenetic groups and this clumping becomes more restricted with more impactful interactions.

Phylogenetic signal in multi-host pest interactions

Quantitative measures that leverage an understanding of the evolutionary ecology of host-pest interactions to assess the relative impacts of generalist pests on their hosts provide important and novel tools to predict threats to ecosystems. By utilizing multiple invasion pathways, multi-host pests present inherently different epidemiological dynamics than single host pests when introduced to naïve plant or animal communities. In particular, generalist pests do not rely on density-dependent transmission of a single host species, which thereby increases the likelihood of pest-induced host extinction (De Castro & Bolker, 2005; Smith et al., 2006). As the majority of plant and animal pests attack multiple host species (Cleaveland et al., 2001; Gilbert et al., 2012; Gilbert & Webb, 2007; Malpica et al., 2006; Novotny et al., 2002; Pearse & Hipp, 2009; Weiblen et al., 2006) these essential evolutionary

tools in species conservation efforts are also broadly applicable. For domesticated mammals, Farrell and Davies (2019) demonstrated that evolutionary distance from an infected host to another mammal host species is a strong predictor of multi-host disease-induced mortality. Similarly, Gilbert et al. (2015) reported that the relative amount of damage done by a natural enemy on plant species declines predictably with increasing evolutionary distance from highly susceptible hosts. Our study affirms that the use of host evolutionary relationships presents a unifying theoretical approach to predicting disease outcomes across multiple host-pest combinations.

Epidemiological implications of host evolutionary relationships

In addition to determining which species are prone to pest-induced mortality, host evolutionary relationships can be used to understand complex epidemiological outcomes and help prioritize surveillance activities in vulnerable, naïve communities. For FD–ISHB, the stronger phylogenetic effects with increasingly severe host impacts correspond to potential epidemiological outcomes. These outcomes are likely consistent with stages of invasion in which non-competent hosts may foster beetle arrival to a new area, competent hosts facilitate beetle-fungal establishment and pest-pathogen persistence, and killed-competent hosts correspond to pest-pathogen spread and ecosystems impact. Because FD–ISHB non-competent hosts exhibit a phylogenetic signal, beetle arrival most likely corresponds to a broad suite of polygenic traits that attract beetles to trees; but other trait aggregates that confer induced defense can prevent beetle establishment. This phenomenon has been

demonstrated for two conspecific cultivars of tea (*Camellia sinensis*) with different susceptibilities to *Euwallacea perbrevis* in Sri Lanka (Karunaratne et al., 2009). Both cultivars are equally attractive to beetle attack, but while beetles established galleries in the susceptible cultivar, they abandoned partly bored galleries the resistant cultivar, suggesting beetle attack induced plant defenses in the resistant cultivar. In systems with such ecological stepping stones of hosts of different susceptibility, a larger pool of closely related susceptible species in a local plant community increases a beetle's chance of encountering a competent host individual; non-competent hosts that do not kill the beetle may therefore facilitate establishment in a new location through contact with individuals representing closely related competent host species.

The even more phylogenetically constrained competent hosts that survive attack represent a low virulence interaction that promotes pest-pathogen persistence in reservoir hosts. The most severely affected competent hosts represent a high-virulence interaction, show the most striking phylogenetic effect, and largely correspond to pest-pathogen spread. Young adult *Euwallacea* females emerging from native galleries prefer to produce and remain in their natal galleries on the same individual tree (Calnaido & Thirugnanasuntharau, 1966; Lynch et al., 2019). Population propagules thus amplify over time until the dying host can no longer support beetle reproduction and beetles escape the tree in a mass dispersal event, aiding in the epidemic spread of the pest-pathogen complex. Thus, our study demonstrates that understanding epidemiological outcomes based on the phylogenetic

structure of the nested outcomes of multi-host pest interactions can help determine which species contribute to different stages of an invasion process.

To optimize the use of limited resources, an understanding of host-evolutionary relationships can be utilized to stratify survey efforts and focus on areas with different combinations of species representing groups that appear to be most important in the arrival, establishment, and spread of the pest-pathogen complex. For example, surveys of wildland forests in South Africa could prioritize locations comprising some combination of species in the Fabaceae, Salicaceae and Sapindaceae, which are common in South Africa (http://pza.sanbi.org/vegetation) and consist of many host species important to all stages of an invasion. Common species in families with many hosts important to beetle arrival (e.g., Podocarpaceae, Proteaceae, Myrtaceae) or establishment (e.g., Myrtaceae, Arecaceae) could also be prioritized. Another way to prioritize survey efforts could be to target species belonging to the genus *Dombeya* (Malvaceae), given that many naturally occur in South Africa but not California, and *D. cacuminum* is a competent host. Targeting species belonging to Annonaceae or Strelitziaceae would be of low priority since these families do not contain host species and are found outside the more susceptible Rosid clade.

Caveats

One limitation to our analysis is that our information on which hosts the *Fusarium* pathogens can grow is not independent of beetle attack. Experimental

inoculations of the fungi on confirmed non-host tree species (no symptoms of beetle attack) would indicate whether the *Fusarium* host range is truly constrained phylogenetically. However, the relationship between the beetles and their fungi is tightly coupled. The *Fusarium* species belong to the monophyletic Ambrosia Fusarium Clade (AFC) (Kasson et al., 2013) and the ~22 Myr old mutualism between AFC members and beetles in the genus *Euwallacea* represents one of 11 known evolutionary origins of fungiculture by ambrosia beetles (O'Donnell et al., 2015). These closely related wood-inhabiting *Fusarium* species are transmitted in mycangia and cultivated by females in galleries as a source of nutrition for the beetle (Kasson et al., 2013; O'Donnell et al., 2015). Key survival structures of the *Fusarium* species that aid in their dispersal have not been observed on *Fusarium*-colonized non-competent hosts, which suggests that their chance of spread without their beetle vector is very low. Therefore, fungal colonization on artificially inoculated plant species outside the phylogenetic constraints of beetle-attacked species may not be as important as the beetle-fungal-host interactions combined.

The strength of the phylogenetic signal seen between different host types provides a working hypothesis as to which species we expect to be new hosts prone to different levels of *Fusarium*-ISHB attack in South Africa. Our California data set is based on eight years of comprehensive and ongoing surveys throughout the infested region, representing the most complete host list available. However, the host list includes additional species in new families based on preliminary surveys in South Africa, which do not occur in California (Calflora, 2020;

https://www.fabinet.up.ac.za/pshb). New species include one new competent host in a new Malvid family within the Rosid clade (Combretaceae: *Combretum kraussii*), and three non-competent hosts representing two new families outside the Rosids (Primulaceae: *Rapanea melanophloeos*; Stilbaceae: *Halleria lucida* and *Nuxia floribunda*). Other new families with non-competent host genera that do not occur in California include Primulaceae (*Rapanea*), Boraginaceae (*Cordia*), and Celastraceae (*Gymnosporia*); all but the latter occur outside the Rosid clade. Interestingly, Aoki et al. (2018) observed attacks by *Euwallacea validus* on tree species in the eastern U.S.A. that occur within the same highly phylogenetically constrained Fabid and Malvid groups as the ISHB beetles. Additionally, all three beetle species (*E. validus, E. fornicatus, E. kuroshio*) share at least seven orders containing competent hosts. Together with all seven new competent host species clumping within the Rosids, and the remaining additional six competent and 19 non-competent host species clustering within existing groups, we can conclude that the overall phylogenetic patterns hold for the growing host list and potentially for host ranges of other *Euwallacea*-AFC members**.**

Phylogenetic models based on evolutionary distances between hosts of generalist pests can be used to evaluate which host species are potentially most vulnerable to pest impacts and most important to their establishment and spread. Certainly, other essential factors that drive host-pest interactions influence host outcomes. Changes in environmental conditions, pathogen virulence, or the host microbiome can amplify or inhibit host susceptibility or damage. In particular, the

phylogenetic structure and host abundance of local communities strongly influence the severity of impact on focal hosts (Parker et al. 2015). Although phylogenetic signal in host range cannot fully explain overall epidemic patterns, it can be used as a first approximation to understanding complex novel pest invasions, serving as a powerful tool to assess risk and guide response priorities.

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Table I. Insect vectors and corresponding fungal pathogens causing Fusarium dieback on tree hosts in California, Israel, and South Africa.

Invasive Shot Hole Borers		Year Detected/ Established	Fusaria Pathogens	Other Weak Mycangial Pathogens	
Species Name	Common Name				
[1-2] *Euwallacea fornicatus*	Polyphagous shot hole borer (PSHB)	[3]Israel: 2005 CA: 2003/2012 ZA: 2016	[4]*Fusarium euwallaceae*	[5]*Graphium euwallaceae*	[5]*Paracremonium pembeum*
[1] *E. kuroshio*	Kuroshio shot hole borer (KSHB)	CA: 2014	[6] *F. kuroshium*	[6] *G. kuroshium*	

[1](Gomez et al., 2018); [2](S. M. Smith et al., 2019); [3](Mendel et al., 2012); [4](Freeman et al., 2013); [5](Lynch et al., 2016); [6](Na et al., 2018)

Table II. Phylogenetic signal for each host type measured by *D* statistic, and the probability of E(D) resulting from Brownian phylogenetic structure.

Host Type	*D*	P of E(D)
Non-host	0.8410635	0
Beetle Only Attacked	0.7404623	0
Fungus	0.7633496	0
Competent	0.7945735	0
Competent Not Killed	0.9098142	0
Competent Killed	0.2993492	0.303

Supplementary Table I. Native range and infested distribution (California—CA or South Africa—ZA) of tree and shrub ISHB host species organized phylogenetically from the most to least ancestral lineages. Non-competent hosts are either attacked by the beetle species alone (A) or attacked by beetles and colonized by *Fusarium* spp. (F). Competent hosts support beetle-pathogen reproduction and are killed (K) or not killed (NK) when attacked.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Pinales	Cupressaceae	*Juniperus chinensis*	F			CA
Pinales	Cupressaceae	*Juniperus virginiana*	A			CA
Pinales	Cupressaceae	*Metasequoia glyptostroboides*	F			CA
Pinales	Cupressaceae	*Taxodium distichum*	F			CA & ZA
Pinales	Podocarpaceae	*Afrocarpus falcatus*	F		ZA	ZA
Pinales	Podocarpaceae	*Afrocarpus gracilior*	A			CA
Pinales	Podocarpaceae	*Podocarpus henkelii*	F		ZA	CA & ZA
Pinales	Pinaceae	*Cedrus atlantica*	A			CA
Pinales	Pinaceae	*Keteleeria evelyniana*	A			CA
Pinales	Pinaceae	*Pinus densiflora*	A			CA
Pinales	Pinaceae	*Pinus douglasiana*	A			CA
Laurales	Lauraceae	*Beilschmiedia miersii*	A			CA
Laurales	Lauraceae	*Cinnamomum camphora*	F			CA & ZA
Laurales	Lauraceae	*Cinnamomum glanduliferum*	A			CA
Laurales	Lauraceae	*Machilus thunbergii*	F			CA
Laurales	Lauraceae	*Nothaphoebe sp.*	A			CA
Laurales	Lauraceae	*Persea americana*		NK		CA & ZA
Laurales	Lauraceae	*Umbellularia californica*	F		CA	CA
Laurales	Monimiaceae	*Peumus boldus*	A			CA
Magnoliales	Magnoliaceae	*Liriodendron tulipifera*	F			CA
Magnoliales	Magnoliaceae	*Magnolia delavayi*	A			CA
Magnoliales	Magnoliaceae	*Magnolia doltsopa*	A			CA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Magnoliales	Magnoliaceae	*Magnolia grandiflora*		NK		CA & ZA
Magnoliales	Magnoliaceae	*Magnolia guatemalensis*	A			CA
Magnoliales	Magnoliaceae	*Magnolia soulangeana*	A			CA
Magnoliales	Magnoliaceae	*Magnolia* sp.	A			CA
Magnoliales	Magnoliaceae	*Magnolia veitchii*	F			CA
Magnoliales	Magnoliaceae	*Magnolia virginiana*		NK		CA
Poales	Poaceae	*Bambusa oldhamii*	A			CA
Poales	Poaceae	*Bambusa* sp.	A			CA
Arecales	Arecaceae	*Archontophoenix cunninghamiana*		NK		CA
Arecales	Arecaceae	*Butia capitata*	A			CA
Arecales	Arecaceae	*Chamaedorea elegans*	F			CA
Arecales	Arecaceae	*Howea forsteriana*		NK		CA
Arecales	Arecaceae	*Livistona chinensis*	F			CA
Arecales	Arecaceae	*Ptychosperma elegans*		NK		CA
Arecales	Arecaceae	*Washingtonia filifera*	F		CA	CA
Arecales	Arecaceae	*Washingtonia robusta*	A			CA
Asparagales	Asparagaceae	*Dracaena draco*	A			CA
Ranunculales	Menispermaceae	*Cocculus laurifolius*		NK		CA
Ranunculales	Menispermaceae	*Cocculus orbiculatus*	F			CA
Ranunculales	Papaveraceae	*Bocconia arborea*	A			CA
Proteales	Proteaceae	*Banksia saxicola*	F			CA
Proteales	Proteaceae	*Macadamia integrifolia*	F			CA & ZA
Proteales	Proteaceae	*Protea mundii*	F		ZA	ZA
Proteales	Platanaceae	*Platanus acerifolia*		K		CA & ZA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Proteales	Platanaceae	*Platanus hispanica*		K		CA
Proteales	Platanaceae	*Platanus mexicana*		NK		CA
Proteales	Platanaceae	*Platanus occidentalis*	F			CA & ZA
Proteales	Platanaceae	*Platanus racemosa*		K	CA	CA & ZA
Proteales	Platanaceae	*Platanus wrightii*	F			CA
Caryophyllales	Tamaricaceae	*Tamarix ramosissima*		NK		CA
Cornales	Cornaceae	*Alangium sp.*	A			CA
Cornales	Cornaceae	*Camptotheca acuminata*	F			CA
Cornales	Cornaceae	*Cornus controversa*	F			CA
Ericales	Pentaphylacaceae	*Cleyera japonica*	F			CA
Ericales	Ebenaceae	*Diospyros dichrophylla*	F		ZA	ZA
Ericales	Ebenaceae	*Diospyros kaki*	A			CA
Ericales	Ebenaceae	*Diospyros lycioides*	F		ZA	ZA
Ericales	Primulaceae	*Rapanea melanophloeos*	F		ZA	ZA
Ericales	Theaceae	*Camellia japonica*	F			CA & ZA
Ericales	Theaceae	*Camellia reticulata*	F			CA
Ericales	Theaceae	*Camellia semiserrata*		NK		CA
Ericales	Ericaceae	*Arbutus unedo*	A			CA
Aquifoliales	Aquifoliaceae	*Ilex cornuta*		NK		CA
Aquifoliales	Aquifoliaceae	*Ilex latifolia*	F			CA
Asterales	Asteraceae	*Baccharis pilularis*		NK		CA
Asterales	Asteraceae	*Baccharis salicina*		NK	CA	CA
Asterales	Asteraceae	*Verbesina gigantea*	A			CA
Dipsacales	Adoxaceae	*Viburnum sinensis*	F			ZA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Apiales	Pittosporaceae	*Hymenosporum flavum*	F			CA
Apiales	Pittosporaceae	*Pittosporum undulatum*	F			CA
Apiales	Araliaceae	*Cussonia spicata*	F		ZA	CA & ZA
Apiales	Araliaceae	*Fatsia japonica*	F			CA
Boraginales	Boraginaceae	*Cordia caffra*	F		ZA	ZA
Boraginales	Boraginaceae	*Wigandia urens*	A			CA
Lamiales	Oleaceae	*Chionanthus retusus*	F			CA
Lamiales	Oleaceae	*Fraxinus excelsior*	F			CA & ZA
Lamiales	Oleaceae	*Fraxinus uhdei*	F			CA
Lamiales	Oleaceae	*Fraxinus velutina*	A		CA	CA
Lamiales	Oleaceae	*Olea europaea*	F			CA & ZA
Lamiales	Oleaceae	*Olea sp.*	F		ZA	ZA
Lamiales	Oleaceae	*Osmanthus fragrans*	A			CA
Lamiales	Scrophulariaceae	*Buddleja saligna*	F		ZA	ZA
Lamiales	Scrophulariaceae	*Myoporum laetum*	F			CA
Lamiales	Stilbaceae	*Halleria lucida*	F		ZA	ZA
Lamiales	Stilbaceae	*Nuxia floribunda*	F		ZA	CA & ZA
Lamiales	Bignoniaceae	*Catalpa speciosa*	F			CA
Lamiales	Bignoniaceae	*Handroanthus impetiginosus*	A			CA
Lamiales	Bignoniaceae	*Jacaranda mimosifolia*		NK		CA & ZA
Lamiales	Bignoniaceae	*Markhamia lutea*	A			CA
Lamiales	Bignoniaceae	*Spathodea campanulata*		NK		CA
Lamiales	Verbenaceae	*Aloysia sp.*	F			CA
Gentianales	Apocynaceae	*Cascabela thevetioides*	A			CA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Gentianales	Apocynaceae	*Plumeria rubra*	F			CA & ZA
Saxifragales	Altingiaceae	*Liquidambar formosana*	F			CA
Saxifragales	Altingiaceae	*Liquidambar styraciflua*		K		CA & ZA
Vitales	Vitaceae	*Vitis vinifera*	F			CA & ZA
Celastrales	Celastraceae	*Gymnosporia buxifolia*	F		ZA	ZA
Oxalidales	Cunoniaceae	*Cunonia capensis*	A			CA & ZA
Oxalidales	Elaeocarpaceae	*Crinodendron patagua*	A			CA
Malpighiales	Phyllanthaceae	*Bischofia javanica*	F			CA
Malpighiales	Salicaceae	*Dovyalis caffra*	F			CA & ZA
Malpighiales	Salicaceae	*Populus fremontii*		K	CA	CA
Malpighiales	Salicaceae	*Populus nigra*		K		CA & ZA
Malpighiales	Salicaceae	*Populus tremuloides*		NK	CA	CA
Malpighiales	Salicaceae	*Populus trichocarpa*		K	CA	CA
Malpighiales	Salicaceae	*Salix alba*		NK		ZA
Malpighiales	Salicaceae	*Salix babylonica*		NK		CA
Malpighiales	Salicaceae	*Salix exigua*	F		CA	CA
Malpighiales	Salicaceae	*Salix gooddingii*		K	CA	CA
Malpighiales	Salicaceae	*Salix laevigata*		K	CA	CA
Malpighiales	Salicaceae	*Salix lasiolepis*		K	CA	CA
Malpighiales	Salicaceae	*Salix mucronata*		NK	ZA	ZA
Malpighiales	Salicaceae	*Xylosma congesta*		NK		CA
Malpighiales	Euphorbiaceae	*Jatropha cinerea*	F			CA
Malpighiales	Euphorbiaceae	*Manihot esculenta*	A			CA
Malpighiales	Euphorbiaceae	*Ricinus communis*		K		CA & ZA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Malpighiales	Euphorbiaceae	*Triadica sebifera*	A			CA
Malpighiales	Euphorbiaceae	*Vernicia fordii*	A			CA
Rosales	Rosaceae	*Chaenomeles sinensis*	A			CA
Rosales	Rosaceae	*Eriobotrya japonica*	F			CA & ZA
Rosales	Rosaceae	*Malus floribunda*	A			CA
Rosales	Rosaceae	*Prunus africana*	F		ZA	ZA
Rosales	Rosaceae	*Prunus caroliniana*	A			CA
Rosales	Rosaceae	*Prunus cerasoides*	A			CA
Rosales	Rosaceae	*Prunus mume*	F			CA
Rosales	Rosaceae	*Prunus nigra*	F			ZA
Rosales	Rosaceae	*Prunus persica*	F			CA & ZA
Rosales	Rosaceae	*Prunus serrulata*	F			CA
Rosales	Rosaceae	*Pyrus calleryana*	F			CA
Rosales	Rosaceae	*Pyrus kawakamii*	F			CA
Rosales	Ulmaceae	*Ulmus alata*	F			CA
Rosales	Ulmaceae	*Ulmus americana*	F			CA
Rosales	Ulmaceae	*Ulmus minor*	F			CA & ZA
Rosales	Ulmaceae	*Ulmus parvifolia*	F			CA & ZA
Rosales	Ulmaceae	*Zelkova serrata*	F			CA
Rosales	Rhamnaceae	*Frangula californica*	A		CA	CA
Rosales	Rhamnaceae	*Ziziphus jujuba*	F			CA
Rosales	Moraceae	*Broussonetia papyrifera*	A			CA
Rosales	Moraceae	*Ficus altissima*		NK		CA
Rosales	Moraceae	*Ficus benjamina*	A			CA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Rosales	Moraceae	*Ficus carica*		NK		CA & ZA
Rosales	Moraceae	*Ficus macrophylla*	F			CA
Rosales	Moraceae	*Ficus maxima*	A			CA
Rosales	Moraceae	*Ficus natalensis*	F		ZA	ZA
Rosales	Moraceae	*Ficus platypoda*	F			CA
Rosales	Moraceae	*Morus alba*	F			CA & ZA
Rosales	Urticaceae	*Pipturus argenteus*	F			CA
Fagales	Fagaceae	*Fagus crenata*		NK		CA
Fagales	Fagaceae	*Fagus sylvatica*	F			CA
Fagales	Fagaceae	*Quercus acutidens*	A		CA	CA
Fagales	Fagaceae	*Quercus acutissima*	A			CA
Fagales	Fagaceae	*Quercus agrifolia*		NK	CA	CA
Fagales	Fagaceae	*Quercus alba*	A			CA
Fagales	Fagaceae	*Quercus buckleyi*	A			CA
Fagales	Fagaceae	*Quercus chrysolepis*		NK	CA	CA
Fagales	Fagaceae	*Quercus coccinea*	A			CA
Fagales	Fagaceae	*Quercus engelmannii*		NK	CA	CA
Fagales	Fagaceae	*Quercus ilex*	F			CA
Fagales	Fagaceae	*Quercus lobata*		K	CA	CA
Fagales	Fagaceae	*Quercus macrocarpa*		NK		CA
Fagales	Fagaceae	*Quercus mexicana*	F			CA
Fagales	Fagaceae	*Quercus palustris*	F			CA & ZA
Fagales	Fagaceae	*Quercus polymorpha*	A			CA
Fagales	Fagaceae	*Quercus robur*		K		CA & ZA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Fagales	Fagaceae	*Quercus rubra*	A			CA
Fagales	Fagaceae	*Quercus rugosa*	A			CA
Fagales	Fagaceae	*Quercus shumardii*	F			CA
Fagales	Fagaceae	*Quercus suber*		NK		CA
Fagales	Fagaceae	*Quercus virginiana*	F			CA
Fagales	Fagaceae	*Quercus wislizeni*	A		CA	CA
Fagales	Juglandaceae	*Carya illinoinensis*	F			CA & ZA
Fagales	Juglandaceae	*Juglans mandshurica*	A			CA
Fagales	Juglandaceae	*Juglans nigra*	A			CA
Fagales	Juglandaceae	*Pterocarya sp.*	A			CA
Fagales	Juglandaceae	*Pterocarya stenoptera*		NK		CA
Fagales	Betulaceae	*Alnus incana*	A		CA	CA
Fagales	Betulaceae	*Alnus rhombifolia*		NK	CA	CA
Fagales	Betulaceae	*Betula pendula*	F		ZA	CA & ZA
Fagales	Betulaceae	*Corylus colurna*	F			CA
Fagales	Casuarinaceae	*Casuarina cunninghamiana*	F			CA
Fagales	Casuarinaceae	*Casuarina equisetifolia*		NK		CA
Fabales	Fabaceae	*Acacia aneura*	F			CA
Fabales	Fabaceae	*Acacia baileyana*	F			CA
Fabales	Fabaceae	*Acacia floribunda*	A			CA
Fabales	Fabaceae	*Acacia mearnsii*		NK		ZA
Fabales	Fabaceae	*Acacia melanoxylon*		NK		CA & ZA
Fabales	Fabaceae	*Acacia saligna*	A			CA
Fabales	Fabaceae	*Acacia sp.*		NK		CA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Fabales	Fabaceae	*Acacia stenophylla*	A			CA
Fabales	Fabaceae	*Acacia victoriae*	A			CA
Fabales	Fabaceae	*Albizia gummifera*	A			CA
Fabales	Fabaceae	*Albizia julibrissin*		NK		CA
Fabales	Fabaceae	*Albizia kalkora*	A			CA
Fabales	Fabaceae	*Bauhinia blakeana*	F			CA
Fabales	Fabaceae	*Bauhinia galpinii*	F		ZA	CA & ZA
Fabales	Fabaceae	*Bauhinia petersiana*	A			CA & ZA
Fabales	Fabaceae	*Bauhinia purpurea*	F			ZA
Fabales	Fabaceae	*Bauhinia variegata*		NK		CA
Fabales	Fabaceae	*Caesalpinia cacalaco*	A			CA
Fabales	Fabaceae	*Calpurnia aurea*	F		ZA	CA & ZA
Fabales	Fabaceae	*Cassia abbreviata*	A		ZA	CA & ZA
Fabales	Fabaceae	*Cassia brewsteri*	F			CA
Fabales	Fabaceae	*Cassia fistula*	A			CA
Fabales	Fabaceae	*Cassia leptophylla*	F			CA
Fabales	Fabaceae	*Castanospermum australe*		NK		CA
Fabales	Fabaceae	*Ceratonia siliqua*	F			CA
Fabales	Fabaceae	*Cercidium floridum subsp. floridum*		NK	CA	CA
Fabales	Fabaceae	*Cercidium microphyllum*	A		CA	CA
Fabales	Fabaceae	*Cercidium sonorae*		NK		CA
Fabales	Fabaceae	*Cercidium* sp. 1	A			CA
Fabales	Fabaceae	*Cladrastis sinensis*	A			CA
Fabales	Fabaceae	*Dalbergia sissoo*	F			CA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Fabales	Fabaceae	*Erythrina abyssinica*	A			CA
Fabales	Fabaceae	*Erythrina caffra*		NK	ZA	CA & ZA
Fabales	Fabaceae	*Erythrina coralloides*		NK		CA
Fabales	Fabaceae	*Erythrina crista-galli*	F			CA
Fabales	Fabaceae	*Erythrina falcata*		NK		CA
Fabales	Fabaceae	*Erythrina folkersii*	F			CA
Fabales	Fabaceae	*Erythrina humeana*	F			CA & ZA
Fabales	Fabaceae	*Erythrina livingstoniana*	F			ZA
Fabales	Fabaceae	*Erythrina lysistemon*	F		ZA	CA & ZA
Fabales	Fabaceae	*Erythrina sykesii*	A			CA
Fabales	Fabaceae	*Gleditsia triacanthos*		NK		CA & ZA
Fabales	Fabaceae	*Inga edulis*	F			CA
Fabales	Fabaceae	*Inga feuilleei*	A			CA
Fabales	Fabaceae	*Lysiphyllum carronii*	F			CA
Fabales	Fabaceae	*Olneya tesota*	A		CA	CA
Fabales	Fabaceae	*Parkinsonia aculeata*		K		CA
Fabales	Fabaceae	*Pithecellobium sp.*	A			CA
Fabales	Fabaceae	*Podalyria calyptrata*		NK	ZA	ZA
Fabales	Fabaceae	*Prosopis articulata*		NK		CA
Fabales	Fabaceae	*Prosopis chilensis*	F			CA
Fabales	Fabaceae	*Prosopis glandulosa*	F			CA
Fabales	Fabaceae	*Prosopis velutina*	F			CA
Fabales	Fabaceae	*Psoralea pinnata*		NK	ZA	ZA
Fabales	Fabaceae	*Schotia brachypetala*	F		ZA	CA & ZA

Supplementary Table I. Continued.

Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Fabales	Fabaceae	*Senegalia caffra*	A			CA & ZA
Fabales	Fabaceae	*Senegalia galpinii*	F		ZA	ZA
Fabales	Fabaceae	*Senegalia visco*	F			CA
Fabales	Fabaceae	*Senna racemosa*	F			CA
Fabales	Fabaceae	*Senna spectabilis*	A			CA
Fabales	Fabaceae	*Senna splendida*	F			CA
Fabales	Fabaceae	*Styphnolobium japonicum*	A			CA
Fabales	Fabaceae	*Tipuana tipu*	A			CA
Fabales	Fabaceae	*Vachellia caven*	A			CA
Fabales	Fabaceae	*Vachellia cochliacantha*	A			CA
Fabales	Fabaceae	*Vachellia etbaica*	A			CA
Fabales	Fabaceae	*Vachellia farnesiana*	F			CA
Fabales	Fabaceae	*Vachellia karroo*	F		ZA	ZA
Fabales	Fabaceae	*Vachellia sieberiana*	F		ZA	ZA
Fabales	Fabaceae	*Virgilia divaricata*	F		ZA	ZA
Fabales	Fabaceae	*Virgilia oroboides*		NK	ZA	ZA
Fabales	Fabaceae	*Wisteria floribunda*		NK		CA
Fabales	Fabaceae	*Wisteria sinensis*	F			CA
Fabales	Fabaceae	*Zenia insignis*	A			CA
Geraniales	Melianthaceae	*Melianthus major*	F		ZA	CA & ZA
Myrtales	Combretaceae	*Combretum erythrophyllum*	F		ZA	ZA
Myrtales	Combretaceae	*Combretum kraussii*		NK	ZA	ZA
Myrtales	Onagraceae	*Hauya elegans*	A			CA
Myrtales	Myrtaceae	*Callistemon salignus*	A			CA

Supplementary Table I. Continued.

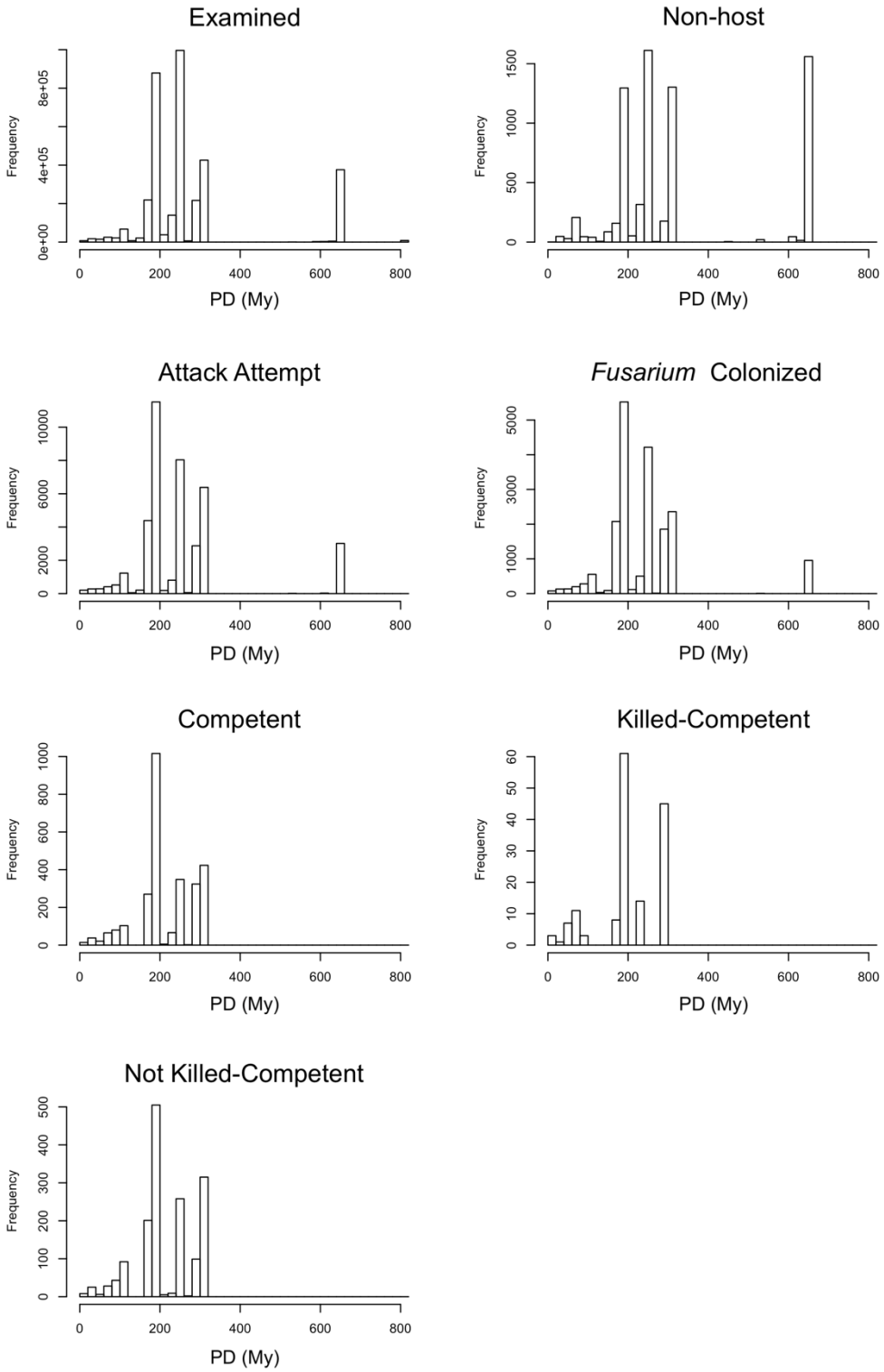
Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Myrtales	Myrtaceae	*Callistemon viminalis*	A			CA
Myrtales	Myrtaceae	*Corymbia ficifolia*		NK		CA
Myrtales	Myrtaceae	*Eucalyptus camaldulensis*	F			CA & ZA
Myrtales	Myrtaceae	*Eucalyptus cinerea*	A			CA
Myrtales	Myrtaceae	*Eucalyptus froggattii*	A			CA
Myrtales	Myrtaceae	*Eucalyptus kitsoniana*	A			CA
Myrtales	Myrtaceae	*Eucalyptus perriniana*	A			CA
Myrtales	Myrtaceae	*Eucalyptus polyanthemos*	F			CA
Myrtales	Myrtaceae	*Eucalyptus torquata*	F			CA
Myrtales	Myrtaceae	*Psidium guajava*	F			CA & ZA
Sapindales	Anacardiaceae	*Harpephyllum caffrum*	F		ZA	CA & ZA
Sapindales	Anacardiaceae	*Pistacia chinensis*	A			CA
Sapindales	Anacardiaceae	*Schinus molle*	F			CA & ZA
Sapindales	Anacardiaceae	*Schinus polygama*	F			ZA
Sapindales	Anacardiaceae	*Schinus terebinthifolia*	F			CA
Sapindales	Burseraceae	*Bursera hindsiana*	A			CA
Sapindales	Sapindaceae	*Acer buergerianum*		K		CA & ZA
Sapindales	Sapindaceae	*Acer caudatifolium*	A			CA
Sapindales	Sapindaceae	*Acer davidii*	A			CA
Sapindales	Sapindaceae	*Acer freemanii*	A			CA
Sapindales	Sapindaceae	*Acer macrophyllum*		K	CA	CA
Sapindales	Sapindaceae	*Acer negundo*		K	CA	CA & ZA
Sapindales	Sapindaceae	*Acer palmatum*		K		CA & ZA
Sapindales	Sapindaceae	*Acer paxii*		NK		CA

Supplementary Table I. Continued.

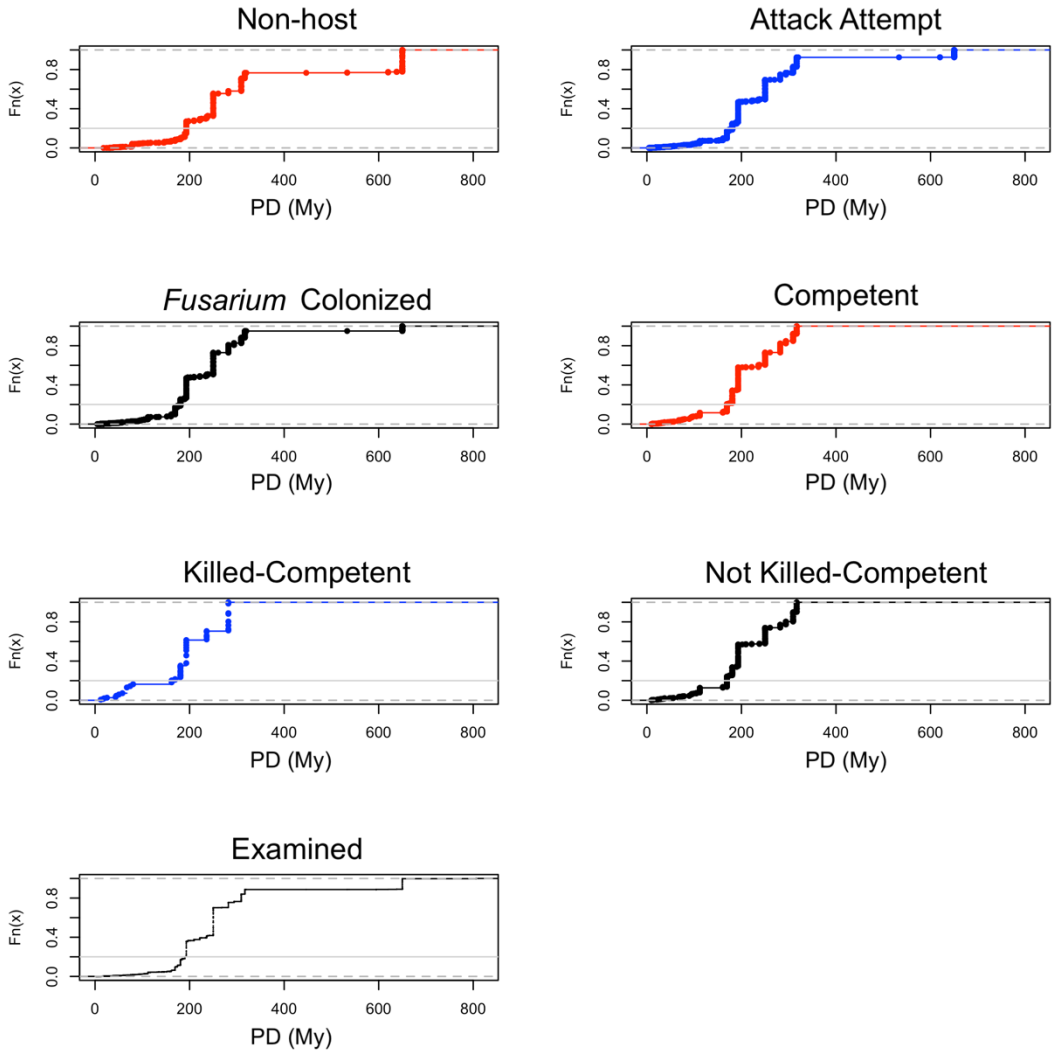
Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Sapindales	Sapindaceae	*Acer pectinatum*	F			CA
Sapindales	Sapindaceae	*Aesculus californica*		NK	CA	CA
Sapindales	Sapindaceae	*Alectryon excelsus*		NK		CA
Sapindales	Sapindaceae	*Cupaniopsis anacardioides*		NK		CA
Sapindales	Sapindaceae	*Harpullia arborea*	F			CA
Sapindales	Sapindaceae	*Harpullia pendula*		NK		CA
Sapindales	Sapindaceae	*Koelreuteria bipinnata*		NK		CA
Sapindales	Sapindaceae	*Koelreuteria elegans*	F			CA
Sapindales	Sapindaceae	*Koelreuteria paniculata*	F			CA
Sapindales	Sapindaceae	*Ungnadia speciosa*	F			CA
Sapindales	Meliaceae	*Aglaia odorata*	A			CA
Sapindales	Meliaceae	*Ekebergia capensis*	F		ZA	ZA
Sapindales	Meliaceae	*Melia azedarach*	F			CA & ZA
Sapindales	Meliaceae	*Swietenia chickrassa*	A			CA
Sapindales	Rutaceae	*Calodendrum capense*	F		ZA	ZA
Sapindales	Rutaceae	*Citrus limon*	F			CA & ZA
Sapindales	Rutaceae	*Citrus sinensis*	F			CA & ZA
Sapindales	Simaroubaceae	*Ailanthus altissima*		NK		CA
Malvales	Malvaceae	*Bombax ceiba*	A			CA
Malvales	Malvaceae	*Brachychiton acerifolius*	F			CA
Malvales	Malvaceae	*Brachychiton australis*	F			CA
Malvales	Malvaceae	*Brachychiton discolor*	F			CA & ZA
Malvales	Malvaceae	*Brachychiton populneus*		NK		CA
Malvales	Malvaceae	*Brachychiton rupestris*	F			CA

Supplementary Table I. Continued.

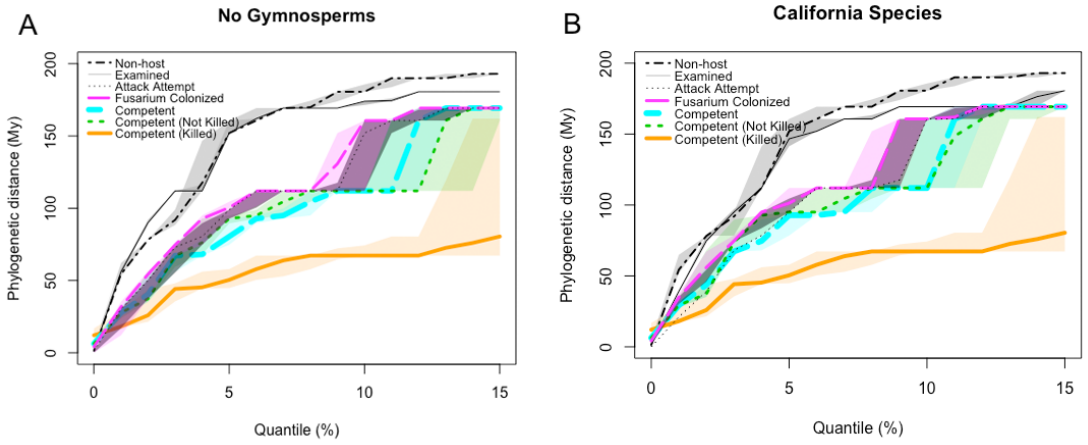
Order	Family	Species	Non-Competent	Competent	Native Range	Infested Distribution
Malvales	Malvaceae	*Ceiba pentandra*	F			ZA
Malvales	Malvaceae	*Ceiba speciosa*	F			CA
Malvales	Malvaceae	*Chiranthodendron pentadactylon*	A			CA
Malvales	Malvaceae	*Dombeya cacuminum*		NK		CA
Malvales	Malvaceae	*Dombeya wallichii*	A			CA
Malvales	Malvaceae	*Firmiana simplex*	F			CA
Malvales	Malvaceae	*Grewia occidentalis*	F		ZA	ZA
Malvales	Malvaceae	*Heliocarpus sp.*	A			CA
Malvales	Malvaceae	*Luehea divaricata*	F			CA
Malvales	Malvaceae	*Pseudobombax ellipticum*	A			CA
Malvales	Malvaceae	*Tilia americana*	F			CA



Supplemental Figure 1. Distribution of pairwise phylogenetic distances (PD) for different subsets of host types.



Supplemental Figure 2. Empirical Cumulative Distribution Function (ECDF) of the phylogenetic distance data for each host type from 0-800 My; 20% or less of the data are at the horizontal abline.



Supplemental Figure 3. Cumulative distribution of phylogenetic distances (CDPD) for all species pairs of each host type from quantiles 1% to 15% after (a) the removal of gymnosperms from the non-competent host data (attack attempt; *Fusarium* colonized) and (b) the removal of South African species data. Intervals for each CDPD represent the 95% confidence interval envelope generated from 10,000 bootstrap simulations on a random sample of 90% of the species within each host type. (a) Species removed from the attack attempt host list include *Juniperus virginiana* (Cupressaceae), *Afrocarpus gracilior* (Podocarpaceae), *Cedrus atlantica*, *Keteleeria evelyniana*, *Pinus densiflora*, *P. douglasiana* (Pinaceae). Species removed from the *Fusarium*-colonized host list include *Juniperus chinensis, Metasequoia glyptostroboides, Taxodium distichum* (Cupressaceae), *Afrocarpus falcatus*, and *Podocarpus henkelii* (Podocarpaceae).

Chapter 3

Microbiome Variation Across a Phylogeographic Range of Tree Hosts Affected by an Emergent Pest–Pathogen Complex

Abstract

Although a large body of research has established that the endophytic plant microbiome is essential to host fitness, the influence of complex interactions between resident microbial communities and pests in their establishment and spread into novel areas is less understood. In this study, we tested whether wood-inhabiting microbial community structure and composition differ across phylogenetically diverse tree host species of an emergent generalist pest-pathogen complex in California and if composition influences host susceptibility to attack. We further explore interactions within the microbiome between endophytic microbes and the pathogen to identify potential mechanisms for shaping disease establishment and spread and evaluate whether endogenous microbes could be utilized for sustainable integrated pest management. Predictive linear discriminant analyses of culturable wood-inhabiting microbial communities revealed consistent differences between *Persea* (avocado), which grows in an agricultural setting, and three genera of wildland host species [*Salix* (willow), *Platanus* (sycamore), and *Quercus* (oak)], but there were no strong, consistent differences among microbial communities based on attack status of the

hosts. However, our analysis did detect enough differences among microbes that the inconsistencies most likely reflect undersampling in the community – a common problem with culture-based studies. Furthermore, we identified 15 fungal species and 11 species of bacteria exhibiting clear *in vitro* antagonism against the pathogen, indicating their potential to confer a protective benefit to tree hosts as biological control agents. This research sets the stage for future studies that integrate a richer data set into our analysis of these communities using a culture-independent approach, and provides an empirical foundation to help stakeholders evaluate the relative importance of biotic and abiotic factors that influence pest-pathogen spread and guide more strategic management decisions.

Introduction

The ecological outcomes of plant pest introductions are fundamentally understood by examining which host, pest, and abiotic factors together favor disease or injury development and pest spread. This approach, however, usually centers on explaining a binary interaction between one pest (e.g., fungi, bacteria, viruses, animals, plants) and one plant host (Ginnan *et al.* 2020). Accidental introductions of pests into areas outside their home range, in particular, can result in more complex novel and unforeseen species interactions because all plants harbor resident microbial communities (Bulgarelli *et al.* 2013; Hardoim *et al.* 2015; Müller *et al.* 2016; Baldrian 2017; Terhonen *et al.* 2019).

It is widely accepted that the endophytic plant microbiome is essential to host fitness by contributing to plant growth promotion, stress tolerance, and extended plant immunity (Hardoim *et al.* 2015; Vandenkoornhuyse *et al.* 2015; Terhonen *et al.* 2019). Indeed, an increasing number of studies in agriculture (Ardanov *et al.* 2012; Gazis & Chaverri 2015; Ginnan *et al.* 2015, 2020; Deyett *et al.* 2017; Deyett & Rolshausen 2019) and forest systems (Arnold *et al.* 2003; Martín *et al.* 2013; Gazis & Chaverri 2015; Kovalchuk *et al.* 2018; Macaya-Sanz *et al.* 2020) indicate a link between microbial community structure and host plant resistance/susceptibility to pathogens or show changes in endophyte community structure after pathogen colonization (Araújo *et al.* 2002; Bulgari *et al.* 2011, 2012; Douanla-Meli *et al.* 2013). Moreover, empirical research reveals that foliar and root endophytes provide

some protection to the host against pathogens and herbivores (Preszler *et al.* 1996; Danielsen & Jensen 1999; Narisawa *et al.* 2002; Arnold *et al.* 2003; Rubini *et al.* 2005; Ganley *et al.* 2008; Mejía *et al.* 2008; Miller *et al.* 2008; Tellenbach & Sieber 2012; Raghavendra & Newcombe 2013; Ridout & Newcombe 2015) by either triggering systemic resistance (Vu *et al.* 2006; Martinuz *et al.* 2012; Singh *et al.* 2013; Mejía *et al.* 2014; Roylawar *et al.* 2015; Martínez-Medina *et al.* 2017) or through antagonistic interactions with the pathogen (i.e., antibiotic inhibition, competition, or pathogen parasitism) (Calhoun *et al.* 1992; Schulz *et al.* 1999; Mejía *et al.* 2008; Sumarah *et al.* 2008, 2015; Hussain *et al.* 2014; Blumenstein *et al.* 2015; Tanney *et al.* 2016). Together, this body of evidence has prompted a wave of studies to assess how beneficial endophytes can be leveraged for biocontrol (Backman & Sikora 2008; Cazorla & Mercado-Blanco 2016; Rabiey *et al.* 2019). However, studies of endophyte-mediated disease modification in agricultural plant pathosystems and economically important plants greatly outnumber those in wild plant systems (Busby *et al.* 2016; Terhonen *et al.* 2019). Furthermore, these studies largely focus on single host species, and with few exceptions (Webber & Hedger 1986; Narisawa *et al.* 2002; Evans *et al.* 2003; Holmes *et al.* 2004; Campanile *et al.* 2007; Pujade-Renaud *et al.* 2019), overwhelmingly focus on foliar or root endophytes (Busby *et al.* 2016).

The Fusarium dieback–invasive shot-hole borers (FD–ISHB) interaction is an emergent pest–pathogen complex from Southeast Asia that kills or causes dieback on over 77 tree species across urban-wildland and agricultural landscapes in Southern California (Eskalen *et al.* 2012; Stouthamer *et al.* 2017), and presents a unique

opportunity to understand microbial composition of many species of attacked and healthy tree hosts from diverse settings. The complex involves two cryptic ambrosia beetles in the *Euwallacea* species complex (Coleoptera: Curculionidae: Scolytinae) (Stouthamer *et al.* 2017; Gomez *et al.* 2018; Smith *et al.* 2019) and the specific symbiotic fungal pathogens each beetle species carries, primarily *Fusarium euwallacea* and *F. kuroshium* (Freeman *et al.* 2013; Lynch *et al.* 2016; Na *et al.* 2018). These closely related wood-limited *Fusarium* species are transmitted and cultivated by females in galleries in the bole and crown of their host as a source of nutrition for the beetle (Kasson et al., 2013; O'Donnell et al., 2015). Preliminary data suggest that *Fusarium* spp. cannot colonize young avocado (*Persea americana*) and sycamore (*Platanus racemosa*) plants inoculated with beneficial endophytes found in non-infested avocado and native sycamore trees in an infested hot spot (Na *et al.* 2014). Hence, while (non)establishment of a beetle in a tree may be due to chance, the endophytic microbiome in wood of host tree individuals may prevent colonization of the beetles' sole food source, preventing beetle establishment and slowing the spread of the pest-pathogen. In addition to microclimate and host-pest factors, identifying the role of the endophytic microbiome of host trees throughout the FD–ISHB infested range could potentially improve modeling the epidemic spread of the beetle-fungus over a landscape, better inform risk assessments and focus phytosanitary actions, and broaden the range of currently limited options for management.

Curiously, although the bole-associated woody biomass of living trees is the essential superhighway linking the rhizosphere and phyllosphere, it remains one of the least explored and understood habitats for microbial communities in plants (Rodríguez *et al.* 2011; Baldrian 2017). Studies that have explored the endophytic microbiome in the wood of trees mostly focus on fungal communities (Terhonen *et al.* 2019). With rare exceptions (Chapela & Boddy 1988; Baum *et al.* 2003; Martín *et al.* 2013; Gazis & Chaverri 2015; Robles *et al.* 2015; Kovalchuk *et al.* 2018; Macaya-Sanz *et al.* 2020), those studies largely focus on fungal communities in small stems that are proximal to the phyllosphere (Carroll 1988; Petrini & Fisher 1988, 1990; Chapela 1989; Fisher & Petrini 1990; Fisher *et al.* 1994; Stone & Petrini 1997; Danti *et al.* 2002; Stone *et al.* 2004; Sieber 2007; Shetty *et al.* 2016) or are biased toward those communities involved in wood decay (Oses *et al.* 2008; Rodríguez *et al.* 2011; Hiscox *et al.* 2015; Skelton *et al.* 2019). The endophytic microbiome of sapwood deserves more attention given the prevalence of ecologically and economically devastating xylem-limited diseases (Appel 1995; Hiemstra & Harris 1998; Gibbs 2003; Juzwik *et al.* 2008; Cameron *et al.* 2015; Pisani *et al.* 2015; Keykhasaber *et al.* 2018; Kyrkou *et al.* 2018), the presence of microbes in woody tissue that have experimentally suppressed their causal pathogens (Brooks *et al.* 1994; Narisawa *et al.* 2002; Aldrich *et al.* 2015; Martínez-Arias *et al.* 2020), and the emergence of new wood-limited pest-pathogen threats (Eskalen *et al.* 2012; Mendel *et al.* 2012; Rabaglia *et al.* 2020). The endophytic microbiome of lignified tissues was characterized in grapevine (*Vitis vinifera*) in the context of Pierce's disease caused by

the bacteria *Xylella fastidiosa* (Deyett *et al.* 2017; Deyett & Rolshausen 2019, 2020), as was the mycobiome in elm species (*Ulmus* spp.) attacked by the fungal pathogen that causes Dutch elm disease (*Ophiostoma novo-ulmi*) (Martín *et al.* 2015; Macaya-Sanz *et al.* 2020) and Norway spruce (*Picea abies*) attacked by the fungal pathogens *Heterobasidion* spp. (Kovalchuk *et al.* 2018). There has not been a comprehensive assessment of wood-inhabiting fungal and bacterial communities in phylogenetically and ecologically diverse tree species. Furthermore, such assessments have not been made comparing diseased and healthy hosts.

Here, we conduct a culture-dependent study using an evolutionary ecology perspective to determine whether community structure of wood-inhabiting endophytes can predict the attack status of phylogenetically diverse hosts of a new pest-pathogen complex. We further explore *in vitro* endophyte-pathogen interactions to identify potential mechanisms for disease establishment and spread and endogenous microbes that could be tested and utilized for sustainable integrated pest management. Specifically, we asked (1) if there are microbial community differences among host species, (2) whether there are differences associated with host species attacked or not attacked by FD-ISHB, and (3) if a potential mechanism for differences can be inferred from interactions between endophyte and pathogen. First, we isolated and identified fungi and bacteria from wood core samples collected from attacked and not-attacked trees across habitats varying in tree species composition in beetle infested and non-infested sites. Next, we conducted *in vitro* bioassays to assess interactions between ISHB's symbiotic *Fusarium* pathogens and all isolated and

molecularly identified endophytic microbes. Finally, we used predictive linear discriminant analyses to test whether wood-limited microbial communities in wood cores differ among host species and attack status, host species of the same attack status, and attack status within host species, and to predict community membership in these naturally occurring groups.

Methods

Site selection

We conducted this study within a network of 234 FD-ISHB monitoring plots that were established between July – November 2017 in riparian forests, oak woodlands, and avocado groves in California (Table I). The plot network covers the range of environmental conditions in which the beetle species have been observed to date. Plots range in size (0.25-2.75-ha; median = 0.27-ha) to account for variation in tree density between plant communities and sites, and to enable an assessment of at least 50 geo-referenced trees varying in species composition and phylogenetic distance from the 77 competent host tree species (Lynch et al. 2020). In each plot, we measured hourly temperature (°C) and relative humidity (%) using iButton Hygrochron data loggers (Maxim Integrated, San Jose, CA, USA), and recorded the species, diameter at breast height (DBH, measured at 1.3 m), health status (1-5; 1= healthy with less than 10% dieback and 5= dead), and FD-ISHB attack severity

(number of beetle attack holes) on every tree. Details of the plot network and associated methodology are described elsewhere (Lynch *in prep*).

We selected a representative sample of 66 beetle infested and 60 non-infested sites (126 total) from the broader plot network. We used an ordination approach to maximize the variability in composition among sites across the state, while selecting pairs of infested and non-infested sites that were as similar to each other as possible. First, we applied nonmetric multidimensional scaling (NMDS) analysis to the larger plot network. We compared the performance of three possible dissimilarity matrices, one based on species abundances and two that incorporate phylogenetic information: (1) Bray-Curtis community dissimilarity (Bray & Curtis 1957), (2) GUniFrac (Lozupone *et al.* 2006; Chen *et al.* 2012), and (3) mean pairwise (phylogenetic) distance (MPD) (Webb 2000). The GUniFrac metric is similar to Bray-Curtis dissimilarity metric in that it is invariant to changes in units; is unaffected by the addition of a new community and additions/removals of species that are not present in two communities; and can recognize differences in total abundances when relative abundances are the same (Lozupone *et al.* 2006, 2007; Swenson 2014; Chen 2018). MPD and GUniFrac have different approaches to accounting for evolutionary similarity among species. MPD relies on mean pairwise phylogenetic distances, but this metric is prone to the swamping effect caused by the disproportionate frequency of many distantly related pairs in phylogenies (Parker *et al.* 2015) GUniFrac dissimilarities instead represent the unique fraction of a phylogeny contained in each plant community (Lozupone *et al.* 2006, 2007; Swenson 2014; Chen 2018). There is

not a clear *a priori* reason that any of the three metrics would be most suitable for ordination of the plots.

We used a dated ultrametric phylogenetic tree of all tree and shrub species in California (Lynch et al. 2020) and the GUniFrac function (α= 1) in the R package GUniFrac v.3.6 (Chen 2018) to calculate the pairwise dissimilarities for each plot. To weight phylogenetic distances by abundance, the difference in relative abundances of a shared species in each of the two communities was multiplied by the branch length from root to tip on the phylogenetic tree holding that species (Swenson 2014; Chen 2018). For MPD, we used the cophenetic function to calculate pairwise phylogenetic distances for each plant species in our phylogenetic tree (Lynch et al., *in review*), and the comdist function to calculate the abundance weighted mean phylogenetic distances for all pairs of communities in our plot network from the R package Picante v.1.2-0 (Kembel et al., 2010). The Bray-Curtis community dissimilarity matrix and corresponding NMDS scores were generated using the metaMDS function (k=2). We used the monoMDS function (Picante v.1.2-0) separately on the GUniFrac and MPD abundance-weighted dissimilarity matrices to generate NMDS scores for each plot. Pairwise comparisons between distance matrices revealed that all three diversity metrics were highly correlated (Fig. S1a). For each metric, we also calculated pairwise Euclidean distances between NMDS scores for each plot using the dist function in base R, which were also highly correlated (Fig. S1b). Inspection of outliers between the phylogenetically-informed measures of diversity indicated that

GUniFrac was better than MPD at accounting for differences in abundances between plots; we chose to use the GUniFrac NMDS approach to select sites for sampling.

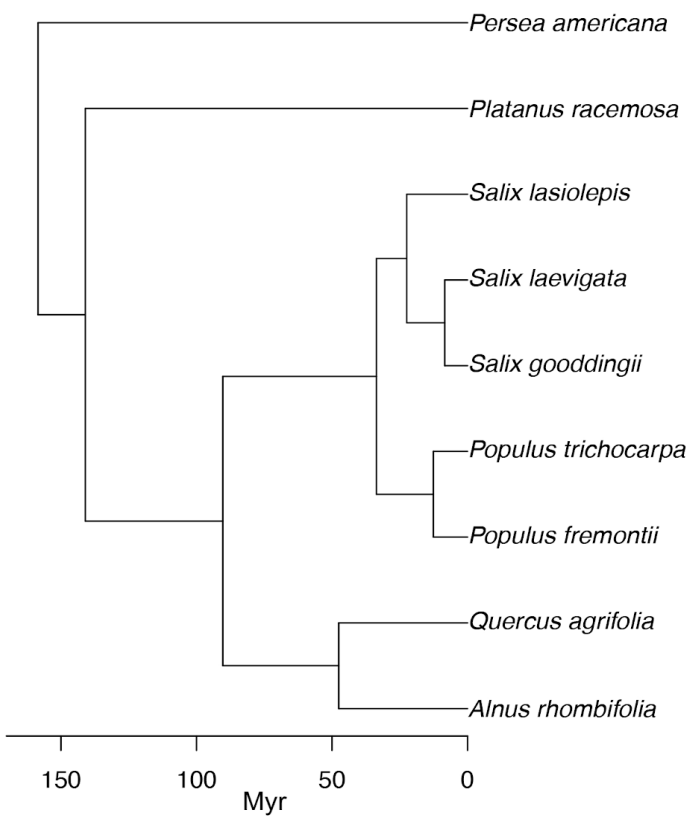
We selected 58 infested plots across the range of NMDS scores representing the GUniFrac-determined species gradient of the plot network. For each infested plot, we selected the non-infested plot with the shortest Euclidean distance in NMDS scores to that infested plot. After visual inspection of sampling plots on a map, we selected another ten to capture geographic variation of species composition throughout infested and non-infested sites.

Tree selection and sampling

To test for microbial community differences among samples based on host relatedness and attack status (not-attacked in 2017 and 2018; first attacked in 2018; attacked in 2017 and 2018; recovered in 2018), we sampled nine representative tree species (Fig. 1) across the phylogeny of 77 competent hosts: *Alnus rhombifolia* (Betulaceae)*, Persea americana* (Lauraceae)*, Platanus racemosa* (Platanaceae)*, Quercus agrifolia* (Fagaceae)*, Populus fremontii* and *P. trichocarpa* (Salicaceae)*, and Salix gooddingii, S. laevigata,* and *S. lasiolepis* (Salicaceae). Within each plot, we collected up to four samples per species per attack status in April-June 2018. Plots were divided into quadrants and one individual tree of the same species and attack status was randomly selected for sampling within each quadrant. For every host species, we subsequently sampled the individual representing each attack status that

was closest to the first randomly selected individual in each quadrant (up to four of each species per status per plot).

A



B

	Alnus rhombifolia	*Quercus agrifolia*	*Populus fremontii*	*Populus trichocarpa*	*Salix gooddingii*	*Salix laevigata*	*Salix lasiolepis*	*Platanus racemosa*
Quercus agrifolia	95							
Populus fremontii	181	181						
Populus trichocarpa	181	181	25					
Salix gooddingii	181	181	67	67				
Salix laevigata	181	181	67	67	17			
Salix lasiolepis	181	181	67	67	45	45		
Platanus racemosa	282	282	282	282	282	282	282	
Persea americana	317	317	317	317	317	317	317	317

Figure 1. **A)** Phylogeny of competent host species sampled in this study, and **B)** pairwise phylogenetic distances for each host species.

We aseptically collected wood core samples from the bole of selected trees using a "quick drill" protocol. All samples were collected from trees at breast height measuring at least 7.0 cm DBH (mean = 27 cm; max = 115 cm). We removed the outer bark with a 1.9-cm diameter drill bit, which was flame sterilized after 2 min in 10% commercial chlorine bleach solution followed by 2 min in 70% ethanol. For each tree, a single-use 5-mm diameter wood flat head drill bit (McMaster-Carr Supply®, autoclaved and flame sterilized prior to use) was inserted at the center of the uncontaminated bark cavity and slowly advanced to a depth of 5 cm into the wood from the cambium. The sawdust sample was collected in a sterile Nasco Whirl-Pak® while affixed to the tree beneath the bark cavity. To avoid sampling fungi actively cultivated by a beetle on attacked trees, we collected samples at a distance of 2-3 cm adjacent to an active gallery. Sawdust samples from wood cores were returned to the laboratory to process for isolations in the present study and high throughput amplicon sequencing (HTAS) for future studies (Supplementary Methods).

Endophyte isolations and in vitro assays

For 88 of the 126 sampled plots, we isolated fungi and bacteria from 575 samples of woody tissues (2-22 samples/plot; mean = 6.5; median= 6) to characterize culturable microbial communities within trees of different attack status and conducted *in vitro* bioassays to assess interactions between ISHB's symbiotic *Fusarium* pathogens and endophytic microbes. We isolated fungi and bacteria from ~70% of the visited plots, haphazardly selected at the end of each collection day, and randomly

selected up to two samples of each collected species-attack status pair per plot (minimum 50%) for isolations. To isolate fungi, we sprinkled 100 mg of sawdust tissue evenly onto 50% potato dextrose agar (Difco^{TM}) amended with 1% tetracycline (PDA-tet) agar. To isolate bacteria, we spread-plated 20 µL of a 10^{-4}–10^{-6} dilution of sawdust suspended in 1 mL phosphate-buffered saline (pH 7.2) onto King's B medium (Etminani & Harighi 2018). All plates were incubated at 25°C in the dark, and colony forming units (CFUs) of distinct morphotypes were counted after five to 10 days. Representative isolates of fungal and bacterial growth were subcultured for identification and long-term storage and purified isolates were putatively identified based on morphology (Barnett & Hunter 2006) to use for *in-vitro* bioassays.

To determine interactions between wood-inhabiting culturable endophytes and the *Fusarium* pathogens, we conducted *in vitro* bioassays using five replicates of each isolated morphotype as available and three isolates each of *F. euwallacea* (UCR-PR3, UCR-1854, UCR-4082) and *F. kuroshium* (UCR-PR5, UCR-3641, UCR-3659). We screened 60 fungal and 40 bacteria species (100 total), which were identified using the aforementioned molecular techniques. For fungi, we placed one 8-mm diameter pure culture mycelial disc of each endophyte-*Fusarium* species pair mycelial side down on 50% PDA-tet approximately 1.0 cm from the edge of the culture plate and diametrically opposite to one another. Interactions between *Fusarium* and bacteria were tested by placing one mycelial disc of a *Fusarium* isolate face down at the center of the plate and a single colony each of up to five bacterial isolates 0.5 cm from the edge and equidistantly spaced around the perimeter of a culture plate

containing King's B medium. For controls, we inoculated two replicate PDA-tet or King's B agar plates with mycelial plugs of each *Fusarium* isolate at one edge or the center of each plate. Plates were incubated at 25°C in the dark and qualitatively evaluated on days seven and 14 for evidence of antagonism (clear inhibition or alteration of growth pattern), coexistence (colonies grow through each other, or lack of visible interaction).

Antagonistic interactions that reduce endophyte or pathogen virulence result from competition between colonies or the excretion and diffusion of inhibitory substances (antibiosis) (Kerr 1999; Frey-Klett *et al.* 2011; Balouiri *et al.* 2016; Krüger *et al.* 2019). We confirmed antibiotic antagonism by the presence of an inhibition zone free of hyphae between the colonies (Fig. 2a). Inhibition by competition was marked by 1) partial replacement, where the inhibitor engulfs or mechanically blocks the contending colony (Fig. 2b-c); 2) reduced colony vigor, where the inhibitor induces morphological changes after physical contact (e.g., mycelial thinning or stunted radial growth) (Fig. 2d); or 3) mutual inhibition (fungal assays only), where neither fungus gains headway and a barrage is formed at the point of mycelial contact (Fig. 2e) (Esser & Meinhardt 1984; Boddy 2000). The barrage is a zone of profuse hyphal tip branching and lethal fusions that produce a clear line of contact between the two colonies and is indicative of an antagonistic reaction when mycelia grow into each other and intermingle (Esser & Meinhardt 1984). We considered fungal colonies to be coexisting if there was an absence of a barrage zone between deadlocked colonies and there was instead mutual intermingling of hyphae

in the zone of contact (Fig. 2f). Coexistence was also recorded for cases in which colony vigor was unaffected at a distance or after physical contact (no interaction).

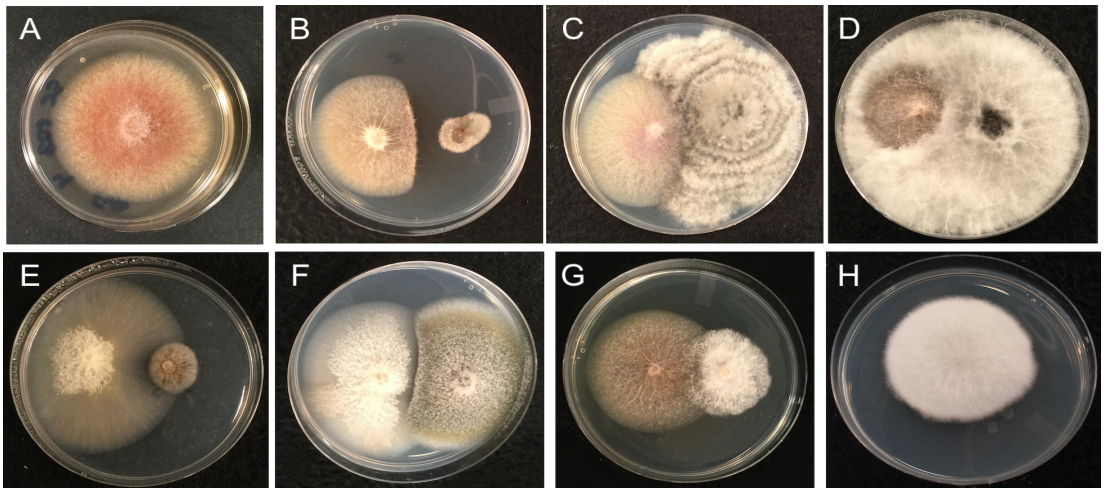


Figure 2. Representative outcomes of interactions between *Fusarium* spp. (left) and endophytes (right) observed *in vitro*. **A)** *Fusarium* colony in the absence of a contending endophyte. **B)** Antibiotic inhibition of *Fusarium* caused by *Pithomyces chartarum.* Outcomes of antagonism by competition include **C-D)** partial replacement (e.g., *Botryosphaeria parva*), **E)** mycelial thinning (e.g., *Aureobasidium* sp.), or **F)** mutual inhibition made evident by the presence of a barrage between deadlocked colonies (e.g., *Alternaria infectoria*). In contrast, coexistence was characterized by **G)** mutual intermingling of hyphae between colonies after physical contact (e.g., *Clonostachys* sp.), or when colony vigor of either microbe was unaffected at a distance. **H)** Commensal interactions in particular resulted in enhanced filamentation and branching of *Fusarium* hyphae after contact with *Paenibacillus* sp.

Culture-based molecular identification

Species-level identification of culturable microbes was further refined through BLASTn searches in GenBank of sequence data from the internal transcribed spacer (ITS) DNA barcode for fungi (Schoch *et al.* 2012)and the 16S DNA barcode for bacteria (Benson *et al.* 2010). Total fungal genomic DNA was extracted from pure culture mycelia of each isolate using methods adapted from Cenis (1992). Primers ITS4 and ITS5 were used to amplify the ribosomal DNA (rDNA) ITS region (White

et al. 1990) for all fungal isolates. Each 30-µL polymerase chain reaction (PCR) mixture contained 20.25 µL of PCR-grade water; 3 µL of ThermoPol Reaction buffer, 0.6 µL of dNTPs, and 0.15 µL of New England Biolab (NEB) Taq DNA polymerase from a Taq PCR core kit (Qiagen); 2.25 µL of each primer at 0.5 mM; and 1.5 µL of template DNA. Thermocycler conditions for fungi were: initial denaturing at 95°C for 2 min; 35 cycles of denaturing at 95°C for 30 s, annealing at 52°C for 45 s; extension at 72°C for 1 min 30 s; and a final extension step of 72°C for 5 min. Bacterial genomic DNA was isolated from a single purified colony suspended in 50 µL lysis buffer (TE + 0.1% Triton-X100), which was boiled for 10 min, and centrifuged at 16,000 x g for 5 min. We used 1 µL of the supernatant as template DNA in each PCR mixture containing 22 µL of PCR-grade water, 25 µL of GoTaq Green® Master Mix (Promega), and 1 µL at 0.5 mM each of U1 and U2 primers to amplify the rDNA 16S region using the following thermocycler conditions: initial denaturing at 94°C for 5 min; 25 cycles of denaturing at 94°C for 1 min, annealing at 60°C for 1 min; extension at 72°C for 2 min; and a final extension step of 72°C for 10 min.

Amplified products were separated by gel electrophoresis in 1% agarose gel with 0.5x Tris-boric acid-EDTA buffer, stained with SYBR Green (Invitrogen, Carlsbad, CA), and viewed under UV light. PCR products were purified for downstream Sanger sequencing using the Exo SAP-IT kit (Affymetrix). The ITS and 16S regions were sequenced in both directions at the College of Biological Sciences UC DNA Sequencing Facility at the University of California, Davis. Sequences were edited and assembled using Sequencher (version 4.6; Gene Codes), locally aligned

using ClustalX 2.1-Mac OSX (Conway Institute) (Thompson *et al.* 1997), and manually aligned using MacClade 4.08 OSX (Sinauer Associates, Inc.) (Maddison, D., Maddison, W. 2001).

For BLASTn searches that did not identify any closely-related species with 100% sequence identity, we conducted phylogenetic analyses using MEGA 7.0 (Stecher *et al.* 2020) with the maximum likelihood heuristic searches and close-neighbor interchange branch swapping. Bootstrap values were calculated using 1,000 replicates and 100 random sequence additions to test branch strength. Sequences for each species recovered in this study were compared with those from previous studies available in GenBank to validate their identities (Table S1).

Data analysis

We used multivariate analyses to assess differences in wood-limited microbial communities among 1) host species and attack status, 2) host species of the same attack status, and 3) attack status within host species (Martiny *et al.* 2006; Anderson *et al.* 2011). For each grouping, we performed a multivariate analysis of variance (MANOVA) to test for significant differences of individual taxa in the microbial communities among groups. Rare microbiota (recovered from < 5 trees) and taxa that were not significantly different ($P \leq 0.05$) among groups in the MANOVAs were excluded from further analyses.

When the results of a MANOVA indicated a significant difference, we used predictive linear discriminant analyses (LDA) to determine which taxa discriminate

between naturally occurring groups, and to predict group membership (Hastie *et al.* 1994; Guo *et al.* 2007). The discriminant functions provide the linear combination of taxa that best separate tree individuals according to groups (e.g., host species, or attacked and not-attacked trees). Data from each analysis were randomly partitioned equally into "training" and "testing" data sets. We used the training data to fit the discriminant model using the lda function in the MASS R package (v. 7.3-51.6), and then applied the model to the test data to predict group membership for each tree based on discriminant scores, and to explore differences among communities. We first used a more inclusive set of microbiota to enter the function (genera recovered from ≥ 5 trees), and then repeated the analyses with more restrictive sets of microbes (genera recovered from ≥ 10 and ≥ 20 trees), which permitted an evaluation of group membership based on rare and common taxa. To account for classification variability on randomly partitioned data, this process was repeated 100 times for each analysis on different random sets of training and testing samples. Models at the 0.025, 0.5, and 0.975 quantile classification rates are reported as representative results.

Results

Overview of wood-endophyte community structure

We isolated 1,428 strains of culturable endophytic fungi (771) and bacteria (657) from wood tissues in 534 of the 575 trees sampled across FD-ISHB -infested and non-infested sites in California (Tables II & SII). All but 51 isolates (including

one bacteria isolate) were identified to genus using BLASTn searches of ITS and 16S rDNA sequence data in GenBank and subsequent phylogenetic analyses (Table SI-SII). Isolate abundance of fungi and bacteria was highly uneven within taxonomic groups, with many rare (53.8% singletons and doubletons) and very few highly abundant taxa (Figs. 2-5, Table SII), consistent with observed patterns of microbial communities in other studies (Nemergut *et al.* 2013). The most common genera were detected across all site-infection categories, including attacked and not-attacked trees within infested and non-infested sites (Figs. 2 & 5; Table SII). Wood samples contained 1-12 distinct culturable taxa (mean = 2.8; median = 2). There was no significant difference in mean generic richness between trees of infested and non-infested sites (Table II).

The fungal isolates were mainly composed of Ascomycota (44 families in 15 orders), with most families representing Dothideomycetes and Sordariomycetes (Fig. 3). In particular, taxonomic richness was highest in the Pleosporales and Hypocreales (Figs. 2-4). Fungal isolates in the Basidiomycota were rare (with the exception of *Cystobasidium* isolates), and comprised one genus each in seven families in five orders (Figs. 2-4; Table SII). Of the 79 fungal genera isolated, the most common were *Cladosporium* (n= 211; Capnodiales, Davidiellaceae), *Aureobasidium* (n= 97; Dothideales, Dothioraceae), *Alternaria* (n= 79; Pleosporales, Pleosporaceae), an unclassified yeast (n= 40), *Didymocyrtis* (n= 33; Pleosporales, Phaeosphaeriaceae), *Penicillium* (n= 32; Eurotiales, Trichocomaceae), *Botryosphaeria* (n= 21;

Botryosphaeriales, Botryosphaeriaceae), *Phragmocamarosporium* (n= 20; Pleosporales, Lentitheciaceae), *Aspergillus* (n= 19; Eurotiales, Trichocomaceae),

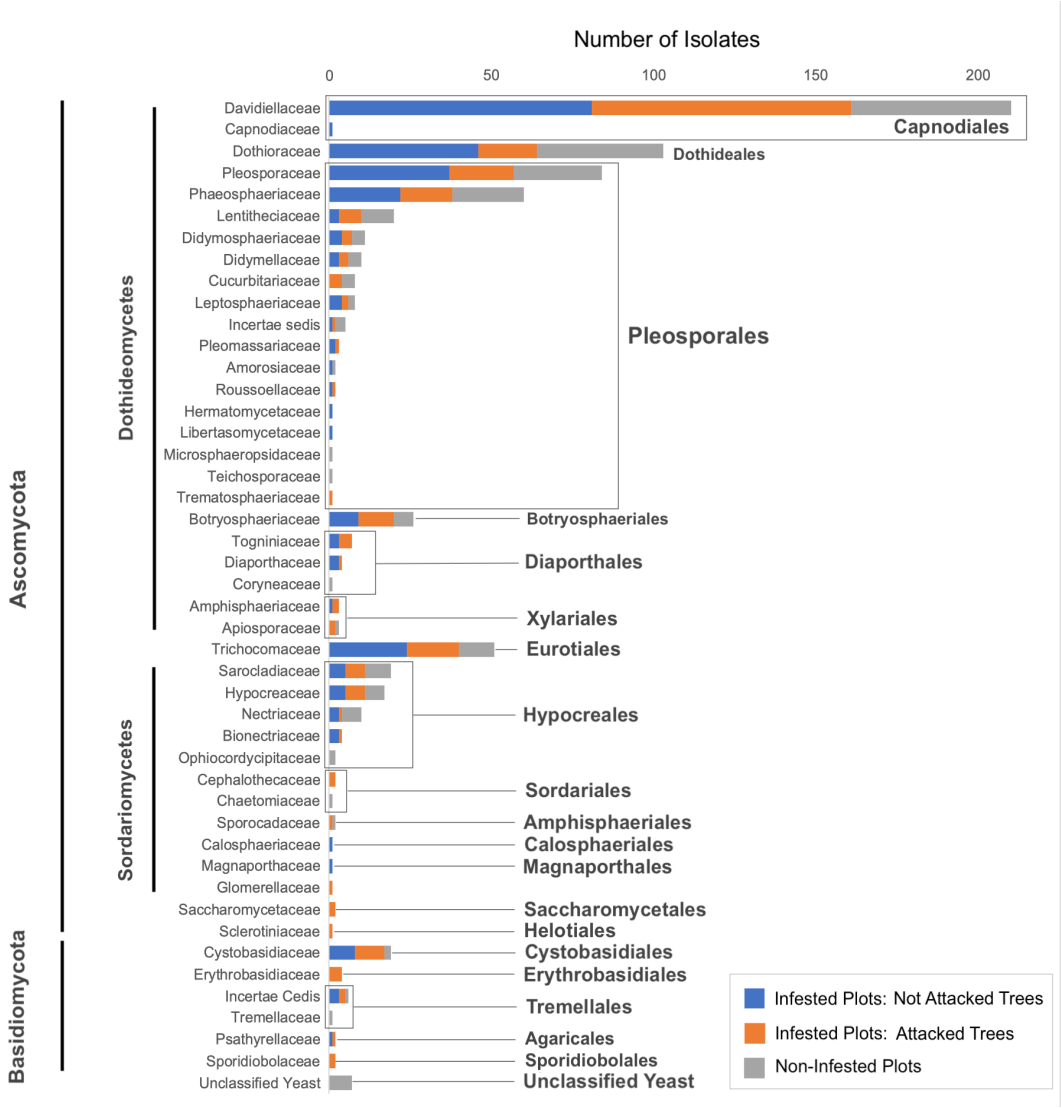


Figure 3. Number of fungal families isolated from trees in FD-ISHB infested and non-infested monitoring plots in southern California, ordered by rank within higher classifications. Higher classifications include the divisions Basidiomycota and Ascomycota, the ascomycete classes Dothidiomycetes and Sordariomycetes, Leotiomycetes (not labeled, represented by Helotiales), and 20 orders, which are labeled to the right of columns.

Sarocladium (n= 19; Hypocreales, Sarocladiaceae), *Cystobasidium* (n= 19; Cystobasidiales, Cystobasidiaceae), and *Neosetophoma* (n= 11; Pleosporales, Phaeosphaeriaceae) (Fig. 3; Table SII). Ten species of *Cladosporium* (Group 1-10), five species of *Aureobasidium* (sp. 1-4b), and one species of *Sarocladium* and *Pleomassaria* belonged to potentially new, previously undescribed, species based on the ITS sequence (Table SI).

Bacterial isolates comprised 39 genera in 22 families. Proteobacteria was the most abundant and taxonomically rich phylum, followed by Actinobacteria, Firmicutes, and Bacteroidetes (Figs. 4-5). All major groups (except Bacteroidetes) represented a common genus, which included *Pseudomonas* (n= 356; Pseudomonadales, Pseudomonadaceae), *Microbacterium* (n= 57; Actinomycetales, Microbacteriaceae), *Pantoea* (n= 56; Enterobacterales, Erwiniaceae), *Paenibacillus* (n= 46; Bacillales, Paenibacillaceae), *Variovorax* (n= 23; Burkholderiales, Comamonadaceae), *Bacillus* (n= 15; Bacillales, Bacillaceae), *Methylobacterium* (n= 14; Rhizobiales, Methylobacteriaceae), and *Brenneria* (n= 13; Enterobacterales, Pectobacteriaceae) (Fig. 5; Table SII).

Microbial interactions

We conducted a total of 1,120 *in vitro* bioassays on 60 and 39 species of wood-inhabiting endophytic fungi and bacteria (Tables III-V). Because many taxa were rare or difficult to isolate, we used one replicate strain for 36 species of fungi and 21 species of bacteria to assess their interactions with *Fusarium*. Here, we focus

on interactions between pathogens and the common endophytes, which include species that were isolated from a minimum of nine trees (Tables III-V; Table SII). Fungal and bacterial interactions and underlying mechanisms in co-culture varied

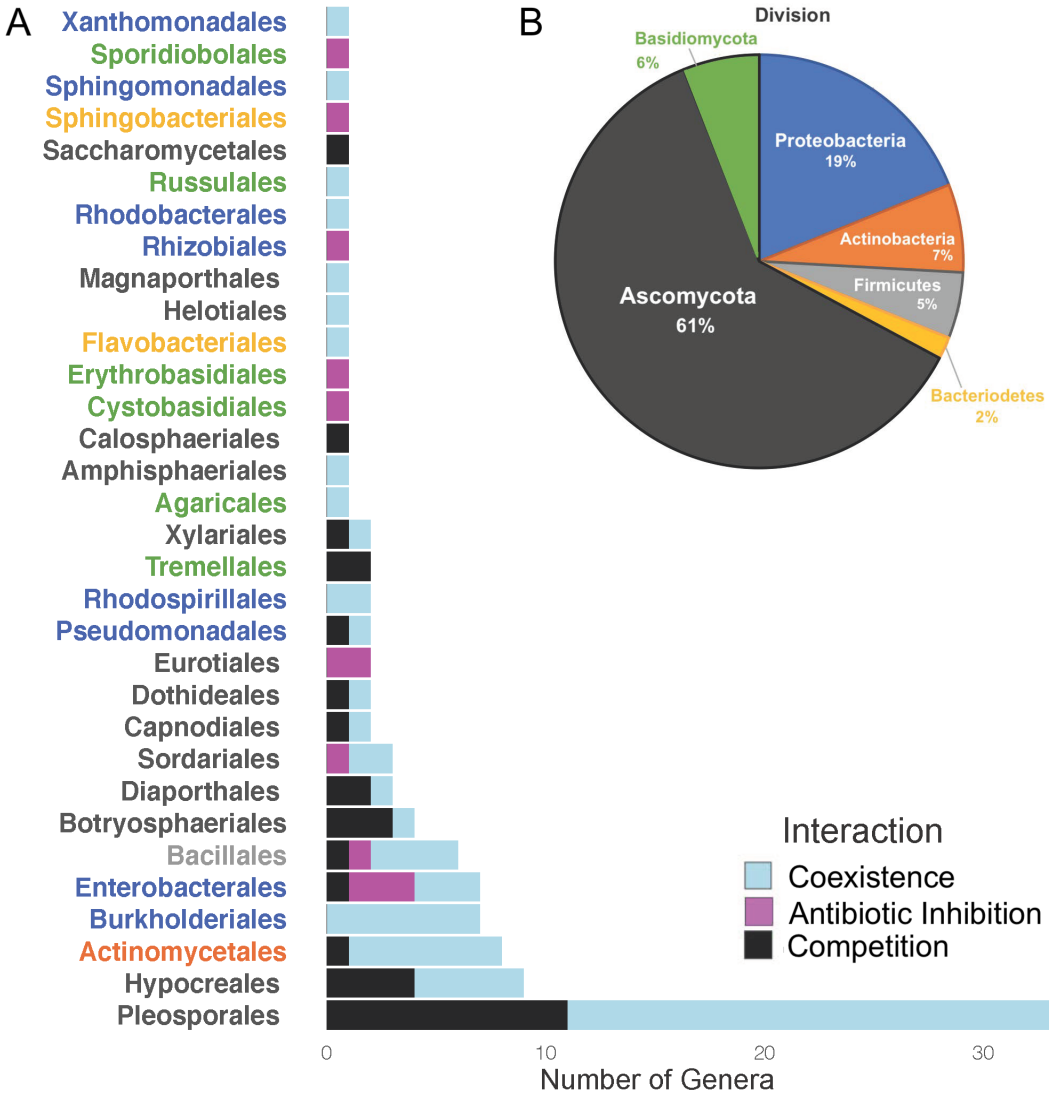


Figure 4. **A)** Number of genera within each order exhibiting coexistence, antibiotic inhibition, or competition with *Fusarium* species *in vitro*. **B)** Number of genera within each division (pie chart). Order colors (A) correspond to the division to which they belong (B).

among species and among isolates of the same species and were mostly antagonistic or neutral (Tables III-V). Uniquely, contact with the bacteria *Paenibacillus* sp. appeared to stimulate filamentation and hyphal branching of all *Fusarium* spp. isolates, producing an unusually thick and fluffy mycelium (Fig. 2h, Table IV). Interactions between all species of *Alternaria* and *Fusarium* were dominated by mutual inhibition (Fig. 2f, Table III).

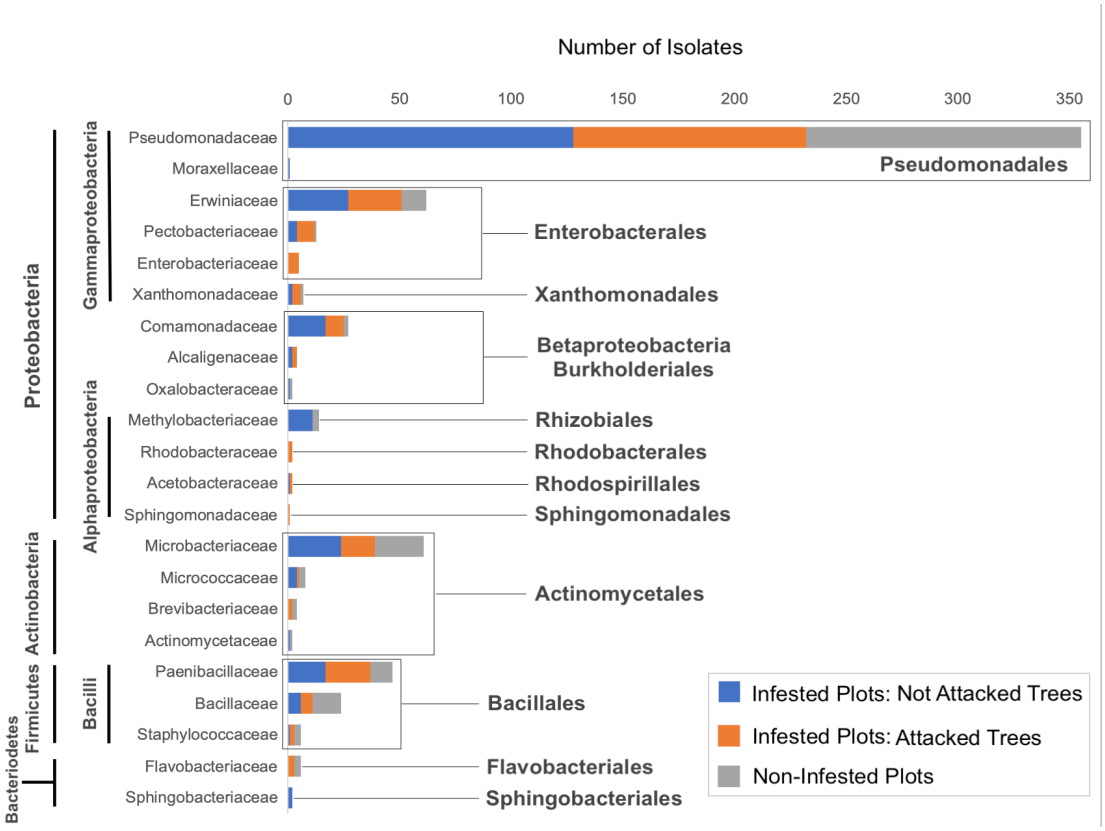


Figure 5. Number of bacteria families isolated from trees in FD-ISHB -infested and non-infested monitoring plots in southern California, ordered by rank within higher classifications. Higher classifications include four divisions, four classes, and 12 orders, which are labeled to the right of columns.

The most common of the 15 endophytic fungal species exhibiting antagonism against all or nearly all *Fusarium* spp. isolates (≥ 94%) included *Aspergillus* sp.,

Didymocyrtis brachylaenae, and *Penicillium nalgiovense* (through antibiosis), and *Botryosphaeria parva,* and *Trichoderma harzianum* (through competition) (Table III). Four of the five replicates of the very common *Cladosporium* Group 5 partially replaced all *Fusarium* spp. isolates and reduced their vigor. In contrast, all pathogen isolates partially replaced or inhibited growth of *Fusicoccum vitifusiforme, Cladosporium aphidis,* and *Hormonema carpetanum*, but these fungi were rare and tests were based on single isolates. The most common of the 11 bacterial endophytes exhibiting antagonism against most *Fusarium* spp. isolates (≥92%) were *Bacillus* sp., *Brenneria* sp., and *Erwinia* sp. The only common bacterial taxon that strongly inhibited pathogen growth exclusively via antibiosis was *Bacillus*. *Pseudomonas fluorescens* and *Pantoea* sp. were very common bacteria that also affected pathogen isolates (0.77 ± 0.32 and 0.68 ± 0.35 respectively) through competition or moderate antibiotic inhibition. For *Pantoea* sp., competition was marked by the production of a rapidly expanding colony, which did not occur in cases of antibiotic inhibition or neutral interactions. This variation was observed among strains and within replicates of six of the ten tested strains. Although rare, isolates of the bacterium *Raoultella terrigena* and fungi *Epicoccum nigrum* and *Pithomyces chartarum* exhibited strong antibiotic inhibition against all *Fusarium* isolates.

Apart from *Aureobasidium* sp. 4, species of *Aureobasidium* on average were never the dominant inhibitor and interactions with the pathogen were highly variable. This variability was largely due to the influence of few replicate strains that were all partially replaced by the pathogen.

Microbial diversity among attacked and not-attacked hosts

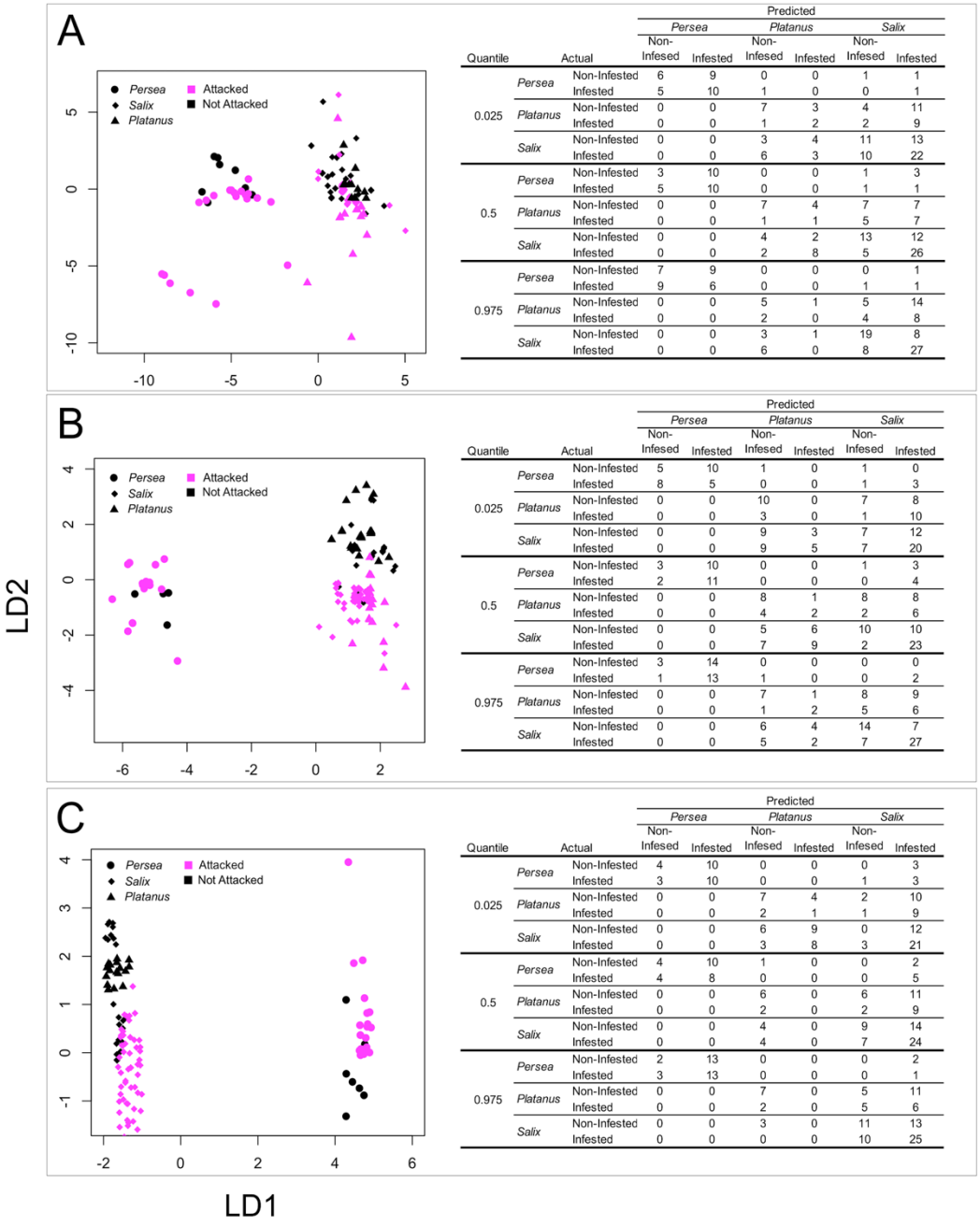
We assessed diversity of culturable microbial communities using microbiota identified to the genus level and host species with the largest sample size: *P. americana* (n= 95), *P. racemosa* (n= 132), *Q. agrifolia* (n= 75), and the three species of *Salix* combined (n= 224) (Table SII). Because there were only three attacked *Q. agrifolia* individuals, we excluded this host from all analyses specifically considering attacked trees. Microbial communities were highly significantly different between 1) host species analyzed together with their attack status, 2) host species of the same attack status (analyzed to compare species separately for attacked and not-attacked trees), and 3) attack status for each host species (MANOVA; $P \leq 2.2e\text{-}16$ each). These significant differences were consistent in analyses of all data sets filtered to include microbial taxa recovered from ≥5, ≥10, and ≥20 trees, suggesting large differences among communities that can be described by discriminant functions.

Discriminant Analysis

We used taxa that were significantly different among groups in each MANOVA to develop the linear discriminant functions for predictive discriminant analyses (Tables VI-X). Our first and most encompassing set of functions used 18, 15, and five microbes recovered from ≥5, ≥10, and ≥20 trees, respectively, to predict group membership in attacked and not-attacked *Salix*, *Platanus*, and *Persea* (six categories) (Table VI). The proportion of separation achieved by each of the five linear discriminant functions was dominated by LD1 (86.1%, 87.4%, 94.2% in each

microbial data set), followed by LD2 (6.1%, 5.1%, 4.0%), indicating that differences in microbial communities are strongly shaped by LD1. The median LD1 coefficients of linear discriminants from 100 analytical repetitions were highly similar among taxa present in each microbial data set (Table VI), suggesting that the most common fungi and bacteria drive differences between groups. Coefficients with the largest absolute values signify taxa with the strongest influence on group separation (Rencher 2003). For LD1, these taxa included *Didymocrytis* and *Paenibacillus*, which were recovered exclusively from *Persea* (Table SII). The identities of influential microbes for LD2 varied slightly between microbial data sets (Table VI), suggesting that group membership is secondarily affected by the inclusion of less common taxa. For example, *Aureobasidium* strongly affected group separation in data sets containing taxa isolated from ≥10 and ≥20 trees but had only a minor influence when included with taxa recovered from ≥5 trees. In contrast, *Methylobacterium* was the most influential taxon in the less inclusive data sets, but was excluded from the discriminant function with fungi and bacteria isolated from ≥20 trees.

We were able to detect consistent differences in microbial communities primarily between *Persea*, which grows in an agricultural setting, and the remaining three genera of wildland host species. Predictive discriminant analysis revealed that among the six host species-attack status categories, testing samples were correctly classified 39% (median value in all three microbial data sets), more than twice the correct classification expected at random (Table VII). For each microbial data set, we visually assessed the relationships among samples from the three attacked and not-



			Predicted					
			Persea		*Platanus*		*Salix*	
Quantile	Actual		Non-Infesed	Infested	Non-Infesed	Infested	Non-Infesed	Infested
0.025	*Persea*	Non-Infested	6	9	0	0	1	1
		Infested	5	10	1	0	0	1
	Platanus	Non-Infested	0	0	7	3	4	11
		Infested	0	0	1	2	2	9
	Salix	Non-Infested	0	0	3	4	11	13
		Infested	0	0	6	3	10	22
0.5	*Persea*	Non-Infested	3	10	0	0	1	3
		Infested	5	10	0	0	1	1
	Platanus	Non-Infested	0	0	7	4	7	7
		Infested	0	0	1	1	5	7
	Salix	Non-Infested	0	0	4	2	13	12
		Infested	0	0	2	8	5	26
0.975	*Persea*	Non-Infested	7	9	0	0	0	1
		Infested	9	6	0	0	1	1
	Platanus	Non-Infested	0	0	5	1	5	14
		Infested	0	0	2	0	4	8
	Salix	Non-Infested	0	0	3	1	19	8
		Infested	0	0	6	0	8	27

			Predicted					
			Persea		*Platanus*		*Salix*	
Quantile	Actual		Non-Infesed	Infested	Non-Infesed	Infested	Non-Infesed	Infested
0.025	*Persea*	Non-Infested	5	10	1	0	1	0
		Infested	8	5	0	0	1	3
	Platanus	Non-Infested	0	0	10	0	7	8
		Infested	0	0	3	0	1	10
	Salix	Non-Infested	0	0	9	3	7	12
		Infested	0	0	9	5	7	20
0.5	*Persea*	Non-Infested	3	10	0	0	1	3
		Infested	2	11	0	0	0	4
	Platanus	Non-Infested	0	0	8	1	8	8
		Infested	0	0	4	2	2	6
	Salix	Non-Infested	0	0	5	6	10	10
		Infested	0	0	7	9	2	23
0.975	*Persea*	Non-Infested	3	14	0	0	0	0
		Infested	1	13	1	0	0	2
	Platanus	Non-Infested	0	0	7	1	8	9
		Infested	0	0	1	2	5	6
	Salix	Non-Infested	0	0	6	4	14	7
		Infested	0	0	5	2	7	27

			Predicted					
			Persea		*Platanus*		*Salix*	
Quantile	Actual		Non-Infesed	Infested	Non-Infesed	Infested	Non-Infesed	Infested
0.025	*Persea*	Non-Infested	4	10	0	0	0	3
		Infested	3	10	0	0	1	3
	Platanus	Non-Infested	0	0	7	4	2	10
		Infested	0	0	2	1	1	9
	Salix	Non-Infested	0	0	6	9	0	12
		Infested	0	0	3	8	3	21
0.5	*Persea*	Non-Infested	4	10	1	0	0	2
		Infested	4	8	0	0	0	5
	Platanus	Non-Infested	0	0	6	0	6	11
		Infested	0	0	2	0	2	9
	Salix	Non-Infested	0	0	4	0	9	14
		Infested	0	0	4	0	7	24
0.975	*Persea*	Non-Infested	2	13	0	0	0	2
		Infested	3	13	0	0	0	1
	Platanus	Non-Infested	0	0	7	0	5	11
		Infested	0	0	2	0	5	6
	Salix	Non-Infested	0	0	3	0	11	13
		Infested	0	0	0	0	10	25

Figure 6. **Left panel:** Plots of discriminant scores for testing samples given by linear discriminant functions distinguishing wood endophyte communities in FD-ISHB attacked and not-attacked *Persea, Platanus,* and *Salix* trees. Plotted discriminant scores represent models with the median classification accuracy in 100 analytical repetitions. **Right panel:** Test classification of samples in models with classification accuracies at the 0.025, 0.5, and 0.975 quantiles. Boxes **A-C** Refer to analyses in which microbial taxa were recovered from ≥ 5, ≥10, and ≥20 trees respectfully.

attacked host species by plotting LD1 and LD2 scores from the test data with the median classification accuracy in 100 analytical repetitions (Fig. 6). The placement of training samples (data not shown) was nearly identical to that of the testing samples.

In all three cases, the samples from wildland host species (*Salix, Platanus*) were clearly distinguished from agricultural host species (*Persea*) along the LD1 axis (Fig. 6a-c). Attacked and not-attacked trees within each host type appeared to differentiate along the LD2 axis. Differences were less pronounced when microbes were isolated from ≥5 trees of wildland species (Fig. 6a) and ≥10 *Persea* trees (Fig. 6b). Further examination of actual and predicted classifications at the 0.025, 0.5, and 0.975 accuracy quantiles showed that LD1 functions consistently predicted differences between host types and classified microbial communities in *Persea* and *Salix*, but poorly classified microbial communities associated with *Platanus* (Fig. 6a-c, right panel). Within correctly classified host species, LD2 functions were better overall at classifying microbial communities in not-attacked *Platanus*, attacked *Salix*, and attacked *Persea*. Test classification of testing samples was best for attacked and not-attacked *Salix* in the most accurate models with the more inclusive microbial data sets (77.1-79.4% truly attacked; 66.7-70.4% truly not-attacked). However, classification by attack status was generally poor, indicating a lack of consistent differences in the microbial communities.

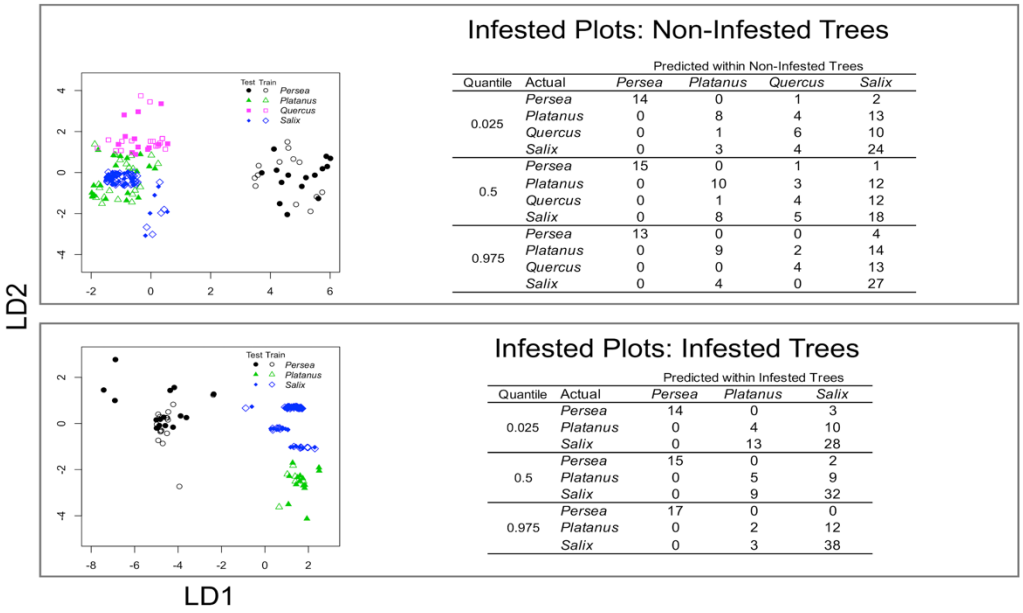
Because coefficients, classification rates, and distributions of linear discriminant scores were similar among the three microbial community data sets within each subsequent analysis (Figs. S2-S4; Tables SIII-VII), we present results of

all other analyses using data sets containing microbiota recovered from ten or more trees (Figs. 7-11; Tables VIII-X).

Host Classification

To account for variation associated with infection status, we further analyzed microbial community differences among hosts separately within not-attacked and attacked trees (Figs. 7 & S2, Tables VIII, SIII, & SVI). Six microbes were associated with group membership in not-attacked *Salix, Platanus, Quercus*, and *Persea*, and seven microbes were associated with attacked *Salix, Platanus,* and *Persea*. The proportion of separation achieved by each of the three linear discriminant functions in not-attacked trees was dominated by LD1 (93.9%), followed by LD2 (5.5%). For attacked trees, the proportion of separation achieved by LD1 was 99.4%. Consistent with our analysis of all six categories together, *Didymocyrtis* and *Paenibacillus* strongly influenced species distinctions for LD1 in both attacked and not-attacked trees (Table VIII). The fungus *Phragmocamarosporium* was commonly found in *Persea* (Table SII) and also influenced species distinctions for LD1 in attacked trees. For LD2, *Methylobacterium* and *Variovorax* drove species differences in not-attacked trees, and *Aureobasidium* and *Pantoea* strongly influenced group membership in attacked trees. These systematic differences in abundance point to a testable hypothesis that these microbes may characteristically differentiate between attacked and not-attacked trees.

We found consistent differences in the microbial communities associated with host type (wildland and agriculture) but not host species. Predictive discriminant analysis revealed that testing samples of not-attacked and attacked trees were



Infested Plots: Non-Infested Trees

Quantile	Actual	Predicted within Non-Infested Trees: *Persea*	*Platanus*	*Quercus*	*Salix*
0.025	*Persea*	14	0	1	2
	Platanus	0	8	4	13
	Quercus	0	1	6	10
	Salix	0	3	4	24
0.5	*Persea*	15	0	1	1
	Platanus	0	10	3	12
	Quercus	0	1	4	12
	Salix	0	8	5	18
0.975	*Persea*	13	0	0	4
	Platanus	0	9	2	14
	Quercus	0	0	4	13
	Salix	0	4	0	27

Infested Plots: Infested Trees

Quantile	Actual	Predicted within Infested Trees: *Persea*	*Platanus*	*Salix*
0.025	*Persea*	14	0	3
	Platanus	0	4	10
	Salix	0	13	28
0.5	*Persea*	15	0	2
	Platanus	0	5	9
	Salix	0	9	32
0.975	*Persea*	17	0	0
	Platanus	0	2	12
	Salix	0	3	38

Figure 7. **Left panel:** Plots of discriminant scores for testing and training samples given by linear discriminant functions distinguishing wood endophyte communities among tree hosts. Plotted discriminant scores represent models using microbial taxa isolated from ≥10 trees, and with the median classification accuracy in 100 analytical repetitions. Analyses were run separately within FD-ISHB attacked and not-attacked trees. **Right panel:** Test classification of samples in models with classification accuracies at the 0.025, 0.5, and 0.975 quantiles.

correctly classified 53% and 72% (median values respectfully), each more than twice the correct classification expected at random (Table VII). In both analyses (Fig. 7), microbial communities in wildland and *Persea* host species were clearly distinguished along the LD1 axis, and differences among wildland host species appeared to be captured by LD2. The inclusion of *Quercus* in the not-attacked tree analysis resulted in less pronounced differences, with *Salix* apparently clustering and

nesting within *Platanus*. However, further examination of actual and predicted classifications at the 0.025, 0.5, and 0.975 accuracy quantiles showed that *Platanus* (in both cases) and *Quercus* were frequently and incorrectly assigned to *Salix,* reflecting the minor influence of LD2 on species distinctions (Fig. 7, right panel). These results indicate that microbial communities are similar among wildland host species and highly distinct from those in *Persea*, and these differences are driven by the presence of *Didymocyrtis, Paenibacillus,* and *Phragmocamarosporium*.

Classification by attack status

To rule out the effect of microbial community variation among host species on discriminating communities by attack status, we developed three separate linear discriminant functions to assess status differences in *Salix*, *Platanus*, and *Persea* trees. Six microbes were used to predict attack status in *Salix* and *Persea*, and five microbes were used for predictions in *Platanus*. *Aureobasidium* and *Pantoea* strongly influenced linear discriminant functions in the wildland species, which was expected as they only occurred within attacked trees in the host classification analysis (Table IX). Microbes with the greatest influence on discriminant functions for *Salix*, *Platanus*, and *Persea* were *Sarocladium*, *Pantoea*, and *Microbacterium* respectfully. While *Didymocyrtis* also influenced predictions for *Persea*, *Paenibacillus* was unexpectedly the least influential, given that it stimulated *Fusarium* growth *in vitro* (Fig. 2, Table IV).

We were unable to detect consistent differences among microbial communities in the attacked and not-attacked hosts using LDA. Using the training samples, functions did a good job distinguishing attacked and non attacked hosts. However, the poor correct classification of the testing samples (Figs. 8 & S3; Table SVII) shows that these differences were not robustly detected across the host individuals, consistent with our analysis of all six categories in which LD2 had a minor influence on separation between attacked and not-attacked trees (Fig. 6). In particular, predictive discriminant analysis revealed that testing samples of not-attacked and attacked *Persea* trees were correctly classified 47% (median), which was below the correct classification expected at random (50%; Table VII). Although poor, discriminant functions were better at predicting not-attacked *Persea* trees (22.2-55.5% truly attacked; 35.3-58.8% truly not-attacked) (Fig. 8). The median classification accuracies for *Salix* and *Platanus* were higher (60% each) but were only 1.2 times more than expected at random. Consistent with our first analysis, discriminant functions were better at predicting attacked *Salix* trees (64.3-78.6% truly attacked; 35.5-54.8% truly not-attacked) and not-attacked *Platanus* trees (26.7-46.7% truly attacked; 51.9-85.2% truly not-attacked) (Fig. 8). Analysis of microbial communities in *Salix* and *Platanus* combined (i.e., wildland species) did not change classification accuracies or predicted attack status outcomes (data not shown). However, the inclusion of rare taxa into the function slightly improved predictions for *Salix* (71.4-83.3% truly attacked; 48.4-64.5% truly not-attacked) (Table SVII). Predicted discriminant scores for trees in non-infested plots were normally distributed

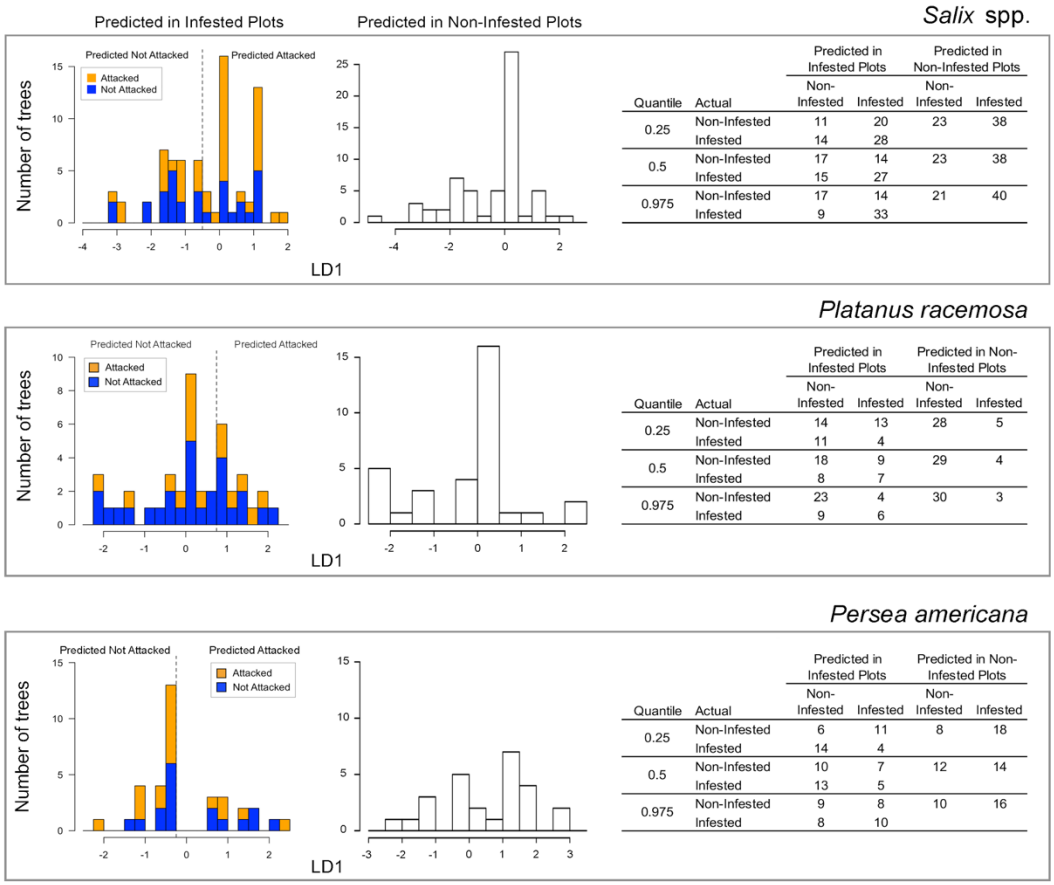


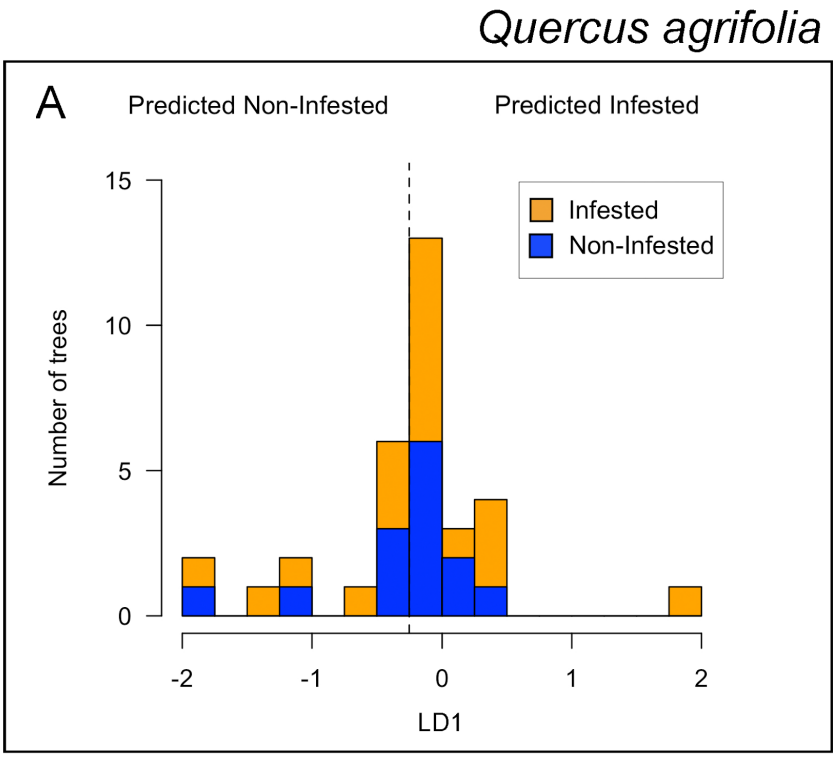
Figure 8. **Left panel:** Predicted discriminant scores for testing samples given by the linear discriminant function distinguishing wood endophyte communities among FD-ISHB attacked and not-attacked *Salix, Platanus,* and *Persea* trees within infested plots. Plotted discriminant scores represent models using microbial taxa isolated from ≥10 trees, and with the median classification accuracy in 100 analytical repetitions. **Middle panel:** Discriminant score predictions for trees in non-infested plots. **Right panel:** Test classification of samples in models with classification accuracies at the 0.025, 0.5, and 0.975 quantiles.

for each host, and discriminant functions predicted that a subset of trees in non-infested plots could become infested based on the combination of microbial taxa in those trees. However, although the predicted distributions of test samples' linear discriminant scores showed distinctions between attacked and not-attacked trees (Fig. 8), the test samples' actual attack status showed scores were normally distributed for

each host (Fig. 8). As such, the ability to say whether trees from non-infested plots are more similar to attacked or not-attacked trees in infested plots is tenuous.

Classification of *Quercus* in infested and non-infested plots

We did not find consistent differences in the microbial communities associated with *Quercus* in infested and non-infested plots. We developed a linear discriminant function to predict group membership of *Quercus*-associated microbial communities in infested and non-infested plots (Fig. 9, Table X). Similar to attack status predictions, test classification of testing samples was nearly equal to values expected at random (52% median; Table VII). The linear discriminant function, which was strongly influenced by *Alternaria* and *Aureobasidium*, classified trees in infested plots better than non-infested plots (57.9-84.2% truly infested vs. 21.4-35.7% truly non-infested) (Fig. 9). However, the inclusion of rare taxa into the function (Table SV) improved its classification performance (61% median; Table VII), and trees in non-infested plots were classified better than infested plots (71.4-92.9% truly non-infested vs. 52.6-63.2% truly infested) (Fig. S4a). Improvements may be largely due to the stronger influence of a completely different set of microbes on the discriminant function (i.e., *Variovorax, Microbacterium,* and *Pantoea*) (Table SV).



B

Quantile	Actual	Predicted: Non-Infested Plots	Predicted: Infested Plots
0.025	Non-Infested Plots	3	11
	Infested Plots	8	11
0.5	Non-Infested Plots	5	9
	Infested Plots	7	12
0.975	Non-Infested Plots	5	9
	Infested Plots	3	16

Figure 9. **A)** Predicted discriminant scores for testing samples given by the linear discriminant function distinguishing wood endophyte communities in *Quercus* among FD-ISHB infested and non-infested plots. Plotted discriminant scores represent models using microbial taxa isolated from ≥10 trees, and with the median classification accuracy in 100 analytical repetitions. **B)** Test classification of samples in models with classification accuracies at the 0.025, 0.5, and 0.975 quantiles.

Discussion

In this study, we assessed endophyte community variation in wood of tree hosts of the emergent generalist pest-pathogen complex Fusarium dieback-Invasive shot hole borers (FD-ISHB) in Southern California. We assessed microbial variation across a phylogenetic diversity of attacked and not-attacked hosts, and sampled across wildland-agriculture communities in infested and non-infested sites that varied in tree species composition. The most common fungi belonged to Capondiales, Dothideales, and Pleosporales (Dothideomycetes), Eurotiales (Eurotiomycetes), and Hypocreales (Sordariomycetes) in Ascomycota, and the most common bacteria were in the Proteobacteria, Actinobacteria, and Firmicutes divisions. Outcomes of fungal and bacterial interactions with *Fusarium in vitro* varied among species and among isolates of the same species, but 15 fungal species and 11 species of bacteria exhibited clear antagonism against the pathogen either through competition or antibiotic inhibition. Linear discriminant analyses of culturable microbial communities in different combinations of attacked and not-attacked host species revealed that the endophytic microbiome was similar in the wildland host species (*Salix, Platanus, Quercus*) and distinct from the agriculture host (*Persea*). However, discriminant analysis could not classify microbial communities by attack status, suggesting that their microbiome is not predictive of attack susceptibility. Group separation by host species was driven by more common taxa and, in particular, the presence of three taxa that were frequently, if exclusively, isolated from *Persea* (*Paenibacillus, Didymocrytis, Phragmocamarosporium*). Similarities between wildland hosts species were

unexpected since they are distantly related to each other (between 181-282 Myr) and the phylogenetic distance between *Persea* and other hosts is 317 Myr (Fig. 1). Recognizing that we cannot generalize microbial community associations to agriculture based on one agriculture host species, these results indicate that wood-limited microbial community differences are likely associated with ecological roles and not host relatedness or attack status. However, effects could be confounded by site or landscape factors, or those factors are more important in explaining microbial variation.

Wood-inhabiting microbial diversity

Our understanding of plant microbiomes and the endosphere in particular stems from numerous studies of important agricultural crops, model plants, grasses, and certain groups of forest trees over the last forty years (Chapela 1989; Clay 1990; Finlay & Clay 2007; Maheshwari & Annapurna 2017; Terhonen *et al.* 2019). New insights have advanced as powerful technological tools like high throughput amplicon sequencing (HTAS), metagenomics, metatranscriptomics, and metaproteomics have become more widely available. However, genus- to species-level identification is not always possible with these tools because they rely on sequence comparisons in databases often with low taxonomic resolution (e.g., "Uncultured Ascomycota"; "Uncultured Endophyte"), making it difficult to assess microbial communities in a meaningful way. Moreover, the diversity of endophytic microbiota in plants is vastly underrepresented in databases, given that numerous species have not been sequenced,

formally described (Terhonen *et al.* 2019), or even discovered (Izumi 2011; Harrison & Griffin 2020). This culture-dependent study provides a species-level library of wood-inhabiting fungi and bacteria from many different tree species. Together with molecular-based identification and phylogenetic analyses, we further identified 17 putative previously undescribed species of fungi (10 *Cladosporium*, five *Aureobasidium,* one *Sarocladium*, one *Pleomassaria*). In conjunction with culture-independent approaches, this work will enable a comprehensive analysis of wood-inhabiting microbial communities in the FD-ISHB pest-pathosystem. For future comparative studies, this work will also contribute a robust set of formally described vouchered endophytes to databases with longer and verified reference sequences.

Among tree-associated microorganisms, endophytic fungal biota are the most intensively examined, particularly in members of the Betulaceae, Fagaceae, Cupressaceae, and Pinaceae (Sieber 2007; Izumi 2011). One exception is the genus *Populus,* in which bacteria have been extensively studied (Izumi 2011). Reviews of endophytic fungi in forest trees conclude that relatedness of dominant endophytes decreases with decreasing relatedness of host trees (Sieber 2007), and wood-inhabiting communities are composed primarily of wood decomposers (i.e., Russulales, Polyporales, and Agaricales in Basidiomycota, and xylariaceous ascomycetes) and taxa in the Diaporthales (Stone *et al.* 2004; Sieber 2007; Porras-Alfaro & Bayman 2011; Terhonen *et al.* 2019). However, those taxa were rare across all hosts in the present study, and communities in distantly related but ecologically similar hosts were similar in species composition. This contrast likely reflects a bias

towards studies of wood decay fungi in the literature. Indeed, our findings are consistent with previous, albeit limited, studies of wood-inhabiting fungal communities in trees that did not focus on wood decay, where Diaporthales were rare, and only 11% of all taxa combined were in Basidiomycota (Tables SVIII-SIX). Although the subset of comparative studies showed distinctions in communities among host species, results were based on a very small number of sampled trees (Table SVIII), making it difficult to use these studies to make generalizations about microbial communities and host specificity.

Community Analysis

One possible explanation for the apparent similarity in culturable microbial communities among wildland hosts and within host species regardless of attack status is that we captured taxa representing a functionally significant wood-associated core microbiome. Based on isolation frequency across hosts, this core microbiome includes four fungal (*Cladosporium, Aureobasidium, Alternaria, Penicillium*) and four bacterial (*Pseudomonas, Microbacterium, Pantoea, Variovorax*) genera. *Cladosporium* and *Pseudomonas* were also signature taxa in avocado. In a culture-independent microbiome analysis of grapevine (*Vitis vinifera*) xylem sap overtime, Deyett & Rolshausen (2019) reported that *Pseudomonas, Cladosporium, Aureobasidium,* and *Alternaria* were also part of the core xylem sap microbiome in all plant phenological stages throughout the growing season. While some species of *Cladosporium* are recognized as foliar and fruit pathogens (Deyett & Rolshausen

2020; Bensch et al. 2012), they have also been used for biocontrol against grapevine wood diseases (Munkvold and Marois 1993; Briceno and Latorre 2008; Iasur-Kruh et al. 2015; Zhang et al. 2017), and have triggered plant growth, early flowering, and increased fruit yield in tobacco (*Nicotiana tabacum*) (Li et al. 2019). Interestingly, isolates of *Pseudomonas* recovered from wood in *Salix sitchensis* and *Populus trichocarpa* promoted the growth of inoculated Douglas-fir (*Pseudotsuga menziesii*) seedlings (Proença *et al.* 2017; Puri *et al.* 2017), demonstrating conferred benefits across phylogenetically distant tree species. *Pseudomonas* is also considered to be a key component of the wood microbiome in pine (*Pinus* spp.) and spruce (*Picea* spp.) (Proença *et al.* 2017; Puri *et al.* 2017). One limitation to this study is that we did not assess the woody microbiome in confirmed non-hosts, many of which are conifers (Eskalen *et al.* 2013). Additional research will need to determine if these microbial taxa together have prevailing conserved functional benefits in wood, but these studies across gymnosperms and angiosperms point to the possibility.

Although predictive discriminant analysis could not detect consistent differences among microbial communities in hosts based on attack or infestation status, the discriminant functions could distinguish between attacked and not-attacked trees (or infested and non-infested sites for *Quercus*) on the training samples. Accordingly, there were enough differences among microbes that the inconsistencies in the testing samples most likely reflect undersampling in the community. Given that the culture-dependent data represent half the number of samples collected in this study, that the culturable taxa represent an even smaller subset of detectable

microbes, and that isolation techniques can favor recovery of some microbes over others, it is conceivable that we missed taxa in our sampling effort. As the inclusion of rare species improved predictions in some cases (i.e., *Salix* and *Quercus*), we expect a richer data set to detect consistent differences in testing samples. β-diversity metrics in other culture-independent studies demonstrated differences in microbial community profiles of wood in diseased and non-diseased grapevine (Pierce's disease) (Deyett *et al.* 2017; Deyett & Rolshausen 2019, 2020), elm (Dutch elm disease) (Martín *et al.* 2015; Macaya-Sanz *et al.* 2020), and spruce (*Heterobasidion* spp. pathogens) (Kovalchuk *et al.* 2018) individuals. Additionally, Proença et al. (2017) used culture-dependent and culture-independent approaches to compare wood-inhabiting bacteria communities among *Pinus pinaster* trees attacked by the pinewood nematode (*Bursaphelenchus xylophilus*) and found that not all taxa detected by HTAS were cultivable. The increased sampling depth achieved in applying HTAS in other studies and the promising culture-dependent evidence in the present study supports the use of HTAS to analyze associations between multi-host microbiomes and FD-ISHB attack. Integrating multiple methodologies will also help to mitigate sampling biases presented in each of these approaches (Palmer *et al.* 2018; Skelton *et al.* 2019).

Microbial interactions and implications

As a first pass, a focus on pairwise *in vitro* interactions is an effective way to understand the potential outcomes between different microbial species (Foster & Bell

2012) and their effects on plant hosts. Numerous studies have demonstrated endophyte effects on pathogens using *in vitro* competition experiments or by exposing pathogens to endophyte metabolites or volatiles (Heather & Sharma 1987; Pandey *et al.* 1993; Bailey *et al.* 2008; Martín *et al.* 2015). Our findings suggest that most endophytes recovered across FD-ISHB host species exhibit some form or degree of antagonism with the *Fusarium* pathogens, consistent with what is reported in studies of other pathosystems (Busby *et al.* 2016). However, the mode of interaction *in vitro* is not always a clear predictor of host outcomes because the approach does not account for higher-order interactions among resident microbial communities in the context of the host environment. Physiological or physical changes arising from microbe-microbe contact can be mediated or exacerbated by host chemistry, nutrient availability, microclimate, or responses to resident microbes (Müller *et al.* 2016; Krüger *et al.* 2019). For example, Adams et al. (2009) reported that bacterial associates of bark beetles (*Dendroctonus* spp. and *Ips grandicollis*) stimulated or inhibited growth and spore production of their symbiotic fungi (*Leptographium* spp.*, Grosmannia clavigera,* and *Ophiostoma* spp.), but exposure to a common conifer volatile (α-pinene) either amplified, reduced, or reversed those interactions. In another study (Ardanov *et al.* 2012), endophytic *Methylobacterium* spp. isolated from Scots pine (*Pinus sylvestris*) did not have direct antagonistic activity towards the fungal pathogen *Gremmeniella abietina*. However, *in planta* experiments showed a strong density dependent effect where high inoculation density resulted in pathogen resistance and low density led to susceptibility. Manipulative studies using synthetic

communities with different combinations of endophytes will be key to further understanding their functional role in the FD-ISHB pest-pathosystem and how they might be leveraged to mitigate disease for restoration and management.

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Table I. Habitat alliance, tree basal area and density and attacked tree density in 2017 and 2018 across sampling sites in Ventura, Orange, and San Diego Counties. Sites are presented in order from north to south.

Site	Habitat Alliance	Basal Area (m^2/ha)	Density (ha^{-1})	Attacked Density (ha^{-1})	Latitude[1]	Longitude[1]
Ventura County						
DAR21[1,5]	Avocado	11.5	369.2	0	34.46	-119.22
RAT194[1]	Willow Riparian	46.3	889.4	0	34.449632	-118.754735
RAT45[1]	Avocado	22.6	348	0	34.45	-118.76
OVLC196[1]	Sycamore-Oak woodland	42.2	178.5	0	34.449313	-119.296109
RAR23[1,4]	Avocado	10.3	228	0	34.44	-119.09
RAR201[1]	Mixed Riparian	44.7	1078.8	0	34.437347	-119.086451
CCP189[1]	Sycamore-Willow Riparian	20.6	372	0	34.424927	-119.260082
STP186[1,4]	Mixed Riparian	28.9	808	0	34.405259	-119.080731
OVLC192[1]	Sycamore-Oak Riparian	41.3	151.4	0	34.395493	-119.309195
TNC204	Mixed Riparian	1.6	45.7	0	34.389163	-118.876101
SAR53[1]	Avocado	11.1	296	0	34.38	-119.31
AKR18[1]	Avocado	15.8	288	0	34.38	-118.88
OVLC193[1]	Willow Riparian	22.5	216	0	34.378373	-119.306152
OVLC191	Mixed Riparian	16.1	762.1	0	34.377852	-119.308041
FDR24[1]	Avocado	13.8	196	0	34.36	-119.08
TNC203	Willow Riparian	30.5	590.5	381	34.357006	-119.028232
PAE20[1]	Avocado	4.5	340	72	34.35	-119.01
RAF25[1]	Avocado	19.2	244	12	34.35	-119.08
HCCRP184	Mixed Riparian	44.4	784	0	34.340816	-118.85957
LIA27[1,5]	Avocado	18.9	256	0	34.33	-119.14
LIA26[1]	Avocado	22.3	324	28	34.33	-119.13
LIA199	Willow Riparian	37.4	480	56	34.329024	-119.131103
TCP180[1]	Willow Riparian	33.8	610.4	0	34.322892	-118.709123
EDJ35[1]	Avocado	13.5	268	0	34.32	-118.96
TNC200[1]	Willow Riparian	24.8	1488.9	29.6	34.290455	-119.129142
LIA29[1,4]	Avocado	23.8	144.4	2.8	34.28	-119.21
DOR38[1]	Avocado	18.2	276	0	34.28	-118.95
BUR32[1,5]	Avocado	20.5	352	0	34.28	-119.12
HAL33[1]	Avocado	10.2	288	0	34.25	-118.90
RHPR48[1]	Avocado	17.1	124	0	34.25	-119.14
TNC202[5]	Willow Riparian	18.9	437.7	0	34.236534	-119.224289
COSCA183[1]	Sycamore-Willow Riparian	14.2	182.5	0	34.212951	-118.928202
COSCA178[1]	Coast live oak woodland	48.4	177.8	0	34.174844	-118.886006
COSCA177[1,4]	Willow Riparian	55.7	756.5	0	34.167766	-118.963559

Site	Habitat Alliance	Basal Area (m^2/ha)	Density (ha^{-1})	Attacked Density (ha^{-1})	Latitude1	Longitude1
Orange County						
GC140[2,3]	Sycamore-Oak Riparian	11	63.9	0	33.858486	-117.707284
GC5[2]	Sycamore-Oak Riparian	4.5	58.1	0	33.847144	-117.705244
SORP97[2,3]	Willow Riparian	41.8	264.6	81.1	33.822629	-117.776623
SORP98[3]	Mixed Riparian	19.2	234.8	128.4	33.82139	-117.774141
SORP99[3]	Mixed Riparian	18.3	243.2	89.6	33.819765	-117.772085
IRP17[3]	Willow Riparian	7.8	169.4	0	33.808969	-117.759633
FC9[2]	Mixed Riparian	23.6	390.7	0	33.791216	-117.717938
PCRP94[2]	Mixed Riparian	43.2	477.2	210.5	33.765458	-117.770114
PCRP93	Mixed Riparian	42.3	366.2	197.2	33.763454	-117.770884
LCNP104[2]	Sycamore-Oak Riparian	7.8	41	0	33.742026	-117.677509
IRC15[2]	Avocado	28.6	223	22	33.73	-117.76
MCWP26	Mixed Riparian	4.5	117.5	0	33.708046	-117.612047
LCNP92	Sycamore-Oak Riparian	6.1	24.2	0	33.703204	-117.694994
WRWP20	Willow Riparian	32.9	4000	228.1	33.682931	-117.663283
WRWP27	Sycamore-Oak Riparian	15.4	126.7	2.5	33.672501	-117.651597
WRWP23	Coast live oak riparian	51	118.9	8.6	33.67146	-117.654673
UCI87	Willow	32	273.7	178.9	33.662277	-117.853062
WMRP65[2]	Mixed Riparian	25.3	472	232	33.656102	-117.825053
UNB54	Willow Riparian	17.9	153.1	37.4	33.651464	-117.871483
ONWP28[2]	Sycamore-Oak Riparian	15.4	93.9	18.8	33.649235	-117.604696
UNB55[2]	Willow Riparian	13.6	344.6	212.3	33.628138	-117.87861
COI170[2]	Mixed Riparian	20	369.7	18.2	33.622951	-117.803642
COI167[2]	Mixed Riparian	30.5	274.9	52.6	33.620873	-117.803012
ONWP145[2]	Mixed Riparian	27.5	127.5	93.8	33.615352	-117.624786
LCWP76[2,6]	Willow Riparian	37.8	207.4	0	33.610166	-117.759713
LCWP80[2]	Sycamore-Oak woodland	23.1	100	34.8	33.597148	-117.755454
LCWP32[2]	Sycamore-Oak Riparian	7.2	79.2	1.5	33.586483	-117.764641
CCSP60	Sycamore-Oak Riparian	25.1	232.6	0	33.582951	-117.796863
AWC46	Willow Riparian	5.8	97.9	61.5	33.581942	-117.710283
LCWP38	Mixed Riparian	26.3	337.7	0	33.573891	-117.786091
CCSP62	Willow Riparian	6.7	260.9	0	33.573672	-117.808666
LCWP35	Willow Riparian	8.7	635.2	0	33.567013	-117.792871
AWC48[2]	Mixed Riparian	11	124.5	85.4	33.564474	-117.74489
AWC49	Mixed Riparian	19.9	94.1	74.2	33.562375	-117.744017
AWC50[2]	Sycamore-Oak woodland	10.8	57.8	12.2	33.560624	-117.742861

Site	Habitat Alliance	Basal Area (m^2/ha)	Density (ha^{-1})	Attacked Density (ha^{-1})	Latitude	Longitude
AWC72[2,6]	Willow Riparian	53.2	157.6	0	33.557446	-117.746867
AWC143[2]	Willow Riparian	7.4	173.2	96.2	33.550581	-117.717643
ONWP148[2]	Willow Riparian	21.9	380.8	175.4	33.54771	-117.660004
AWC69[2]	Willow Riparian	13.2	151.5	142.4	33.544333	-117.725248
AWC43	Mixed Riparian	18.8	374.4	177.3	33.543091	-117.733586
AWC42[2]	Mixed Riparian	7.5	99.6	60.2	33.535715	-117.741441
AWC67[2]	Willow Riparian	13.3	342.8	295.4	33.532109	-117.741628
AWC66[2]	Willow Riparian	7	294.5	198.6	33.527715	-117.739541
AWC41[2]	Willow Riparian	12.2	285.7	29.8	33.523026	-117.737924
San Diego County						
WGP107[2]	Sycamore-Oak Riparian	4.9	54.3	1.7	33.353243	-117.031194
HA58[2]	Avocado	31	117.6	80	33.33	-117.12
HA57[2]	Avocado	64.2	228	0	33.32	-117.04
HA56[2]	Avocado	76.2	212	40	33.32	-117.12
CALT128[4,6]	Mixed Riparian	21.8	816	0	33.314081	-117.180371
CALT127[4]	Mixed Riparian	14.6	272.7	0	33.313209	-117.183121
CALT138	Willow Riparian	19.3	759.2	195.9	33.291701	-117.222963
CDFW119[2]	Mixed Riparian	7.8	160.8	7	33.276011	-117.230468
CALT137	Mixed Riparian	14	243.2	59.5	33.260272	-117.238243
CNLM118[2]	Willow Riparian	10.3	215.2	81.1	33.25949	-117.263498
CNF129[2]	Coast live oak riparian	119.7	1128.4	0	33.256735	-116.797467
CNF133	Sycamore-Oak Riparian	32.5	143.8	0	33.251218	-116.791261
HA55[2]	Avocado	69.3	380	292	33.25	-117.17
CNF135	Sycamore-Willow Riparian	43.5	315.1	0	33.244721	-116.781169
GRP109[2]	Willow Riparian	29.5	776	12	33.243553	-117.273148
GRP108[2]	Mixed Riparian	15.1	400	12	33.243452	-117.270912
HA54[2]	Avocado	69.5	508	248	33.24	-117.17
CDFW113[2]	Willow Riparian	15.1	158	0	33.179562	-117.314499
CDFW112[2]	Willow Riparian	14.4	217	0	33.179502	-117.317238
CDFW114	Willow Riparian	18.5	214.7	0	33.178532	-117.310761
CA14[2]	Avocado	4.4	51	21	33.16	-117.07
CDFW151	Willow Riparian	15.7	180	4	33.143613	-117.307916
HA8[2]	Avocado	23.1	168	150	33.14	-117.03
CNLM150	Willow Riparian	422.8	237.7	82.7	33.131579	-117.300064
DS12[2]	Avocado	18.2	157	105	33.12	-117.03
HA3[2]	Avocado	33.6	104	104	33.11	-117.02
HA11[2,4]	Avocado	26.1	97	37	33.10	-117.03

Site	Habitat Alliance	Basal Area (m^2/ha)	Density (ha^{-1})	Attacked Density (ha^{-1})	Latitude	Longitude
HA1[2]	Avocado	14.2	172	128	33.10	-117.03
HA2	Avocado	22.8	156	0	33.08	-116.97
SDRP176[2]	Sycamore-Oak Riparian	49.2	135.5	0	33.07851	-117.115402
TECC120[2]	Sycamore-Oak Riparian	34.6	256.7	0	33.076355	-117.159615
SDRP175[2]	Willow Riparian	16	612	0	33.064094	-117.064334
TECC122[2]	Mixed Riparian	15.8	174.8	17.5	33.05355	-117.204286
SDRP173[6]	Willow Riparian	11.3	360.4	0	33.042541	-117.154207
SEER111[2]	Willow Riparian	19.5	204	152	33.012032	-117.273317
LCOP172[2]	Willow Riparian	13.1	357.4	25.5	33.010024	-117.167398
SDCP171[2]	Sycamore-Willow Riparian	19.4	175.3	80.6	33.002351	-117.234756
FSCP164	Sycamore-Oak Riparian	52.2	229.5	42.4	32.847837	-116.861699
MBNP207[2]	Sycamore-Oak Riparian	43.7	484.6	0	32.845069	-117.199031
TCNP208[2]	Mixed Riparian	28	381	0	32.798004	-117.179396
SR115[2]	Mixed Riparian	32	145.4	101.5	32.777135	-116.874573
CDFW155	Mixed Riparian	13.2	362.7	0	32.771991	-116.808345
SR117[2]	Sycamore-Oak woodland	33.5	114.8	32.4	32.762775	-116.846311
PCOS213[2]	Sycamore-Oak Riparian	2.5	71.8	0	32.695786	-117.051046
CDFW158	Sycamore-Willow Riparian	15.9	311.6	0	32.640867	-116.879603
OVRP165[2]	Willow Riparian	13.1	220	0	32.597954	-116.949348
OVRP160[2]	Sycamore-Willow Riparian	15.6	140.8	56.3	32.589843	-117.066133
TRVRP159	Willow Riparian	19.1	351.4	281.1	32.555394	-117.088553

[1]Avocado locations are accurate to one km to maintain privacy

[2]Selected for culturing

[3]Burned in Canyon 2 Fire (10/9/2017 - 10/18/2017)

[4]Burned in Lilac Fire (12/7/2017-12/16/2017)

[5]Burned in Thomas Fire (12/7/2017-1/12/2017

[6]Site became infested in 2018

Table II. Mean and median richness of culturable fungi and bacteria genera in wood samples collected from FD-ISHB not-attacked trees in infested plots (IN), attacked trees in infested plots (II), and trees in non-infested plots (NN).

	Generic Richness			Trees surveyed	Isolates Recovered
Site-Host Status	Mean ± SD[1]	Median	Range	*n*	
IN	2.73 ± 1.54	2	1 - 9	215	545
II	2.76 ± 1.62	2	1 - 8	171	452
NN	2.54 ± 1.57	2	1 - 8	189	431
Grand Total	2.67 ± 1.57	2		575	1428

[1]Standard Deviation

Table III. *In vitro* interaction outcomes between endophytic fungi and *Fusarium* pathogens. "Dominant Inhibitor" refers to which microbe "won" in the interaction. "Dominant Mechanism" refers to the type of interaction (i.e., antibiosis, competition, coexistence). Values indicate the average (± standard deviation) number of cases among replicate strains in which a given outcome was observed between endophyte and pathogen.

			Dominant Inhibitor			Dominant Mechanism				
							Competition		Coexistence	
Fungal Endophyte	*n* Strains	Isolate Abundance	Endophyte	Pathogen	Mutual Inhibition[1]	Antibiosis	Mycelial Thinning[2]	Partial Replacemet[3]	Mutual Intermingling	No Contact
Aspergillus sp.	1	19	1			1				
Cladosporium cladosporioides	1	3	1			1				
Didymocyrtis brachylaenae	1	33	1			1				
Epicoccum nigrum	2	4	1 ± 0			1 ± 0				
Leptoxyphium kurandae	1	1	1			1				
Pithomyces chartarum	2	2	1 ± 0			1 ± 0				
Penicillium nalgiovense	4	32	0.94 ± 0.13			0.94 ± 0.13			0.06 ± 0.13	
Ascochyta phacae	1	3	0.67		0.33	0.67				
Phaeoacremonium sp.	2	7	0.75 ± 0.35			0.75 ± 0.35			0.25 ± 0.35	
Dothideomycetes	1	1	1			0.50	0.50			
Botryosphaeria parva	8	11	1 ± 0					1 ± 0		
Trichoderma harzianum	2	9	1 ± 0					1 ± 0		
Botryosphaeria iberica	1	2	1					1		
Botryosphaeria obtusa	1	3	1					1		
Fusarium brachygibbosum	1	1	1					1		
Lasiodiplodia gilanensis	1	2	1					1		
Neocucurbitaria salicis-albae	1	4	1					1		
Ulocladium sp.	1	3	1			0.33		0.67		
Cladosporium Group 5	5	56	0.80 ± 0.45		0.03 ± 0.07		0.78 ± 0.36	0.80 ± 0.45	0.17 ± 0.37	
Botryosphaeria sp.	1	3	0.67		0.33			0.67		
Cladosporium Group 1	3	57	0.67 ± 0.58	0.11 ± 0.19		0.33 ± 0.58	0.33 ± 0.38	0.53 ± 0.41	0.22 ± 0.38	
Neosetophoma italica	2	7	0.63 ± 0.18		0.13 ± 0.18	0.50 ± 0	0.38 ± 0.53		0.25 ± 0.35	
Aureobasidium sp. 4b	3	7	0.56 ± 0.10		0.39 ± 0.10		0.80 ± 0.05		0.06 ± 0.10	
Querciphoma carteri	2	8	0.50 ± 0.35		0.25 ± 0.35		0.75 ± 0		0.25 ± 0	
Cladosporium sp.	4	86	0.50 ± 0.43	0.08 ± 0.17	0.33 ± 0.47	0.06 ± 0.13	0.75 ± 0.32	0.17 ± 0.19	0.08 ± 0.17	
Fusicoccum vitifusiforme	1	2		1		1				

[1]Evident through the formation of a barrage between deadlocked colonies, with the exception of *Cladosporium* Group 10 and *Querciphoma carteri*

[2]Effect on pathogen

[3]Effect on endophyte or pathogen

Table III. Continued

			Dominant Inhibitor			Dominant Mechanism				
							Competition		Coexistence	
Fungal Endophyte	*n* Strains	Isolate Abundance	Endophyte	Pathogen	Mutual Inhibition[1]	Antibiosis	Mycelial Thinning[2]	Partial Replacemet[3]	Mutual Intermingling	No Contact
Cladosporium aphidis	1	5		1				1		
Hormonema carpetanum	1	6		1				1		
Aureobasidium melanogenum	2	4	0.25 ± 0.35	0.63 ± 0.53	0.13 ± 0.18		0.38 ± 0.18	0.63 ± 0.53		
Aureobasidium sp. 3	4	8	0.19 ± 0.24	0.48 ± 0.34	0.33 ± 0.12		0.46 ± 0.22	0.56 ± 0.43		
Aureobasidium pullulans	6	43	0.35 ± 0.27	0.42 ± 0.49	0.23 ± 0.26	0.24 ± 0.28	0.33 ± 0.38	0.42 ± 0.49		
Alternaria multiformis	1	2			1					
Aureobasidium sp. 4a	1	2			1		1			
Cladosporium Group 10	1	7			1		1			
Phialemonium sp.	1	2			1		0.50			
Libertasomyces myopori	1	1			1		0.25			
Cladosporium Group 8	1	2			1					
Diaporthe sp.	1	2			1					
Paraconiothyrium brasiliense	1	3			1					
Pleiochaeta carotae	1	1			1					
Alternaria sp.	3	15	0.08 ± 0.14		0.91 ± 0.14		0.25 ± 0.25	0.08 ± 0.14		
Alternaria alternata	17	50	0.01 ± 0.06		0.89 ± 0.21		0.20 ± 0.21	0.11 ± 0.22	0.09 ± 0.17	
Alternaria infectoria	6	31	0.04 ± 0.10		0.88 ± 0.21		0.08 ± 0.13		0.08 ± 0.20	
Acrostalagmus luteoalbus	4	7		0.13 ± 0.25	0.83 ± 0.24	0.13 ± 0.14	0.17 ± 0.24	0.06 ± 0.13	0.04 ± 0.08	
Stemphylium sp.	1	2			0.75		0.25		0.25	
Aureobasidium sp. 2	2	4		0.38 ± 0.53	0.63 ± 0.53		0.25 ± 0.35	0.38 ± 0.53		
Pyricularia caricis	1	1	0.25		0.50		0.75		0.25	
Pseudocamarosporium	1	6	0.25		0.50	0.25	0.50		0.25	
Hermatomyces sp.	1	1			0.50		0.50		0.50	
Alternaria atra	1	1			0.50				0.50	
Cystobasidium slooffiae	1	1		0.50				0.50		0.50
Sarocladium sp. nov.	2	18		0.38 ± 0.53	0.50 ± 0.35	0.13 ± 0.18	0.25 ± 0	0.38 ± 0.53	0.13 ± 0.18	
Brachysporiella navarrica	1	1								1
Didymosphaeria variabile	1	7							1	
Phragmocamarosporium hederae	2	11								1 ± 0

[1]Evident through the formation of a barrage between deadlocked colonies, with the exception of *Cladosporium* Group 10 and *Querciphoma carteri*

[2]Effect on pathogen

[3]Effect on endophyte or pathogen

Table III. Continued

			Dominant Inhibitor			Dominant Mechanism				
							Competition		Coexistence	
Fungal Endophyte	*n* Strains	Isolate Abundance	Endophyte	Pathogen	Mutual Inhibition[1]	Antibiosis	Mycelial Thinning[2]	Partial Replacemet[3]	Mutual Intermingling	No Contact
Clonostachys sp.	3	4			0.17 ± 0.14		0.17 ± 0.14		0.83 ± 0.14	
Populocrescentia forlicesenensis	1	1	0.25				0.25			0.75
Pleurostoma richardsiae	1	1	0.33				0.33		0.67	
Aureobasidium subglaciale	2	3		0.10 ± 0.14	0.35 ± 0.21		0.42 ± 0.12	0.17 ± 0.24	0.55 ± 0.07	
Pleomassaria sp. nov	1	3			0.50				0.50	

[1]Evident through the formation of a barrage between deadlocked colonies, with the exception of *Cladosporium* Group 10 and *Querciphoma carteri*

[2]Effect on pathogen

[3]Effect on endophyte or pathogen

Table IV. *In vitro* interaction outcomes between endophytic bacteria (*E*) and *Fusarium* pathogens (*P*). "Dominant Mechanism" refers to interaction type (i.e., antibiosis, competition). Values are the average (± standard deviation) number of times a given outcome observed between *E* and *P* among replicate strains.

			Dominant Mechanism		Other Interaction		
Bacterial Endophyte	**n Strains**	**Isolate Abundance**	**Antibiosis**	**Competition**	**Neutral**	**Commensal**	**Observation**
Bacillus sp.	4	18	1 ± 0				Inhibited fungal growth
Raoultella terrigena	1	2	1				Inhibited fungal growth
Pantoea agglomerans	5	6	0.75 ± 0.31		0.25		Inhibited fungal growth
Pantoea sp.[1]	10	55	0.50	0.22	0.27 ± 0.36		Inhibited fungal growth, mycelial thinning
Acidovorax sp.	1	2		1			Mycelial thinning
Acinetobacter johnsonii	1	1		1			Stunted radial growth, enhanced filamentation
Brenneria sp.	1	12		1			Mycelial thinning
Gibbsiella quercinecans	1	2		1			Mycelial thinning
Lysinibacillus fusiformis	1	2		1			Stunted radial growth, enhanced filamentation
Novosphingobium resinovorum	1	1		1			Stunted radial growth, mycelial thinning
Pantoea ananatis	1	1		1			Mechanical blocking, reduced growth or enhanced filamentation •Enhanced bacterial biofilm
Stenotrophomonas sp.	4	5		0.88 ± 0.25	0.13		Mycelial thinning
Pseudomonas aeruginosa	1	1		0.83	0.17		Mycelial thinning
Arthrobacter sp.	1	5		0.75			Mycelial thinning
Flavobacterium sp.	3	3		0.69 ± 0.05			Mycelial thinning
Pseudomonas fluorescens[3]	14	273	0.07	0.70	0.23 ± 0.32		Mycelial thinning, mechanical blocking
Erwinia sp.[4]	3	6	0.27	0.64	0.13		Mycelial thinning, mechanical blocking, reduced fungal growth • Enhanced bacterial biofilm
Paenibacillus sp.[2]	8	47				1 ± 0	Enhanced filamentation
Brenneria populi	1	2		0.50		0.50	Reduced (*F. euwallacea*) and enhanced (*F. kuroshium*) filamentation

[1]0.68 ± 0.35 Antibiosis and competition combined

[2]Effect on *Fusarium* spp. potentially commensal

[3]0.77 ± 0.32 Antibiosis and competition combined

[4]0.92 ± 0.14 Antibiosis and competition combined

Table V. Endophytic bacteria in which *in vitro* interactions with *Fusarium* spp. were neutral. Values indicate the average (± standard deviation) number of cases among replicate strains in which a given outcome was observed between endophyte and pathogen.

		Observation		Other Interaction	
Bacterial Endophyte	***n* Strains**	**Mixing**	**No Contact**	**Antagonistic**	**Commensal**
Achromobacter xylosoxidans	1	1			
Lysinibacillus sphaericus	1	1			
Microbacterium sp.	3	1 ± 0			
Pseudarthrobacter phenanthrenivorans	1	1			
Pseudomonas graminis	1	1			
Pseudomonas koreensis	1	1			
Variovorax paradoxus	1	1			
Massilia sp.	1	0.83	0.17		
Pedobacter cryoconitis	1	0.83		0.17	
Staphylococcus hominis	1	0.83		0.17	
Variovorax sp.	3	0.83 ± 0.29	0.10	0.20	
Microbacterium oxydans	2	0.80 ± 0		0.20	
Methylobacterium sp.	8	0.79 ± 0.15		0.21	
Paracoccus caeni	2	0.75 ± 0.35		0.25	
Staphylococcus epidermidis	3	0.75 ± 0.25		0.14	
Stenotrophomonas rhizophila	2	0.71 ± 0.06		0.30	
Brevibacterium epidermidis	2	0.63 ± 0.53		0.38 ± 0.53	
Brenneria salicis	4	0.61 ± 0.44	0.05	0.24	0.10
Enterobacter sp.[1]	2	0.50		0.50	
Pseudomonas orientalis	1	0.17	0.50	0.33	
Curtobacterium flaccumfaciens	1	0.40	0.40		0.20

[1]Variation between strains

Table VI. Linear discriminant functions given by predictive discriminant analysis of microbial communities in samples collected from FD-ISHB infested and non-infested *Salix* spp., *Platanus racemosa,* and *Persea americana.* Coefficients are presented from analyses using taxa recovered from five, ten, and 20 or more trees, respectively.

		Median Coefficients					95% confidence interval				
Microbe		LD1	LD2	LD3	LD4	LD5	LD1	LD2	LD3	LD4	LD5
Analysis using taxa recovered from five or more trees											
Alternaria		0.25	-0.09	-0.15	-0.17	0.06	-0.08—0.46	-1.59—1.87	-1.48—1.47	-1.46—0.92	-1.10—1.18
Aspergillus		0.30	0.37	0.39	0.13	0.16	-0.13—0.66	-2.26—2.62	-1.78—2.64	-1.42—1.90	-2.12—1.51
Aureobasidium	*	0.24	0.17	0.53	0.19	-0	-0.14—0.59	-2.19—2.03	-1.62—1.98	-0.87—1.14	-1.17—1.13
Bacillus	*	0.42	0.57	-0.95	0.66	-0.3	-0.45—1.22	-2.86—3.91	-3.68—3.07	-3.78—4.53	-4.07—3.05
Brenneria	*	0.91	-0.44	-0.45	-0.52	0.22	0.11—1.54	-2.75—2.19	-1.71—2.29	-3.13—2.19	-3.60—2.18
Didymocyrtis	**	-5.4	0.20	-0.23	0.35	0.08	-8.65— -4.26	-0.83—1.65	-2.31—1.43	-2.46—3.19	-2.70—2.39
Erwinia	*	0.66	-0.14	-0.29	-0.17	-0.50	-0.61—1.71	-2.89—4.52	-3.15—3.82	-5.63—5.72	-4.47—4.75
Fusarium		-0.3	0.37	-0.21	-0.11	0.55	-1.00—0.57	-2.56—3.18	-3.03—3.36	-4.57—4.55	-3.91—3.98
Methylobacterium	*	-0.3	0.71	-0.67	-0.24	-0.4	-2.14—0.6	-4.32—3.72	-4.44—4.05	-2.91—3.30	-3.09—2.48
Microbacterium	*	0.11	-0.26	0.56	-0.20	-0.2	-0.60—0.68	-2.06—1.49	-1.58—2.43	-2.39—2.22	-2.37—2.37
Neosetophoma		0.27	-0.26	0.34	-0.47	0.18	-0.26—0.78	-3.66—2.38	-2.55—3.47	-3.31—3.79	-2.68—3.21
Paenibacillus	**	-4.80	0.0004	0.02	-0.10	0.16	-8.37— -3.73	-1.34—0.75	-0.96—1.05	-1.88—1.34	-1.46—1.36
Pantoea	*	0.70	0.02	-0.35	-0.04	0.03	0.25—0.97	-1.66—1.72	-2.07—1.69	-2.23—1.81	-1.70—2.01
Phragmocamarosporium	*	-1.50	-0.16	-0.02	-0.09	-0.2	-3.22—0.11	-1.99—1.13	-2.12—2.01	-3.56—3.35	-3.77—2.21
Pseudomonas	*	0.99	-0.03	-0.05	0.08	0.06	0.44—1.45	-0.93—0.85	-0.91—1.09	-1.13—1.09	-1.08—0.90
Sarocladium	*	0.72	0.23	-1.24	-0.13	-0.1	0.12—1.59	-3.27—3.62	-4.14—4.92	-3.99—3.19	-3.72—3.73
Variovorax	*	0.07	0.08	0.93	0.17	0.14	-0.37—0.63	-3.27—2.45	-3.07—3.52	-2.37—2.35	-2.58—2.21
Yeast		0.24	-0.11	-0.22	0.03	0.18	-0.46—0.75	-1.36—1.23	-1.35—1.49	-1.21—1.41	-1.29—1.82

**Taxa with the strongest influence on group separation

*Taxa with moderate to strong influence on group separation

Table VI. Continued

Microbe		Median Coefficients LD1	LD2	LD3	LD4	LD5	95% confidence interval LD1	LD2	LD3	LD4	LD5
Analysis using taxa recovered from ten or more trees											
Alternaria		0.21	0.34	-0.05	-0.24	-0.1	-0.08—0.37	-1.17—1.69	-1.56—1.65	-1.71—1.51	-1.78—1.51
Aspergillus	*	0.38	1.04	-0.14	0.24	-0	-0.06—0.78	-3.38—2.81	-2.28—3.08	-1.85—1.91	-2.11—2.35
Aureobasidium	*	0.28	1.08	-0.11	0.16	0.05	-0.16—0.54	-2.17—2.31	-1.98—2.00	-1.73—1.70	-1.09—1.38
Bacillus	*	0.57	-0.08	-0.40	0.10	0.01	-0.51—1.44	-3.50—5.44	-4.46—5.53	-5.74—5.08	-4.84—5.09
Brenneria	*	0.86	-0.55	0.19	-0.09	0.30	0.25—1.44	-2.71—2.09	-2.28—2.71	-3.66—3.11	-2.78—2.77
Didymocyrtis	**	-5.4	0.33	-0.27	0.01	-0.1	-7.06— -4.53	-0.48—1.63	-2.31—1.69	-2.33—2.97	-2.59—3.05
Methylobacterium	*	-0.02	2.42	0.04	0.02	-0.5	-1.37—0.66	-4.15—4.37	-5.01—4.12	-2.94—4.05	-2.96—3.48
Microbacterium		0.19	0.21	0.38	-0.34	0.26	-0.62—0.61	-2.01—1.93	-1.59—2.98	-3.02—2.46	-2.20—2.43
Paenibacillus	**	-4.9	0.12	-0.05	-0.06	-0.2	-6.71— -3.86	-1.06—0.97	-1.36—1.43	-1.77—1.31	-1.56—1.80
Pantoea	*	0.62	0.29	-0.16	-0.02	0.05	0.37—1.02	-1.34—1.72	-1.84—1.86	-1.92—1.95	-1.66—1.95
Phragmocamarosporium	*	-1.6	-0.37	-0.01	-0.07	-0.1	-3.02—0.18	-1.55—1.76	-2.70—1.89	-4.25—4.64	-2.64—3.29
Pseudomonas	*	0.92	-0.30	-0.08	0.06	0.10	0.37—1.44	-1.18—1.18	-0.95—0.94	-1.15—1.26	-1.16—1.26
Sarocladium	*	0.68	-0.07	-0.55	-0.11	-0.2	0.18—1.44	-2.70—3.77	-3.50—3.44	-4.82—4.63	-4.32—4.47
Variovorax	*	0.07	-0.53	0.10	0.17	0.08	-0.40—0.44	-2.59—2.23	-3.68—3.57	-2.57—2.56	-2.42—2.81
Yeast		0.15	-0.18	-0.20	0.005	0.06	-0.61—0.66	-0.90—1.04	-1.12—1.60	-1.41—2.59	-1.68—1.82
Analysis using taxa recovered from 20 or more trees											
Alternaria		0.24	0.07	-0.29	0.54	-0	-0.47—0.47	-1.83—2.29	-2.68—2.51	-2.64—2.67	-2.03—1.87
Aureobasidium	*	0.01	0.50	-0.02	-0.02	-0	-0.43—0.52	-2.74—2.71	-2.04—2.41	-1.69—1.82	-1.09—1.09
Didymocyrtis	**	-4.5	-0.10	-0.24	-0.13	0.23	-6.87—6.00	-3.18—1.92	-3.53—3.05	-2.77—2.77	-3.22—3.32
Microbacterium		0.10	0.15	-0.24	-0.03	0.52	-0.49—0.47	-2.22—1.91	-3.26—3.32	-3.39—3.15	-3.60—3.48
Paenibacillus	**	-4.5	0.37	0.16	0.10	-0.5	-6.93—6.08	-1.02—1.41	-1.25—1.61	-1.45—1.39	-1.81—1.65

**Taxa with the strongest influence on group separation

*Taxa with moderate to strong influence on group separation

Table VII. Test classification accuracies for each predictive linear discriminant analysis on testing samples in the present study. Included are accuracy values reflecting differences between groups at random, compared to the median and 95% confidence interval values calculated from the 100 repetitions in each analysis.

			Classification Accuracy		
Classification	*n* Categories	Microbe Isolation Frequency	Expected at Random	Median	95% Confidence Interval
Host-attack status	6	≥ 5 Trees	0.17	0.39	0.33—0.44
		≥ 10 Trees		0.39	0.32—0.46
		≥ 20 Trees		0.39	0.33—0.44
Host within not-attacked Trees	4	≥ 5 Trees	0.25	0.51	0.43—0.58
		≥ 10 Trees		0.52	0.42—0.59
		≥ 20 Trees		0.50	0.43—0.57
Host within attacked trees	3	≥ 5 Trees	0.33	0.74	0.62—0.79
		≥ 10 Trees		0.72	0.64—0.79
		≥ 20 Trees		0.72	0.66—0.79
Attack status: *Salix*	2	≥ 5 Trees	0.50	0.63	0.54—0.71
		≥ 10 Trees		0.60	0.53—0.67
		≥ 20 Trees		0.60	0.53—0.68
Attack status: *Platanus*	2	≥ 5 Trees	0.50	0.57	0.48—0.69
		≥ 10 Trees		0.60	0.44—0.69
		≥ 20 Trees		0.58	0.45—0.67
Attack status: *Persea*	2	≥ 5 Trees	0.50	0.47	0.37—0.56
		≥ 10 Trees		0.47	0.32—0.56
		≥ 20 Trees		0.47	0.38—0.59
Plot status: *Quercus*	2	≥ 5 Trees	0.50	0.61	0.48—0.73
		≥ 10 Trees		0.52	0.42—0.62
		≥ 20 Trees		0.52	0.39—0.61

Table VIII. Linear discriminant functions given by predictive discriminant analyses of microbial communities in host species (*Salix* spp., *Platanus racemosa, Quercus agrifolia,* and *Persea americana*). Differences between host species were analyzed separately for samples collected from FD-ISHB attacked and not-attacked trees in infested plots. Host classification of attacked trees excludes *Quercus*. Coefficients are presented from analyses using taxa recovered from ten or more trees.

		Median Coefficients			95% confidence interval		
Microbe		LD1	LD2	LD3	LD1	LD2	LD3
Classification for not-attacked trees[1]							
Aureobasidium		-0.17	-0.15	0.12	-0.57—0.28	-2.00—2.06	-2.24—2.24
Didymocyrtis	**	5.99	-0.05	0.03	4.77—9.66	-1.02—1.04	-1.17—1.46
Methylobacterium	*	0.72	-1.43	0.31	-0.27—2.25	-3.72—3.23	-3.83—3.92
Paenibacillus	**	5.76	0.01	-0.23	4.45—9.72	-1.49—1.59	-1.73—1.94
Pseudomonas		-0.57	-0.06	-0.07	-0.97—0.05	-1.68—1.53	-1.78—1.94
Variovorax	*	-0.33	1.63	0.09	-0.63— -0.07	-3.59—3.51	-2.71—2.62
Classification for attacked trees							
Aureobasidium	*	0.15	-2.48		-0.14—0.52	-3.95—0.13	
Didymocyrtis	**	-5.55	-0.87		-9.25— -4.02	-2.26—0.57	
Microbacterium	*	-0.22	0.62		-1.95—0.99	-1.65—2.64	
Paenibacillus	**	-5.21	-0.50		-8.13— -3.63	-1.57—0.81	
Pantoea	*	0.62	-1.77		0.14—1.16	-3.01—0.64	
Phragmocamarosporium	*	-1.94	0.75		-4.82—0.08	-0.86—2.41	
Pseudomonas	*	0.80	0.35		0.37—1.42	-1.51—1.63	

[1]*Aureobasidium* had a stronger influence in models with taxa recovered from 5 or more 20 or more trees (see Table SIII)

**Taxa with the strongest influence on group separation

*Taxa with moderate to strong influence on group separation

Table IX. Linear discriminant functions given by predictive discriminant analyses of microbial communities in samples collected from FD-ISHB attacked and not-attacked trees. Differences in attack status were analyzed separately for each host species (*Salix* spp., *Platanus racemosa,* and *Persea americana*). Coefficients (Coeff.) are presented from analyses using taxa recovered from ten or more trees.

	Salix			*Platanus*			*Persea*		
Microbe		Median LD1 Coeff.	95% confidence interval		Median LD1 Coeff.	95% confidence interval		Median LD1 Coeff.	95% confidence interval
Alternaria	*	-1.02	-1.95—0.31	*	1.13	-0.77—3.05			
Aureobasidium	**	-1.95	-2.61— -0.85	**	-1.35	-2.20— -0.41			
Cladosporium					0.56	-0.80—1.64		0.09	-1.80—1.72
Didymocyrtis							**	-1.12	-3.55—1.02
Microbacterium	**	-1.48	-3.89—2.71				**	1.87	-0.58—4.03
Pantoea		-0.30	-1.70—0.97	**	1.40	-0.90—2.59			
Paenibacillus								0.04	-2.43—2.02
Phragmocamarosporium								0.17	-2.87—3.52
Pseudomonas		0.67	-0.64—1.60					-0.06	-1.74—2.04
Sarocladium	**	2.06	-1.77—5.43						
Yeast				*	-1.05	-2.56—1.29			

**Taxa with the strongest influence on group separation
*Taxa with moderate to strong influence on group separation

Table X. Linear discriminant function given by predictive discriminant analysis of microbial communities isolated from *Quercus agrifolia* in FD-ISHB infested and non-infested plots. Coefficients are presented from analyses using taxa recovered from ten or more trees.

Microbe		Median LD1 Coefficients	95% confidence interval
Alternaria	**	1.77	0.01—3.22
Aureobasidium	**	-1.26	-2.81—1.39
Cladosporium		-0.27	-1.60—1.33
Pseudomonas	*	-0.96	-1.98—0.68

**Taxa with the strongest influence on group separation
*Taxa with moderate to strong influence on group separation

Table SI. Reference species from GenBank used for phylogenetic analysis-based species identification of fungal endophytes isolated from wood cores in this study.

Species	GenBank Accession Number
Acrocalymma fici	NR137953.1
Albatrellus citrinus	NR132801.1
Amylostereum chailletii	AF506406.1
Amylostereum chailletii	MH861504.1
Angustimassarina acerina	NR138406.1
Angustimassarina camporesii	NR168223.1
Angustimassarina populi	KP899137.1
Angustimassarina populi	MF409170.1
Angustimassarina populi	MG763958.1
Angustimassarina quercicola	KP899133.1
Ascochyta medicaginicola	GU237749.1
Ascochyta nigripycnidia	GU237756.1
Ascochyta phacae	NR135942.1
Ascochyta pisi	GU237763.1
Asteromassaria berberidicola	MH863491.1
Asteromassaria olivaceohirta	AY313953.1
Aureobasidium melanogenum	KT693729.1
Aureobasidium melanogenum	MG589133.1
Aureobasidium melanogenum	MT119458.1
Aureobasidium melanogenum	MT119459.1
Aureobasidium melanogenum	MT119460.1
Aureobasidium melanogenum	NR159598.1
Aureobasidium namibiae	KT693730.1
Aureobasidium namibiae	MF398842.1
Aureobasidium namibiae	MK782285.1
Aureobasidium namibiae	MK782286.1
Aureobasidium namibiae	MK782288.1
Aureobasidium namibiae	MK782292.1
Aureobasidium namibiae	MK782297.1
Aureobasidium namibiae	MN994074.1
Aureobasidium namibiae	MT325792.1
Aureobasidium namibiae	NR147362.1
Aureobasidium pullulans	JN051490.1
Aureobasidium pullulans	JX188091.1
Aureobasidium pullulans	JX188092.1
Aureobasidium pullulans	KC345715.1
Aureobasidium pullulans	KF801105.1
Aureobasidium pullulans	KJ825980.1

Table SI. Continued.

Species	GenBank Accession Number
Aureobasidium pullulans	KP204332.1
Aureobasidium pullulans	KT693709.1
Aureobasidium pullulans	KT898629.1
Aureobasidium pullulans	KT898722.1
Aureobasidium pullulans	KU751863.1
Aureobasidium pullulans	MH864403.1
Aureobasidium pullulans	MK782479.1
Aureobasidium pullulans	MK782488.1
Aureobasidium pullulans	MN371874.1
Aureobasidium pullulans	MN922047.1
Aureobasidium pullulans	MN922054.1
Aureobasidium pullulans	MN922087.1
Aureobasidium pullulans	MN922111.1
Aureobasidium pullulans	MN922113.1
Aureobasidium pullulans	MT000590.1
Aureobasidium pullulans	MT035961.1
Aureobasidium pullulans	NR144909.1
Aureobasidium subglaciale	KT693735.1
Aureobasidium subglaciale	NR147323.1
Auriscalpium vulgare	MK211170.1
Bannoa bischofiae	NR153592.1
Bannoa hahajimensis	NR121198.1
Biatoropsis hafellneri	NR154873.1
Blistum tomentosum	AB208109.1
Bondarzewia montana	MH857893.1
Botryosphaeria lutea	AY259091.1
Botryosphaeria obtusa	AY259094.2
Bullera alba	KY101819.1
Bullera penniseticola	KY101792.1
Bullera unica	KY101799.1
Bulleribasidium oberjochense	NR121467.1
Bulleromyces albus	KC460892.1
Capnodium coffeicola	KU358921.1
Chaetocapnodium placitae	NR132831.1
Chaetodermella luna	KP814482.1
Cladosporium aggregatocicatricatum	NR152300.1
Cladosporium allicinum	MH863126.1
Cladosporium allicinum	NR152266.1
Cladosporium angustisporum	MH863862.1
Cladosporium angustisporum	NR111530.1

Table SI. Continued.

Species	GenBank Accession Number
Cladosporium aphidis	MK347815.1
Cladosporium aphidis	MK513829.1
Cladosporium aphidis	NR120010.1
Cladosporium austrohemisphaericum	MF472935.1
Cladosporium austrohemisphaericum	MK111441.1
Cladosporium austrohemisphaericum	MT520550.1
Cladosporium austrohemisphaericum	NR152289.1
Cladosporium cladosporioides	KF938442.1
Cladosporium cladosporioides	KU743946.1
Cladosporium cladosporioides	KY563276.1
Cladosporium cladosporioides	LN834358.1
Cladosporium cladosporioides	MG385086.1
Cladosporium cladosporioides	MH395154.1
Cladosporium cladosporioides	MH647073.1
Cladosporium cladosporioides	NR119839.1
Cladosporium delicatulum	MT548673.1
Cladosporium dominicanum	DQ780353.1
Cladosporium dominicanum	MK336562.1
Cladosporium dominicanum	NR119603.1
Cladosporium halotolerans	KU059910.1
Cladosporium halotolerans	MF473002.1
Cladosporium halotolerans	MF473009.1
Cladosporium halotolerans	NR119605.1
Cladosporium herbarum	MT524447.1
Cladosporium limoniforme	MN826827.1
Cladosporium oryzae	MK140687.1
Cladosporium oxysporum	KY400090.1
Cladosporium oxysporum	MK140684.1
Cladosporium oxysporum	NR152267.1
Cladosporium perangustum	MH863874.1
Cladosporium perangustum	MT427730.1
Cladosporium perangustum	MT466522.1
Cladosporium perangustum	NR119851.1
Cladosporium phaenocomae	NR119950.1
Cladosporium psychrotolerans	MF473224.1
Cladosporium psychrotolerans	NR119607.1
Cladosporium pulvericola	MF473226.1
Cladosporium pulvericola	MF473227.1
Cladosporium pulvericola	MF473228.1
Cladosporium ramotenellum	KU933442.1

Table SI. Continued.

Species	GenBank Accession Number
Cladosporium ramotenellum	MH102075.1
Cladosporium ramotenellum	MK267417.1
Cladosporium ramotenellum	MK722198.1
Cladosporium ramotenellum	MK910072.1
Cladosporium ramotenellum	MN636231.1
Cladosporium ramotenellum	MT223790.1
Cladosporium ramotenellum	MT312770.1
Cladosporium ramotenellum	NR119658.1
Cladosporium rhusicola	NR152299.1
Cladosporium sloanii	MF473253.1
Cladosporium sphaerospermum	LT821488.1
Cladosporium sphaerospermum	MF473270.1
Cladosporium sphaerospermum	MG228420.1
Cladosporium sphaerospermum	MK332486.1
Cladosporium sphaerospermum	MN518383.1
Cladosporium sphaerospermum	MT520554.1
Cladosporium sphaerospermum	MT520602.1
Cladosporium sphaerospermum	MT534178.1
Cladosporium tenellum	MH205932.1
Cladosporium tenellum	MH863130.1
Cladosporium tenuissimum	MK140685.1
Cladosporium tenuissimum	MT497424.1
Cladosporium tenuissimum	MT497425.1
Cladosporium varians	MH863938.1
Cladosporium varians	NR119856.1
Cladosporium velox	DQ780361.1
Cladosporium velox	MF473308.1
Cladosporium velox	MF473309.1
Cladosporium velox	MF473310.1
Cladosporium velox	MK814792.1
Cladosporium velox	MK814793.1
Cladosporium velox	MK814794.1
Comoclathris rosarum	NR157507.1
Conidiocarpus betle	MN749294.1
Conidiocarpus betle	MN749295.1
Conidiocarpus plumeriae	KU358919.1
Conidiocarpus siamensis	KU358926.1
Coprinellus amphithallus	HQ846978.1
Coprinellus amphithallus	KT804055.1
Coprinellus angulatus	MN096853.1

Table SI. Continued.

Species	GenBank Accession Number
Coprinellus angulatus	MN121285.1
Coprinellus aureogranulatus	GQ249274.1
Coprinellus aureogranulatus	MH862611.1
Coprinellus bisporiger	HQ846974.1
Coprinellus bisporus	GU227704.1
Coprinellus bisporus	MH856988.1
Coprinellus brevisetulosus	GU227709.1
Coprinellus brevisetulosus	GU227711.1
Coprinellus callinus	HQ847003.1
Coprinellus callinus	MH856994.1
Coprinellus callinus	MH868510.1
Coprinellus canistri	HQ846985.1
Coprinellus canistri	KT804062.1
Coprinellus christianopolitanus	KC992944.1
Coprinellus christianopolitanus	NR166369.1
Coprinellus congregatus	JN943131.1
Coprinellus congregatus	MH856803.1
Coprinellus curtus	AY461824.1
Coprinellus curtus	KT804095.1
Coprinellus deminutus	JN159572.1
Coprinellus disseminatus	MK077874.1
Coprinellus disseminatus	MK077878.1
Coprinellus domesticus	AB817976.1
Coprinellus ellisii	MH858016.1
Coprinellus ellisii	MK460875.1
Coprinellus eurysporus	HQ846992.1
Coprinellus eurysporus	JN943114.1
Coprinellus flocculosus	KM403380.1
Coprinellus flocculosus	MK656240.1
Coprinellus heptemerus	JN159553.1
Coprinellus heptemerus	KC176321.1
Coprinellus heterosetulosus	MH856805.1
Coprinellus heterosetulosus	MH856806.1
Coprinellus heterothrix	FM878018.1
Coprinellus hiascens	MH856807.1
Coprinellus hiascens	MH856808.1
Coprinellus impatiens	FM163177.1
Coprinellus impatiens	MH856810.1
Coprinellus marculentus	MH856481.1
Coprinellus micaceus	FJ850969.1

Table SI. Continued.

Species	GenBank Accession Number
Coprinellus micaceus	HM240519.1
Coprinellus mitrinodulisporum	HQ180171.1
Coprinellus pellucidus	KR869758.1
Coprinellus pellucidus	MH856811.1
Coprinellus plagioporus	MH856812.1
Coprinellus plagioporus	MH856816.1
Coprinellus radians	HM997120.1
Coprinellus radians	KM272008.1
Coprinellus radicellus	GU227716.1
Coprinellus radicellus	GU227719.1
Coprinellus saccharinus	MG696612.1
Coprinellus sassii	FN396101.1
Coprinellus sassii	MH856817.1
Coprinellus sclerocystidiosus	HQ846991.1
Coprinellus sclerocystidiosus	NR164277.1
Coprinellus silvaticus	KC992943.1
Coprinellus subdisseminatus	MH856997.1
Coprinellus subdisseminatus	MH857000.1
Coprinellus subimpatiens	MH857004.1
Coprinellus subimpatiens	MH868526.1
Coprinellus subpurpureus	MH856824.1
Coprinellus subpurpureus	MH856830.1
Coprinellus truncorum	FM878006.1
Coprinellus truncorum	FM878007.1
Coprinellus velatopruinatus	HQ847002.1
Coprinellus velatopruinatus	MK843938.1
Coprinellus verrucispermus	AY521250.1
Coprinellus verrucispermus	MN523239.1
Coprinellus xanthothrix	MK573918.1
Coprinus doverii	HQ846983.1
Coprinus pseudoamphithallus	HQ846973.1
Coprinus radians	AF345822.1
Coprinus silvaticus	EU520144.1
Cucurbitaria berberidis	NR153946.1
Cucurbitaria oromediterranea	MF795763.1
Curreya austroafricana	HQ428123.1
Curreya grandicipis	JN712456.1
Curreya pityophila	MH855249.1
Curreya pityophila	MH859500.1
Cyrenella elegans	KR075687.1

Table SI. Continued.

Species	GenBank Accession Number
Cyrenella elegans	NR145383.1
Cystobasidium calyptogenae	KY103129.1
Cystobasidium fimetarium	KP053250.1
Cystobasidium laryngis	KY103133.1
Cystobasidium lysinophilum	MT337408.1
Cystobasidium minutum	NR149346.1
Cystobasidium pallidum	KY103146.1
Cystobasidium pinicola	KY103147.1
Cystobasidium psychroaquaticum	KY103148.1
Cystobasidium ritchiei	NR154854.1
Cystobasidium slooffiae	KY103150.1
Delphinella abietis	KX364384.1
Delphinella balsameae	KY997059.1
Delphinella strobiligena	MH860318.1
Dendrothyrium longisporum	JX496115.1
Dendrothyrium longisporum	MH861658.1
Dentipellis coniferarum	NR132865.1
Didymocyrtis banksiae	KY979757.1
Didymocyrtis banksiae	NR154037.1
Didymocyrtis brachylaenae	NR165522.1
Didymocyrtis slaptoniensis	KT383842.1
Didymocyrtis trassii	MG519614.1
Didymosphaeria variabile	MH860201.1
Didymosphaeria variabile	MH860405.1
Didymosphaeria variabile	NR137006.1
Diplodia corticola	NR111152.1
Diplodia mutila	NR144906.1
Diplodia rosacearum	MG015747.1
Diplodia seriata	NR111151.1
Dothiora cactacearum	NR155064.1
Dothiora cannabinae	NR144904.1
Dothiora europaea	NR145339.1
Dothiora prunorum	NR138366.1
Dothiora rhamni-alpinae	NR155043.1
Dothiorella iberica	NR111165.1
Echinodontium tinctorium	AF506430.1
Ectophoma multirostrata	NR158226.1
Ectophoma pomi	NR158236.1
Emarellia grisea	LT726708.1
Epicoccum nigrum	FJ424240.1

Table SI. Continued.

Species	GenBank Accession Number
Epicoccum nigrum	FJ424241.1
Epicoccum thailandicum	NR152926.1
Epicoccum tritici	KX926426.1
Erythrobasidium elongatum	NR73306.1
Erythrobasidium hasegawianum	NR111008.1
Erythrobasidium yunnanense	NR155098.1
Falciformispora aquatica	NR168785.1
Falciformispora senegalensis	MH861195.1
Fissuroma maculans	NR120003.1
Fumiglobus pieridicola	NR153985.1
Gloeocystidiellum porosum	AY048881.1
Gloeohypochnicium analogum	GQ411521.1
Halojulella avicenniae	MK028713.1
Hannaella coprosmae	NR165939.1
Hannaella oryzae	NR165938.1
Hannaella pagnoccae	KC169793.1
Hannaella zeae	NR144771.1
Haptocillium glocklingiae	NR137654.1
Harposporium cylindrosporum	MH861596.1
Harposporium harposporiferum	NR160171.1
Hasegawazyma lactosa	FJ515187.1
Hasegawazyma lactosa	NR73295.1
Hirsutella liboensis	NR166545.1
Hirsutella rhossiliensis	NR145063.1
Hirsutella uncinata	NR111154.1
Hirsutella vermicola	NR137547.1
Holtermannia corniformis	GU937755.1
Hormonema carpetanum	AY616210.1
Hormonema macrosporum	NR145340.1
Hormonema viticola	NR137620.1
Hybogaster giganteus	KR230053.1
Hymenostilbe odonatae	AB104725.1
Katumotoa bambusicola	NR154103.1
Keissleriella dactylidis	NR155219.1
Keissleriella quadriseptata	NR145135.1
Kwoniella botswanensis	NR119822.1
Lachnocladium brasiliense	MH260037.1
Lasiodiplodia gilanensis	NR147328.1
Lasiodiplodia theobromae	NR111174.1
Lentithecium aquaticum	NR160229.1

Table SI. Continued.

Species	GenBank Accession Number
Lentithecium carbonneanum	NR158534.1
Lentithecium clioninum	NR154137.1
Lentithecium pseudoclioninum	NR154108.1
Leptoxyphium fumago	MT223811.1
Leptoxyphium kurandae	JF951150.1
Leptoxyphium madagascariense	NR137731.1
Libertasomyces aloeticus	MK876395.1
Libertasomyces aloeticus	NR165566.1
Libertasomyces myopori	NR145200.1
Libertasomyces platani	NR155336.1
Libertasomyces quercus	NR155337.1
Lophiostoma multiseptatum	NR138018.1
Lophiostoma rugulosum	MH863273.1
Lophiostoma rugulosum	NR160228.1
Massaria campestris	NR137583.1
Massaria mediterranea	NR137764.1
Massarina pandanicola	NR164265.1
Medicopsis romeroi	NR130697.1
Melanomma japonicum	NR154215.1
Microsphaeropsis arundinis	KX463004.1
Microsphaeropsis arundinis	MH236168.1
Microsphaeropsis olivacea	MH685169.1
Microsphaeropsis olivacea	MH793434.1
Microsphaeropsis ononidicola	MG967670.1
Microsphaeropsis spartii-juncei	NR160346.1
Microxyphium leptospermi	MH855514.1
Montagnula aloes	NR111757.1
Murilentithecium clematidis	NR154174.1
Murilentithecium lonicerae	NR164442.1
Murispora hawksworthii	NR138414.1
Muritestudina chiangraiensis	NR156402.1
Naohidea sebacea	DQ911616.1
Naohidea sebacea	NR121324.1
Neoastrosphaeriella krabiensis	NR120004.1
Neocucurbitaria acanthocladae	NR156354.1
Neocucurbitaria acerina	NR154254.1
Neocucurbitaria prunicola	NR166273.1
Neocucurbitaria salicis-albae	NR163365.1
Neofusicoccum parvum	NR119487.1
Neofusicoccum vitifusiforme	MH862869.1

Table SI. Continued.

Species	GenBank Accession Number
Neoophiosphaerella sasicola	NR154263.1
Neophaeosphaeria agaves	NR137833.1
Neophaeosphaeria filamentosa	JF740259.1
Neoroussoella entadae	NR163325.1
Neoroussoella leucaenae	NR165226.1
Neoroussoella lignicola	KU314953.1
Neosetophoma italica	KP711356.1
Neosetophoma italica	LC206631.1
Neosetophoma samarorum	KF251162.1
Neosetophoma samarorum	MH862569.1
Neosetophoma shoemakeri	MG844346.1
Neothyrostroma encephalarti	NR166314.1
Nodulosphaeria thalictri	NR168786.1
Ophiocordyceps sphecocephala	AY646402.1
Papiliotrema siamensis	NR155608.1
Paraconiothyrium archidendri	MH861045.1
Paraconiothyrium brasiliense	LC489893.1
Paraconiothyrium brasiliense	MH857941.1
Paraconiothyrium brasiliense	MH863203.1
Paraconiothyrium estuarinum	MH862842.1
Paraisaria orthopterorum	NR165221.1
Paraisaria phuwiangensis	NR165224.1
Paraisaria yodhathaii	NR165219.1
Peniophora crassitunicata	MH862292.1
Phaeosphaeria breonadiae	NR155675.1
Phaeosphaeria podocarpi	NR137933.1
Phaeosphaeria sinensis	MK347803.1
Phaeosphaeria sinensis	NR163350.1
Phaeosphaeriopsis agapanthi	NR145197.1
Phaeosphaeriopsis grevilleae	NR164457.1
Phaeosphaeriopsis pseudoagavacearum	NR164458.1
Phoma aloes	NR137837.1
Phoma herbarum	MH855910.1
Phoma schachtii	NR137713.1
Phragmocamarosporium hederae	MK359435.1
Pithomyces chartarum	MH861960.1
Pleiochaeta carotae	NR154371.1
Pleiochaeta setosa	KR536610.1
Pleiochaeta setosa	MH854808.1
Pleomassaria acericola	MH863515.1

Table SI. Continued.

Species	GenBank Accession Number
Pleomassaria siparia	MH860853.1
Poaceascoma helicoides	NR154317.1
Podocarpomyces knysnanus	MN562155.1
Polycephalomyces sinensis	NR119928.1
Polycephalomyces yunnanensis	KF977849.1
Populocrescentia forlicesenensis	NR154326.1
Preussia aemulans	MH858743.1
Preussia subticinensis	MH858931.1
Pseudocamarosporium propinquum	NR154309.1
Pseudomassariosphaeria bromicola	NR164235.1
Pseudomurilentithecium camporesii	NR168228.1
Pseudoroussoella chromolaenae	NR168861.1
Pseudotrichia thailandica	NR138405.1
Purpureocillium lavendulum	MH864976.1
Purpureocillium lavendulum	NR166039.1
Purpureocillium lilacinum	MH855800.1
Purpureocillium lilacinum	NR165946.1
Pyrenochaeta nobilis	NR103598.1
Querciphoma carteri	KF251209.1
Querciphoma carteri	KF251210.1
Readerielliopsis fuscoporiae	NR137978.1
Rhodotorula dairenensis	KY104735.1
Rhodotorula evergladensis	NR137709.1
Roussoella neopustulans	NR155715.1
Roussoella siamensis	NR155716.1
Roussoella thailandica	NR155717.1
Roussoella verrucispora	NR155714.1
Roussoellopsis macrospora	KJ739604.1
Russula sarnarii	KY284154.1
Saccothecium rubi	NR148096.1
Sakaguchia cladiensis	KY105299.1
Sakaguchia dacryoidea	KY105301.1
Sakaguchia lamellibrachiae	KY105306.1
Sakaguchia meli	FJ807683.1
Sakaguchia oryzae	KY105307.1
Schizophyllum commune	KX363707.1
Sclerostagonospora cycadis	NR160231.1
Sclerostagonospora ericae	NR145199.1
Sclerostagonospora lathyri	NR158956.1
Sclerostagonospora rosae	NR157541.1

Table SI. Continued.

Species	GenBank Accession Number
Scorias mangiferae	NR154422.1
Septoriella oudemansii	KR873250.1
Septoriella oudemansii	MN966618.1
Septoriella phragmitis	NR132926.1
Setoarthopyrenia chromolaenae	NR168860.1
Setoseptoria arundelensis	NR157545.1
Setoseptoria magniarundinacea	NR154457.1
Sirotrema translucens	LC203431.1
Splanchnonema platani	MH855894.1
Splanchnonema pupula	MH863514.1
Sporobolomyces patagonicus	NR137666.1
Sporormiella isomera	MH860653.1
Stagonospora duoseptata	MH866088.1
Stagonospora lomandrae	NR156671.1
Stagonospora perfecta	NR138388.1
Stagonospora tainanensis	NR155769.1
Stemphylium alfalfae	AF442775.1
Stemphylium botryosum	NR163547.1
Stemphylium lycopersici	MH863236.1
Stemphylium mali	MH863225.1
Stemphylium solani	NR154934.1
Stemphylium vesicarium	MH863402.1
Teichospora mariae	KU601583.1
Teichospora melanommoides	NR154632.1
Teichospora rubriostiolata	NR154634.1
Teichospora trabicola	NR154635.1
Tetraploa nagasakiensis	NR119403.1
Tetraploa yakushimensis	NR119405.1
Tolypocladium nubicola	MH861780.1
Tolypocladium parasiticum	MH861597.1
Tolypocladium tundrense	MH861781.1
Towyspora aestuari	NR148095.1
Trematosphaeria grisea	NR132039.1
Trichomerium deniquelatum	NR132965.1
Trichomerium dioscoreae	NR137946.1
Trichomerium eucalypti	NR156672.1
Trichomerium foliicola	NR144963.1
Trimorphomyces sakaeraticus	NR77088.1
Tsuchiyaea wingfieldii	AF444327.1
Ulocladium dauci	FJ266484.1

Table SI. Continued.

Species	GenBank Accession Number
Ulocladium oudemansii	FJ266488.1
Ulocladium sorghi	MH864494.1
Ulocladium zantedeschiae	MH864493.1
Venturia saliciperda	NR168752.1

Table SII. Counts of microbial taxa isolated across hosts.

		Alnus (n =14)			*Persea* (n =96)			*Platanus* (n =132)			*Populus* (n=33)			*Quercus* (n= 75)			*Salix* (n = 224)			
Site/Tree Status	Host Species Site/Tree Status	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	Grand
n Trees Sampled	n Trees Sampled	(5)	(5)	(4)	(34)	(36)	(26)	(57)	(35)	(40)	(12)	(7)	(14)	(36)	(3)	(36)	(71)	(86)	(67)	Total
Bacteria																				
Order	**Family**	**Genus**																		
Pseudomonadale	Pseudomonadaceae	*Pseudomonas*	3	3	4	10	8	12	41	21	28	8	6	12	21	2	22	45	64	46	356
Actinomycetales	Microbacteriaceae	*Microbacterium*	1		1	4	7	10	4	1	1	2		1	4	1	1	6	5	8	57
Enterobacterales	Erwiniaceae	*Pantoea*							8	7		1		2	4	1	1	12	12	8	56
Bacillales	Paenibacillaceae	*Paenibacillus*				17	20	9													46
Burkholderiales	Comamonadaceae	*Variovorax*							6	1		1			6	1		1	5	2	23
Bacillales	Bacillaceae	*Bacillus*				1		2		1	1						5	1	2	3	16
Rhizobiales	Methylobacteriaceae	*Methylobacterium*				1			1		1	1					1	8		1	14
Enterobacterales	Pectobacteriaceae	*Brenneria*					1			1				1	1			3	6		13
Bacillales	Bacillaceae	*Lysinibacillus*				2	2	2							2						8
Xanthomonadale	Xanthomonadaceae	*Stenotrophomonas*				1										1		1	3	1	7
Enterobacterales	Erwiniaceae	*Erwinia*							1	2						1		1	1		6
Bacillales	Staphylococcaceae	*Staphylococcus*									1							1	2	1	5
Actinomycetales	Micrococcaceae	*Arthrobacter*									1				2				1	1	5
Actinomycetales	Brevibacteriaceae	*Brevibacterium*								1									1	2	4
Burkholderiales	Alcaligenaceae	*Achromobacter*							1	1									1		3
Actinomycetales	Microbacteriaceae	*Curtobacterium*										1			1			1			3
Flavobacteriales	Flavobacteriaceae	*Enterobacter*											1						2		3
Flavobacteriales	Flavobacteriaceae	*Flavobacterium*									1						1			1	3
Actinomycetales	Micrococcaceae	*Pseudarthrobacter*							1									1		1	3
Burkholderiales	Comamonadaceae	*Acidovorax*																2			2
Burkholderiales	Comamonadaceae	*Delftia*							1							1					2
Enterobacterales	Enterobacteriaceae	*Gibbsiella*																	2		2
Rhodobacterales	Rhodobacteraceae	*Paracoccus*					1			1											2
Sphingobacteriale	Sphingobacteriaceae	*Pedobacter*																2			2

Table SII. Continued

		Host Species	*Alnus* (n =14)			*Persea* (n =96)			*Platanus* (n =132)			*Populus* (n=33)			*Quercus* (n= 75)			*Salix* (n = 224)			
Site/Tree Status		Site/Tree Stat	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	Grand
n Trees Sampled		n Trees Sample	(5)	(5)	(4)	(34)	(36)	(26)	(57)	(35)	(40)	(12)	(7)	(14)	(36)	(3)	(36)	(71)	(86)	(67)	Total
Bacteria																					
Order	**Family**	**Genus**																			
Enterobacterales	Enterobacteriaceae	*Raoultella*																	2		2
Pseudomonadale	Moraxellaceae	*Acinetobacter*				1															1
Actinomycetales	Actinomycetaceae	*Actinomyces*	1																		1
Bacillales	Bacillaceae	*Anoxybacillus*									1										1
Burkholderiales	Alcaligenaceae	*Bordetella*				1															1
Bacillales	Paenibacillaceae	*Brevibacillus*												1							1
Burkholderiales	Oxalobacteraceae	*Herbaspirillum*				1															1
Burkholderiales	Oxalobacteraceae	*Massilia*															1				1
Sphingomonadal	Sphingomonadaceae	*Novosphingobium*								1											1
Enterobacterales	Enterobacteriaceae	*Rahnella*																	1		1
Actinomycetales	Microbacteriaceae	*Rathayibacter*					1														1
Rhodospirillales	Acetobacteraceae	*Roseococcus*				1															1
Rhodospirillales	Acetobacteraceae	*Roseomonas*					1														1
Actinomycetales	Actinomycetaceae	*Streptomyces*						1													1
		Unclassified													1						1
Subtotal		**Subtotal**	**5**	**3**	**5**	**40**	**41**	**36**	**64**	**38**	**35**	**14**	**7**	**17**	**41**	**8**	**32**	**85**	**##**	**75**	**657**

Table SII. Continued

Fungi		Host Species	*Alnus* (n =14)			*Persea* (n =96)			*Platanus* (n =132)			*Populus* (n=33)			*Quercus* (n= 75)			*Salix* (n = 224)			
		Site/Tree Status	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	Grand
Order	**Family**	n Trees Sample	(5)	(5)	(4)	(34)	(36)	(26)	(57)	(35)	(40)	(12)	(7)	(14)	(36)	(3)	(36)	(71)	(86)	(67)	Total
		Genus																			
Capnodiales	Davidiellaceae	*Cladosporium*	1	2		12	14	6	26	17	8	5	4	5	13	1	10	25	43	19	211
Dothideales	Dothioraceae	*Aureobasidium*		2		1	1		21	6	11	1	2	5	4	1	7	18	7	10	97
Pleosporales	Pleosporaceae	*Alternaria*		1		2	2	2	8	6	5	2	3	5	7	1	2	14	8	11	79
		Unclassified Yea				3	1	1	7	2	3	1		2	1		2	5	11	1	40
Pleosporales	Phaeosphaeriaceae	*Didymocyrtis*				11	9	13													33
Eurotiales	Trichocomaceae	*Penicillium*				2	2		1	3	3				4	1	1	4	6	5	32
Botryosphaeriales	Botryosphaeriaceae	*Botryosphaeria*		1		2	1		2	1	1			1				4	6	3	22
Pleosporales	Lentitheciaceae	*Phragmocamarosporium*				3	5	8									1		2	1	20
Eurotiales	Trichocomaceae	*Aspergillus*				1			4	1			1		3			5	2	2	19
Cystobasidiales	Cystobasidiaceae	*Cystobasidium*				2	1		3	2		1	1		1			1	5	2	19
Hypocreales	Sarocladiaceae	*Sarocladium*	1							1	2				2	1	2	2	4	4	19
Pleosporales	Phaeosphaeriaceae	*Neosetophoma*					1		2			1	1	1				1	2	2	11
Hypocreales	Nectriaceae	*Fusarium*				2		1						1	1				1	3	9
Hypocreales	Hypocreaceae	*Trichoderma*						1	1					1	1			1	2	2	9
Pleosporales	Leptosphaeriaceae	*Querciphoma*							1						3	1	1		1	1	8
Pleosporales	Phaeosphaeriaceae	*Didymosphaeria*							1					1			1	2		2	7
Diaporthales	Togniniaceae	*Phaeoacremonii*				2	2											1	2		7
Hypocreales	Hypocreaceae	*Acrostalagmus*					2						1					1	1	1	6
Dothideales	Dothioraceae	*Hormonema*							1				1	1						3	6
Pleosporales	Didymosphaeriaceae	*Pseudocamarosporium*										2			1				2	1	6
		Ascomycete 1						5													5
Pleosporales	Didymosphaeriaceae	*Dendrothyrium*												1			1	1	1	1	5
Tremellales		*Hannaella*							2	1		1							1		5
Pleosporales	Cucurbitariaceae	*Cucurbitariaceae*								1									1	2	4
Diaporthales	Diaporthaceae	*Diaporthe*							1									2	1		4
Pleosporales	Didymellaceae	*Epicoccum*			1	1			1	1											4

Table SII. Continued

		Host Species	*Alnus* (n =14)			*Persea* (n =96)			*Platanus* (n =132)			*Populus* (n=33)			*Quercus* (n= 75)			*Salix* (n = 224)			
Fungi		Site/Tree Status	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	Grand
Order	**Family**	n Trees Sample	(5)	(5)	(4)	(34)	(36)	(26)	(57)	(35)	(40)	(12)	(7)	(14)	(36)	(3)	(36)	(71)	(86)	(67)	Total
Erythrobasidiales	Erythrobasidiaceae	*Erythrobasidium*																	4		4
Xylariales	Apiosporaceae	*Arthrinium*									1		1						1		3
Pleosporales	Didymellaceae	*Ascochyta*								1									1	1	3
Hypocreales	Bionectriaceae	*Clonostachys*							1									2			3
Pleosporales	Didymellaceae	*Ectophoma*						2							1						3
Pleosporales	Cucurbitariaceae	*Neocucurbitaria*								1				1					1		3
Pleosporales	Pleomassariaceae	*Pleomassaria*				2	1														3
Xylariales	Amphisphaeriaceae	*Truncatella*																1	2		3
Pleosporales	Pleosporaceae	*Ulocladium*						1										2			3
Hypocreales	Hypocreaceae	*Acremonium*							1											1	2
Agaricales	Psathyrellaceae	*Coprinellus*				1	1														2
Botryosphaeriales	Botryosphaeriaceae	*Fusicoccum*																1	1		2
Botryosphaeriales	Botryosphaeriaceae	*Lasiodiplodia*					2														2
Pleosporales	Phaeosphaeriaceae	*Nodulosphaeria*										1								1	2
Hypocreales	Ophiocordycipitacea	*Ophiocordycipitaceae*									1						1				2
Pleosporales	Phaeosphaeriaceae	*Paraconiothyriur*													1				1		2
Sordariales	Cephalothecaceae	*Phialemonium*								1									1		2
Pleosporales	Pleosporaceae	*Pithomyces*										1						1			2
Sporidiobolales	Sporidiobolaceae	*Rhodotorula*														1			1		2
Amphisphaeriales	Sporocadaceae	*Seimatosporium*																	1	1	2
Pleosporales	Phaeosphaeriaceae	*Septoriella*				1	1														2
Saccharomycetales	Saccharomycetacea	*Yamadazyma*								1									1		2
Pleosporales	Roussoellaceae									1								1			2
Pleosporales	Amorosiaceae	*Angustimassarin*																		1	1
		Ascomycete 2						1													1
		Ascomycete 3															1				1
Sordariales	Chaetomiaceae	*Botryotrichum*						1													1

Table SII. Continued

		Host Species	*Alnus* (n =14)			*Persea* (n =96)			*Platanus* (n =132)			*Populus* (n=33)			*Quercus* (n= 75)			*Salix* (n = 224)			
Fungi		Site/Tree Status	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	IN	II	NN	Grand
Order	**Family**	n Trees Sample	(5)	(5)	(4)	(34)	(36)	(26)	(57)	(35)	(40)	(12)	(7)	(14)	(36)	(3)	(36)	(71)	(86)	(67)	Total
Helotiales	Sclerotiniaceae	*Botrytis*																	1		1
Sordariales	Incertae sedis	*Brachysporiella*							1												1
Invertae sedis	Glomerellaceae	*Colletotrichum*																	1		1
Diaporthales	Coryneaceae	*Coryneum*												1							1
Hypocreales	Nectriaceae	*Cosmospora*															1				1
Pleosporales	Cucurbitariaceae	*Curreya*									1										1
Hypocreales	Bionectriaceae	*Gliomastix*					1														1
Russulales		*Gloeohypochnicium*						1													1
Pleosporales	Hermatomycetaceae	*Hermatomyces*													1						1
Capnodiales	Capnodiaceae	*Leptoxyphium*																1			1
Pleosporales	Libertasomycetaceae	*Libertasomyces*										1									1
	Amorosiaceae	*Lophiostoma*				1															1
Pleosporales	Microsphaeropsidaceae	*Microsphaeropsi*																		1	1
Tremellales	Tremellaceae	*Papiliotrema*						1													1
Pleosporales	Phaeosphaeriaceae	*Phaeosphaeria*																	1		1
Pleosporales	Incertae sedis	*Pleiochaeta*																		1	1
Calosphaeriales	Calosphaeriaceae	*Pleurostoma*				1															1
Pleosporales	Phaeosphaeriaceae	*Populocrescenti*																		1	1
Pleosporales		*Pseudopassalor*																	1		1
Magnaporthales	Magnaporthaceae	*Pyricularia*							1												1
Pleosporales		*Sclerostagonospora*						1													1
Pleosporales	Phaeosphaeriaceae	*Stemphylium*							1												1
Pleosporales	Teichosporaceae	*Teichospora*															1				1
Pleosporales	Trematosphaeriacea	*Trematosphaeria*																	1		1
											1										1
Subtotal			**1**	**1**	**7**	**50**	**47**	**45**	**87**	**47**	**37**	**17**	**15**	**26**	**44**	**7**	**32**	**96**	**128**	**84**	**771**
Grand Total			**6**	**4**	**12**	**90**	**88**	**81**	**151**	**85**	**72**	**31**	**22**	**43**	**86**	**15**	**64**	**181**	**238**	**159**	**1428**

Table SIII. Linear discriminant functions given by predictive discriminant analyses of microbial communities in host species (*Salix* spp., *Platanus racemosa, Quercus agrifolia*, and *Persea americana*). Differences between host species were analyzed separately for samples collected from FD-ISHB infested and non-infested trees in infested plots. Host classification of infested trees excludes *Quercus*. Coefficients are presented from analyses using taxa recovered from five and 20 or more trees, respectively.

		Infested Plots: Non-Infested Trees							Infested Plots: Infested Trees			
		Median Coefficients			95% confidence interval				Median Coefficients		95% confidence interval	
Microbe		LD1	LD2	LD3	LD1	LD2	LD3		LD1	LD2	LD1	LD2
Analysis using taxa recovered from five or more trees												
Aureobasidium	*	-0.26	0.45	-0.88	-0.63—0.16	-1.89—2.09	-2.20—2.45	*	0.19	-2.09	-0.14—0.49	-3.45—1.09
Didymocyrtis	**	6.05	-0.02	-0.38	5.03—9.64	-0.83—1.24	-1.32—1.07	**	-5.68	-1.06	-10.86— -3.63	-2.32—0.30
Methylobacterium		0.03	0.17	0.38	-0.32—1.93	-3.82—3.69	-4.21—4.24	*	0.22	0.78	-1.25—1.43	-1.54—2.76
Paenibacillus	**	5.86	0.04	-0.45	4.68—9.70	-1.36—1.77	-1.70—1.56	**	-4.92	-0.64	-10.00— -3.48	-1.58—0.50
Pantoea								*	0.63	-1.92	0.05—1.02	-3.35—1.79
Phragmocamarosporium								*	-1.82	0.83	-5.36—0.29	-0.98—3.40
Pseudomonas		-0.45	0.11	-0.21	-0.92—0.19	-1.38—1.71	-1.87—1.66	*	0.87	0.14	0.12—1.46	-1.55—1.42
Variovorax	*	-0.30	-1.09	-0.05	-0.60— -0.05	-3.93—3.39	-2.75—2.18					
Analysis using taxa recovered from 20 or more trees												
Alternaria		-0.24	0.25	0.02	-0.40— -0.03	-1.83—1.47	-1.90—2.12					
Aureobasidium	*	-0.22	-0.73	0.0009	-0.55—0.24	-2.32—2.35	-2.13—1.82	*	0.18	-2.11	-0.21—0.49	-3.82—0.74
Didymocyrtis	**	5.88	-0.03	-0.02	4.69—9.67	-1.40—1.32	-1.06—1.02	**	-5.46	-0.93	-9.12 — -4.10	-2.48—0.80
Microbacterium								*	0.02	0.71	-1.44—1.04	-1.41—2.92
Paenibacillus	**	5.73	-0.33	0.04	4.45—9.62	-1.91—1.76	-1.66—1.52	**	-4.96	-0.36	-9.07— -3.73	-1.63—0.68
Pantoea								*	0.62	-1.83	0.18—0.91	-3.14—1.70
Phragmocamarosporium								*	-2.02	0.71	-4.81—0.17	-0.82—2.65
Pseudomonas		-0.50	-0.31	-0.003	-0.88—0.08	-1.78—1.82	-1.74—1.71	*	0.77	0.36	0.21—1.40	-1.57—1.56
Variovorax		-0.34	-0.10	-0.16	-0.58— -0.12	-3.52—3.21	-3.74—4.00					

**Taxa with the strongest influence on group separation

*Taxa with moderate to strong influence on group separation

Table SIV. Linear discriminant functions given by predictive discriminant analyses of microbial communities in samples collected from FD-ISHB attacked and not-attacked trees. Differences in attack status were analyzed separately for each host species (*Salix* spp., *Platanus racemosa,* and *Persea americana*). Coefficients are presented from analyses using taxa recovered from five and 20 or more trees, respectively.

	Salix			*Platanus*			*Persea*		
Microbe		Median LD1 Coefficients	95% confidence interval		Median LD1 Coefficients	95% confidence interval		Median LD1 Coefficients	95% confidence interval
Analysis using taxa recovered from five or more trees									
Alternaria	*	-1.10	-1.90–0.02	*	1.05	-0.29–2.49			
Aspergillus	*	-1.37	-3.57–0.29		-0.87	-3.37–5.04			
Aureobasidium	*	-1.21	-2.35– -0.07	*	-1.09	-1.93–0.15			
Brenneria		0.39	-1.61–2.59						
Cladosporium					-0.05	-1.08–1.26		-0.25	-1.99–1.57
Didymocyrtis							*	-1.00	-2.71–2.31
Lysinibacillus								-0.17	-3.93–4.87
Methylobacterium	*	-2.62	-3.39– -1.64						
Microbacterium	*	-1.21	-3.2–1.11	*	-1.44	-3.13–2.05	*	1.69	-1.29–3.42
Paenibacillus								0.05	-2.04–1.80
Pantoea		-0.41	-1.40–0.66	*	1.31	0.05–2.71			
Phragmocamarosporium								0.40	-3.02–2.70
Pseudomonas		0.70	-0.18–1.84		-0.50	-1.50–0.89		-0.28	-1.99–1.56
Sarocladium	*	1.63	-1.35–4.40						
Variovorax	*	1.06	-0.94–2.76	*	-1.35	-3.21–1.14			
Yeast		0.74	-0.53–1.88		-0.78	-3.61–1.14			
Analysis using taxa recovered from 20 or more trees									
Alternaria	*	-1.03	-2.13–0.56	*	0.92	-1.09–2.53			
Aureobasidium	*	-1.96	-2.93– -0.84	*	-1.72	-2.32– -0.50			
Cladosporium					0.33	-1.21–1.52		-0.04	-1.77–1.76
Didymocyrtis							*	-1.07	-3.64–1.74
Microbacterium							*	1.81	-1.37–3.67
Paenibacillus								0.09	-2.34–2.10
Pantoea		-0.67	-1.91–0.74						
Pseudomonas		0.43	-0.85–1.68		-0.40	-2.05–1.41		-0.25	-2.03–1.57
Yeast	*	1.01	-0.48–2.61						

**Taxa with the strongest influence on group separation
*Taxa with moderate to strong influence on group separation

Table SV. Linear discriminant function given by predictive discriminant analysis of microbial communities isolated from *Quercus agrifolia* in FD-ISHB infested and non-infested plots. Coefficients are presented from analyses using taxa recovered from five and 20 or more trees, respectively.

Microbe		Median LD1 Coefficients	95% confidence interval
Analysis using taxa recovered from five or more trees			
Alternaria	**	1.43	-0.24—2.60
Aureobasidium	*	-1.08	-2.64—0.21
Cladosporium		-0.07	-1.37—0.90
Microbacterium	**	1.86	-0.33—4.01
Pantoea	**	1.81	-0.34—2.97
Pseudomonas		-0.41	-1.83—0.90
Querciphoma		-0.21	-3.50—1.54
Sarocladium		-0.44	-2.61—2.22
Variovorax	**	2.24	1.35—4.77
Analysis using taxa recovered from 20 or more trees			
Cladosporium		0.32	-1.77—2.02
Pseudomonas	**	-1.94	-2.37—1.31

**Taxa with the strongest influence on group separation.

*Taxa with moderate to strong influence on group separation.

Table SVI. Confusion matrices of host classification.

		Predicted within not-attacked Trees				Predicted within attacked trees		
Quantile	Actual	*Persea*	*Platanus*	*Quercus*	*Salix*	*Persea*	*Platanus*	*Salix*
	Analysis using taxa recovered from five or more trees							
0.025	*Persea*	14	0	1	2	14	0	3
	Platanus	0	6	8	11	0	3	11
	Quercus	0	1	5	11			
	Salix	0	5	12	14	0	4	37
0.5	*Persea*	15	1	0	1	14	0	3
	Platanus	0	8	5	12	0	5	9
	Quercus	0	0	3	14			
	Salix	0	10	1	20	0	7	34
0.975	*Persea*	15	0	0	2	16	0	1
	Platanus	0	6	3	16	0	2	12
	Quercus	0	0	8	9			
	Salix	0	2	6	23	0	2	39
	Analysis using taxa recovered from ten or more trees							
0.025	*Persea*	14	0	1	2	14	0	3
	Platanus	0	8	4	13	0	4	10
	Quercus	0	1	6	10			
	Salix	0	3	4	24	0	13	28
0.5	*Persea*	15	0	1	1	15	0	2
	Platanus	0	10	3	12	0	5	9
	Quercus	0	1	4	12			
	Salix	0	8	5	18	0	9	32
0.975	*Persea*	13	0	0	4	17	0	0
	Platanus	0	9	2	14			
	Quercus	0	0	4	13	0	2	12
	Salix	0	4	0	27	0	3	38
	Analysis using taxa recovered from 20 or more trees							
0.025	*Persea*	14	0	2	1	14	0	3
	Platanus	0	7	3	15	0	3	11
	Quercus	0	4	5	8			
	Salix	0	10	8	13	0	11	30
0.5	*Persea*	16	1	0	0	15	0	2
	Platanus	0	6	2	17	0	4	10
	Quercus	0	3	5	9			
	Salix	0	7	6	18	0	8	33
0.975	*Persea*	16	0	0	1	15	0	2
	Platanus	0	8	2	15	0	2	12
	Quercus	0	2	4	11			
	Salix	0	6	2	23	0	1	40

Table SVII. Confusion matrices of status classification for each host species.

Host	Quantile	Actual	Predicted in Infested Plots: Not-attacked	Predicted in Infested Plots: Attacked	Predicted in Non-Infested Plots: Not-attacked	Predicted in Non-Infested Plots: Attacked
Salix	*Analysis using taxa recovered from five or more trees*					
	0.025	Not-attacked	15	16	17	44
		Attacked	12	30		
	0.5	Not-attacked	20	11	16	45
		Attacked	12	30		
	0.975	Not-attacked	19	12	21	40
		Attacked	7	35		
	Analysis using taxa recovered from 20 or more trees					
	0.025	Not-attacked	17	14	24	37
		Attacked	21	21		
	0.5	Not-attacked	16	15	19	42
		Attacked	14	28		
	0.975	Not-attacked	15	16	24	37
		Attacked	7	35		
Platanus	*Analysis using taxa recovered from five or more trees*					
	0.025	Not-attacked	15	12	29	4
		Attacked	10	5		
	0.5	Not-attacked	16	11	16	17
		Attacked	7	8		
	0.975	Not-attacked	23	4	29	4
		Attacked	10	5		
	Analysis using taxa recovered from 20 or more trees					
	0.025	Not-attacked	15	12	14	19
		Attacked	11	4		
	0.5	Not-attacked	19	8	30	3
		Attacked	9	6		
	0.975	Not-attacked	23	4	30	3
		Attacked	9	6		
Persea	*Analysis using taxa recovered from five or more trees*					
	0.025	Not-attacked	6	11	8	18
		Attacked	14	4		
	0.5	Not-attacked	9	8	14	12
		Attacked	12	6		
	0.975	Not-attacked	10	7	9	17
		Attacked	8	10		
	Analysis using taxa recovered from 20 or more trees					
	0.025	Not-attacked	2	15	11	15
		Attacked	8	10		
	0.5	Not-attacked	10	7	16	10
		Attacked	12	6		
	0.975	Not-attacked	10	7	9	17
		Attacked	8	10		

Table SVIII. Studies that characterized wood-inhabiting fungal communities in different tree hosts; "n" refers to the total number of trees sampled in the study.

Source		Host	n	Location
1	Baum et al. 2003	*Fagus sylvatica*	10	Europe
2	Chapela 1989	*Fagus grandifolia*	6	USA
		Populus tremuloides	7	
3	Chapela & Boddy 1988	*Fagus sylvatica*	34	Europe
4	Evans et al. 2003	*Theobroma gileri*	80	South America
5	Fisher and Petrini 1990	*Alnus glutinosa*	2	Europe
6	Fisher et al. 1994	*Quercus ilex*	9	Europe
7	Gazis & Chaverri 2015	*Hevea brasiliensis*	190	South America
8	Kovalchuk et al. 2018	*Picea abies*	6	Europe
9	Kowalski & Kehr 1992	*Abies alba*	unk	Europe
		Larix decidua	unk	
		Picea abies	unk	
		Pinus sylvestris	unk	
		Acer pseudoplatanus	unk	
		Alnus glutinosa	unk	
		Betula pendula	unk	
		Carpinus betulus	unk	
		Fagus sylvatica	unk	
		Fraxinus excelsior	unk	
		Quercus robur	unk	
10	Macaya-Sanz et al. 2020	*Ulmus spp.*	8	Europe
11	Petrini & Fisher 1988	*Fagus sylvatica*	10	Europe
		Pinus sylvestris	10	
12	Petrini & Fisher 1990	*Salix fragilis*	3	Europe
		Quercus robur	1	
13	Robles et al. 2015	*Platanus acerifolia*	34	South America

3: Average 4.25 (1-9) trees/site in 8 sites

4: 20 trees each in four sites

6: Three trees per site

7&13: Sampled the bole

8: Three trees each with and without *Heterobasidion*

Table SIX. Wood-inhabiting fungal taxa isolated from host species in previous studies. Host species are presented in phylogenetic order from the most to least basal lineages.

Species	Abies alba	Larix decidua	Picea abies	Pinus sylvestris	Fraxinus excelsior	Hevea brasiliensis	Platanus acerifolia	Populus tremuloides	Salix fragilis	Alnus glutinosa	Betula pendula	Carpinus betulus	Ulmus spp.	Fagus sylvatica	Fagus grandifolia	Quercus ilex	Quercus robur	Acer pseudoplatanus	Theobroma gileri	Order	Source
Ascomycota																					
Ascomycete sp.1														x							6
Ascomycete sp.2														x							6
Ascomycete sp. 3	x																				9
Ascomycete sp. 8						x							x								2
Cephalosporiopsis sp.																	x				4
Coleomycete sp. 82						x															2
Coleomycete spp.						x							x								2
Dothideomycetes																					
Diplodia microsperma							x													Botryosphaeriales	12
Diplodia sp.															x					Botryosphaeriales	12
Guignardia spp.					x												x			Botryosphaeriales	4;7
Lasiodiplodia					x															Botryosphaeriales	7
Lasiodiplodia theobromae																	x			Botryosphaeriales	4
Neofusicoccum mediterraneum											x									Botryosphaeriales	10
Capnodiales		x																		Capnodiales	8
Cladosporium cladosporioides						x					x									Capnodiales	10;13
Cladosporium tennuissimum								x												Capnodiales	5
Cladosprium herbarum								x												Capnodiales	5
Petrophila											x									Capnodiales	10
Trimmato stroma									x											Capnodiales	9
Aureoasidium pullans		x				x		x			x									Dothideales	12
Hormonema sp.			x									x								Dothideales	11
Kabatina sp.								x												Dothideales	5
Cyclothyrium juglandis				x																Incertae sedis	9
Hansfordiellopsis sp.																	x			Microthyriales	4
Alternaria alternata						x					x									Pleosporales	13
Alternaria infectoria											x									Pleosporales	10
Aposphaeria		x		x				x	x	x		x			x	x				Pleosporales	9
Bipolaris australiensis						x														Pleosporales	13
Camarosporium quercus															x					Pleosporales	12

Table SIX. Continued.

Species	Abies alba	Larix decidua	Picea abies	Pinus sylvestris	Fraxinus excelsior	Hevea brasiliensis	Platanus acerifolia	Populus tremuloides	Salix fragilis	Alnus glutinosa	Betula pendula	Carpinus betulus	Ulmus spp.	Fagus sylvatica	Fagus grandifolia	Quercus ilex	Quercus robur	Acer pseudoplatanus	Theobroma gileri	Order	Source
Cochliobolus lunatus					x															Pleosporales	13
Coniothyrium fuckeli	x																x			Pleosporales	4;9
Coniothyrium pini			x																	Pleosporales	11
Epicoccum nigrum					x															Pleosporales	13
Microphaeriopsis olivacea			x																	Pleosporales	11
Paraconiothyrium				x																Pleosporales	7
Phoma cava						x										x				Pleosporales	12
Phoma eupyrena					x															Pleosporales	13
Phoma herbarum												x								Pleosporales	10
Phoma sp. 1																	x			Pleosporales	4
Pleurophomopsis ligniola									x											Pleosporales	5
Pseudodiplodia sp.																	x			Pleosporales	4
Pyrenochaeta												x								Pleosporales	10
Ochroconis crassihumicola																	x			Venturiales	4
Dematiaccous spp.						x								x							2
Dermatiaceous sp.						x															2
Eurotiomycetes																					
Chaetothyriales		x																		Chaetothyriales	8
Cladophialophora sp.			x																	Chaetothyriales	9
Exophiala																				Chaetothyriales	10
Phialophora fastigiata						x														Chaetothyriales	2
Phialophora spp.									x								x			Chaetothyriales	4;9
Rhinocladiella atrovirens													x							Chaetothyriales	11
Aspergillus niger					x															Eurotiales	13
Aspergillus reptans					x															Eurotiales	13
Aspergillus ustus					x															Eurotiales	13
Penicillium aculeatum																	x			Eurotiales	4
Penicillium glabrum												x					x			Eurotiales	4;10
Phaeococcus sp.						x								x						Eurotiales	2
Talaromyces sp.		x																		Eurotiales	8

Table SIX. Continued.

Species	Abies alba	Larix decidua	Picea abies	Pinus sylvestris	Fraxinus excelsior	Hevea brasiliensis	Platanus acerifolia	Populus tremuloides	Salix fragilis	Alnus glutinosa	Betula pendula	Carpinus betulus	Ulmus spp.	Fagus sylvatica	Fagus grandifolia	Quercus ilex	Quercus robur	Acer pseudoplatanus	Theobroma gileri	Order	Source
Hyphomycetes																					
Acrodictys sp.																	x				4
Virgariella sp.													x								1
Incertae sedis																					
Periconiella sp.			x										x							Incertae sedis	11
Virgaria nigra																	x			Incertae sedis	4
Lecanoromycetes																					
Rinodina pyrina											x									Caliciales	10
Scoliciosporum umbrinum		x																		Lecanorales	8
Leotiomycetes																					
Cryptocline sp. 3													x							Helotiales	11
Cryptosporiopsis sp. 1								x												Helotiales	5
Mollisia cinerea				x																Helotiales	9
Pezicula livida		x	x																	Helotiales	9
Pezizales sp.																	x			Helotiales	4
Sirodothis spp.	x	x	x																	Helotiales	9
Sporonema sp.			x										x							Helotiales	11
Tympanis alne								x												Helotiales	5;9
Oidiodendron sp.																	x			Incertae sedis	4
Geomyces											x									Thelebolales	10
Orbiliomycetes																					
Vermispora sp.																	x			Orbiliales	4
Pezizomycetes																					
Caloscypha sp.																	x			Pezizales	4
Oedcephalum glomerulosum															x					Pezizales	12
Saccharomycetes																					
Geotrichum candidum																	x			Saccharomycetals	4
Sordariomycetes																					

Table SIX. Continued.

Species	Abies alba	Larix decidua	Picea abies	Pinus sylvestris	Fraxinus excelsior	Hevea brasiliensis	Platanus acerifolia	Populus tremuloides	Salix fragilis	Alnus glutinosa	Betula pendula	Carpinus betulus	Ulmus spp.	Fagus sylvatica	Fagus grandifolia	Quercus ilex	Quercus robur	Acer pseudoplatanus	Theobroma gileri	Order	Source
Coniochaeta hoffmannii		x																		Coniochaetales	9
Apiognomonia errabunda												x				x				Diaporthales	9;12
Coryneum umonatum																x				Diaporthales	12
Cryptospora betulae										x										Diaporthales	9
Cryptospora suffusa								x												Diaporthales	9
Cryptosporella suffusa								x												Diaporthales	5
Cytospora sp.							x													Diaporthales	12
Melanconium apiocarpum								x												Diaporthales	5;9
Phomopsis salicina							x													Diaporthales	12
Phomopsis spp.			x									x	x	x		x			x	Diaporthales	1;2;4;6;11
Pseudovalsa longipes																x				Diaporthales	9
Colletotrichum sp.																			x	Glomerellales	4
Glomerella cingulata																			x	Glomerellales	4
Verticicladium trifidum			x									x								Glomerellales	11
Verticillium fungicola																			x	Glomerellales	4
Verticillium luteoalbum																			x	Glomerellales	4
Acremonium exiguum																			x	Hypocreales	4
Acremonium furcatum																			x	Hypocreales	4
Acremonium spp.																			x	Hypocreales	4
Acremonium zeylanicum																			x	Hypocreales	4
Beauveria alba							x													Hypocreales	12
Beauveria sp.																			x	Hypocreales	4
Clonostachys byssicola																			x	Hypocreales	4
Clonostachys grammicospora																			x	Hypocreales	4
Clonostachys pseudochroleuca																			x	Hypocreales	4
Clonostachys pseudostriata																			x	Hypocreales	4
Clonostachys rogersoniana																			x	Hypocreales	4
Clonostachys rosea												x							x	Hypocreales	1;4
Clonostachys theobromae																			x	Hypocreales	4
Cylindrocarpon destructans																			x	Hypocreales	4

Table SIX. Continued.

Species	Abies alba	Larix decidua	Picea abies	Pinus sylvestris	Fraxinus excelsior	Hevea brasiliensis	Platanus acerifolia	Populus tremuloides	Salix fragilis	Alnus glutinosa	Betula pendula	Carpinus betulus	Ulmus spp.	Fagus sylvatica	Fagus grandifolia	Quercus ilex	Quercus robur	Acer pseudoplatanus	Theobroma gileri	Order	Source
Cylindrocarpon spp.													x							Hypocreales	3
Cylindrocarpon theobromicola																	x			Hypocreales	4
Cylindrocladiella infestans																	x			Hypocreales	4
Fusarium decemcellulare																	x			Hypocreales	4
Fusarium eumartii																	x			Hypocreales	4
Fusarium lateritium								x												Hypocreales	12
Fusarium merismoides																	x			Hypocreales	4
Fusarium radicicola																	x			Hypocreales	4
Fusarium solani					x												x			Hypocreales	4;13
Fusarium sp.				x									x				x			Hypocreales	3;4;7
Fusarium stilboides																	x			Hypocreales	4
Gliocephalis sp.																	x			Hypocreales	4
Gliocladium penicillioides					x								x							Hypocreales	1;13
Lanatonectria flavolanata																	x			Hypocreales	4
Lecanicillium sp.																	x			Hypocreales	4
Mariannaea sp.																	x			Hypocreales	4
Myrothecium cinctum																	x			Hypocreales	4
Myxormia sp.			x																	Hypocreales	11
Nectria coccine													x							Hypocreales	3
Paecilomyces lilacinus																	x			Hypocreales	4
Sarocladium strictum					x															Hypocreales	13
Stilbella albominuta																	x			Hypocreales	4
Tolypocladium				x																Hypocreales	7
Torrubiella sp.																	x			Hypocreales	4
Trichoderma atrovirde					x															Hypocreales	13
Trichoderma hamatum																	x			Hypocreales	4
Trichoderma harzianum					x												x			Hypocreales	4;13
Trichoderma spp.				x		x							x				x			Hypocreales	1;2;4;7
Trichoderma virens																	x			Hypocreales	4
Trichoderma viride																	x			Hypocreales	4

Table SIX. Continued.

Species	*Abies alba*	*Larix decidua*	*Picea abies*	*Pinus sylvestris*	*Fraxinus excelsior*	*Hevea brasiliensis*	*Platanus acerifolia*	*Populus tremuloides*	*Salix fragilis*	*Alnus glutinosa*	*Betula pendula*	*Carpinus betulus*	*Ulmus* spp.	*Fagus sylvatica*	*Fagus grandifolia*	*Quercus ilex*	*Quercus robur*	*Acer pseudoplatanus*	*Theobroma gileri*	Order	Source
Cephalotrichum stemonitis																	x			Microascales	4
Graphium penicilloides																	x			Microascales	4
Pseudallascheria boydii					x															Microascales	13
Chaetomium elatum													x							Sordariales	3
Chaetomium funicola					x															Sordariales	13
Chaetomium globosum					x															Sordariales	13
Phialemonium curvatum					x															Sordariales	13
Phomopsis pittospori					x															Sordariales	13
Anthostomella pedemontana													x							Xylariales	9
Arthrinium phaeospermum					x															Xylariales	13
Arthrinium sp.					x												x			Xylariales	4;13
Colletotrichum acutatum				x											x					Xylariales	6;7
Cryptosphaeria populina						x														Xylariales	2
Daldinia sp.		x					x				x			x						Xylariales	9;11;12
Entoleuca												x								Xylariales	10
Hansfordia sp.																	x			Xylariales	4
Hypoxylon bipapillatum		x					x	x					x			x				Xylariales	11;12
Hypoxylon fragiforme													x		x					Xylariales	1
Hypoxylon sp.					x											x				Xylariales	12;13
Liberomyces saliciphilus												x								Xylariales	10
Pestalotia sp.						x														Xylariales	2
Pestalotiopsis guepini					x															Xylariales	13
Pestalotiopsis sp.				x													x			Xylariales	4;7
Trichothecium roseum												x								Xylariales	10
Xylaria 1													x							Xylariales	1
Xylariales sp.																	x			Xylariales	4
Xylariaceous spp.						x														Xylariales	2
Basidiomycota																					
Agaricomycetes																					
Agaricales sp. 1																	x			Agaricales	4

Table SIX. Continued.

Species	*Abies alba*	*Larix decidua*	*Picea abies*	*Pinus sylvestris*	*Fraxinus excelsior*	*Hevea brasiliensis*	*Platanus acerifolia*	*Populus tremuloides*	*Salix fragilis*	*Alnus glutinosa*	*Betula pendula*	*Carpinus betulus*	*Ulmus* spp.	*Fagus sylvatica*	*Fagus grandifolia*	*Quercus ilex*	*Quercus robur*	*Acer pseudoplatanus*	*Theobroma gileri*	Order	Source
Coprinopsis cinera				x																Agaricales	13
Granulobasidium vellereum				x																Agaricales	13
Moniliophthora roreri																x				Agaricales	4
Psilocybe sp.																x				Agaricales	4
Basidioradulum radula												x								Hymenochaetales	1
Inonotus rickii				x																Hymenochaetales	13
Coriolopsis sp.																x				Polyporales	4
Daedaleopsis sp.																x				Polyporales	4
Fomes fomentarius												x								Polyporales	1
Perenniporia sp.																x				Polyporales	4
Phanerochaete chrysosporium				x																Polyporales	13
Trametes sp.																x				Polyporales	4
Cystobasidiomycetes																					
Buckleyzyma aurantiaca																				Incertae sedis	10
Tremellomycetes																					
Filobasidium magnum											x									Filobasidiales	10
Trichosporon sporotrichoides				x																Tremellales	13
Vishniacozyma carnescens											x									Tremellales	10
Cryptococcus																					10
Basidiomycete spp.																x					4
Zygomycota																					
Mucorales sp.1																x				Mucorales	4

SA= South America

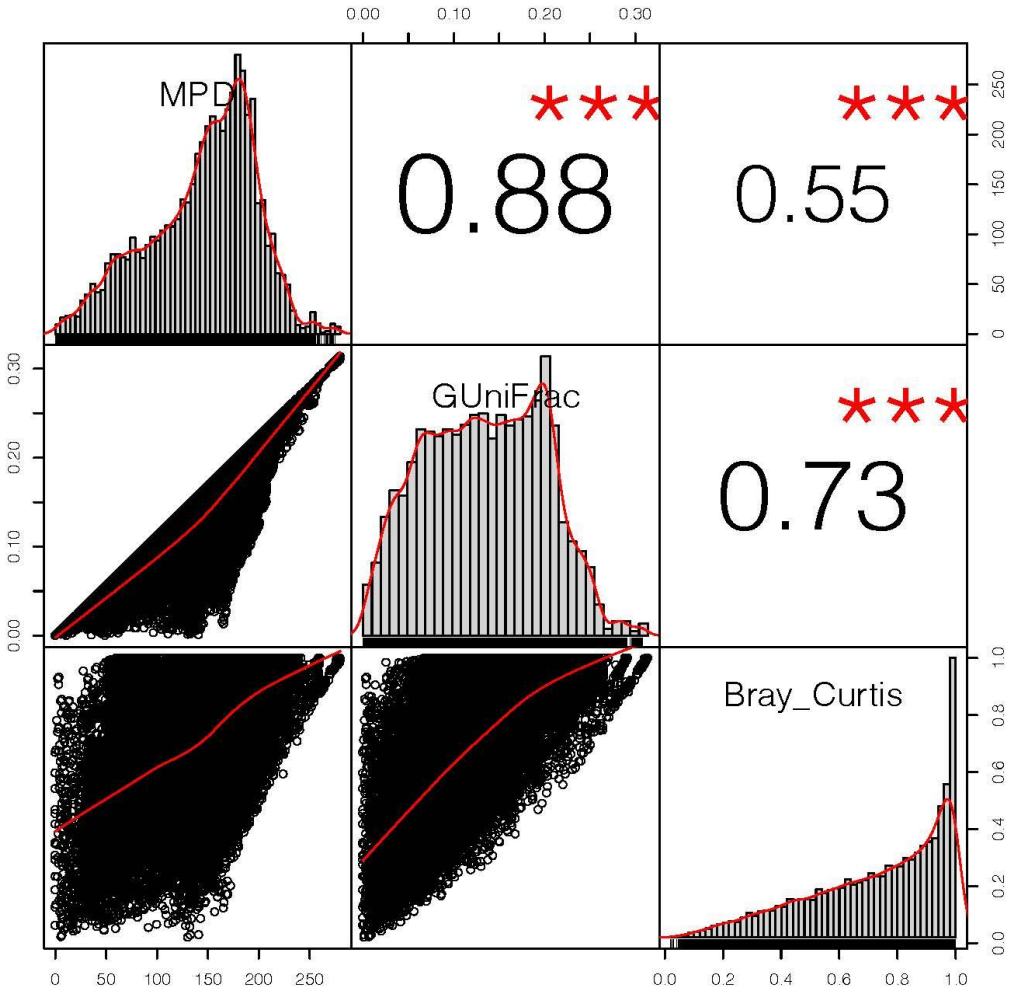


Figure S1a. Pairwise comparisons of distance matrices used to calculate NMDS scores in the mean phylogenetic distance (MPD), GUniFrac, and Bray-Curtis community dissimilarity metrics. Correlations were highly significant (Mantel test; *P* = 1e-04 each). Scores were used to evaluate plant communities and select a representative sample of sites for the present study across a network of 234 FD-ISHB monitoring plots.

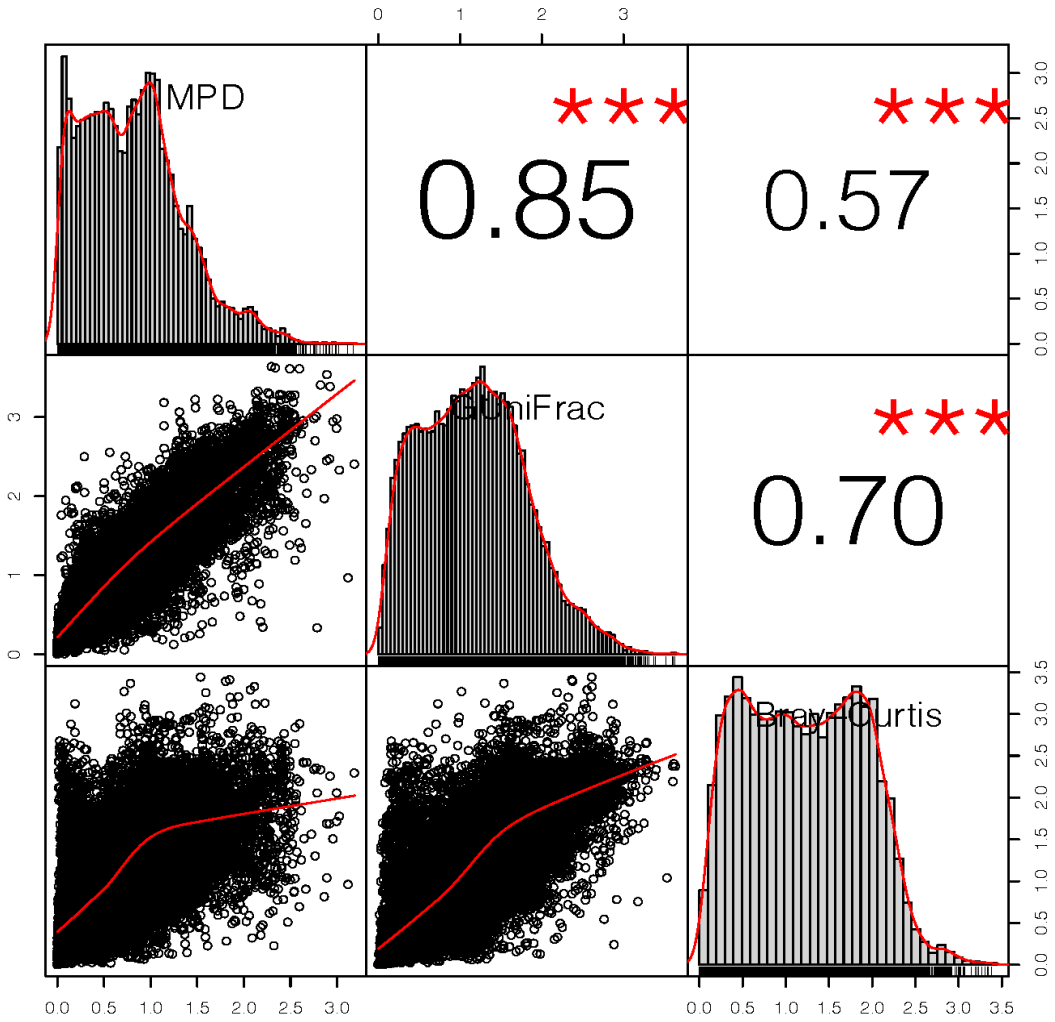


Figure S1b. Diagnostic plots comparing the Euclidean distances of NMDS scores in the mean phylogenetic distance (MPD), GUniFrac, and Bray-Curtis community dissimilarity metrics.

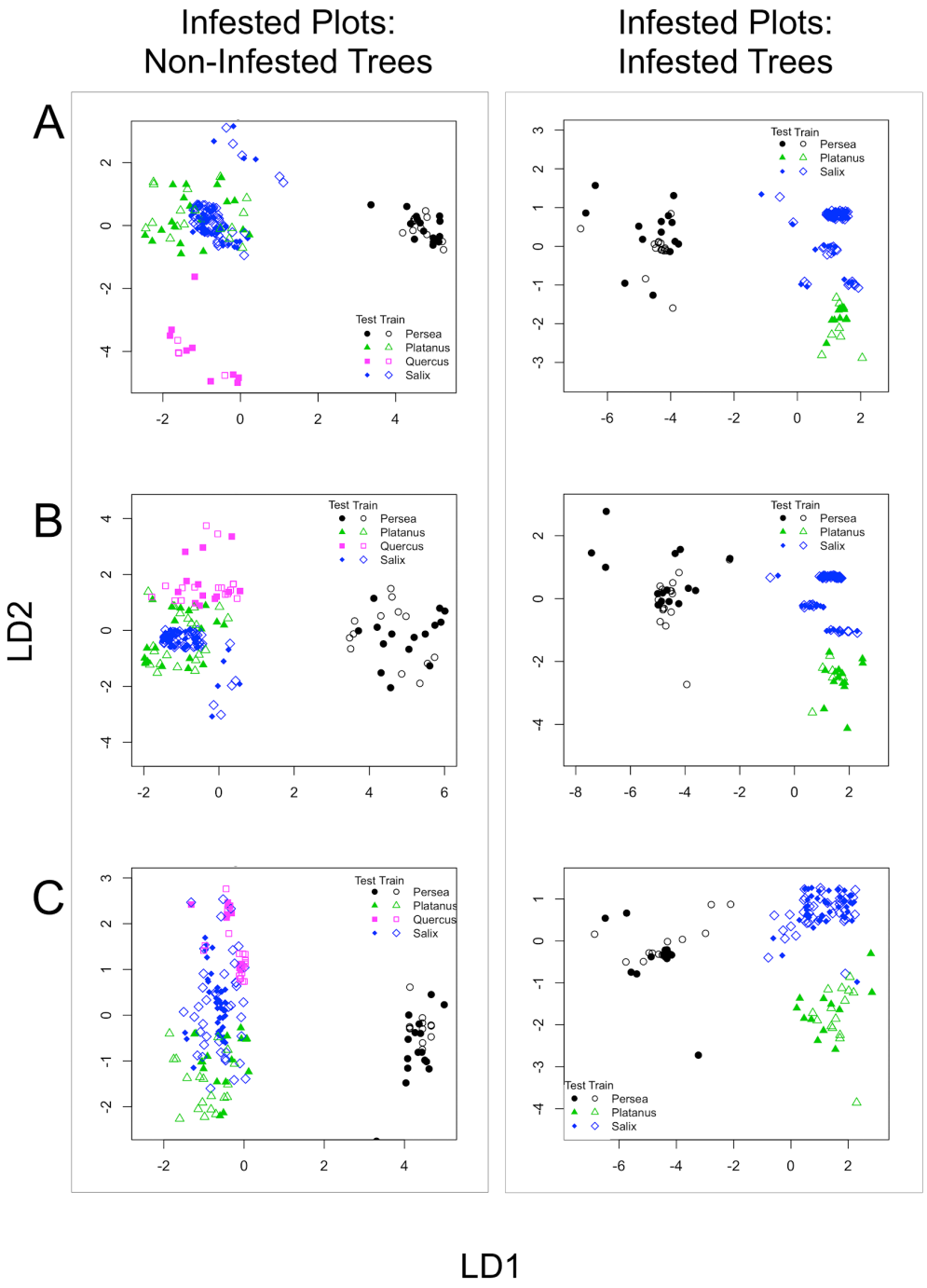


Figure S2. Plots of discriminant scores for testing and training samples given by linear discriminant functions distinguishing wood endophyte communities among tree hosts. Plotted discriminant scores represent models using microbial taxa isolated from **A)** ≥5 trees, **B)** ≥10 trees **C)** ≥20 trees, and with the median classification accuracy in 100 analytical repetitions. Analyses were run separately within FD-ISHB attacked (**left panel**) and not-attacked trees (**right panel**).

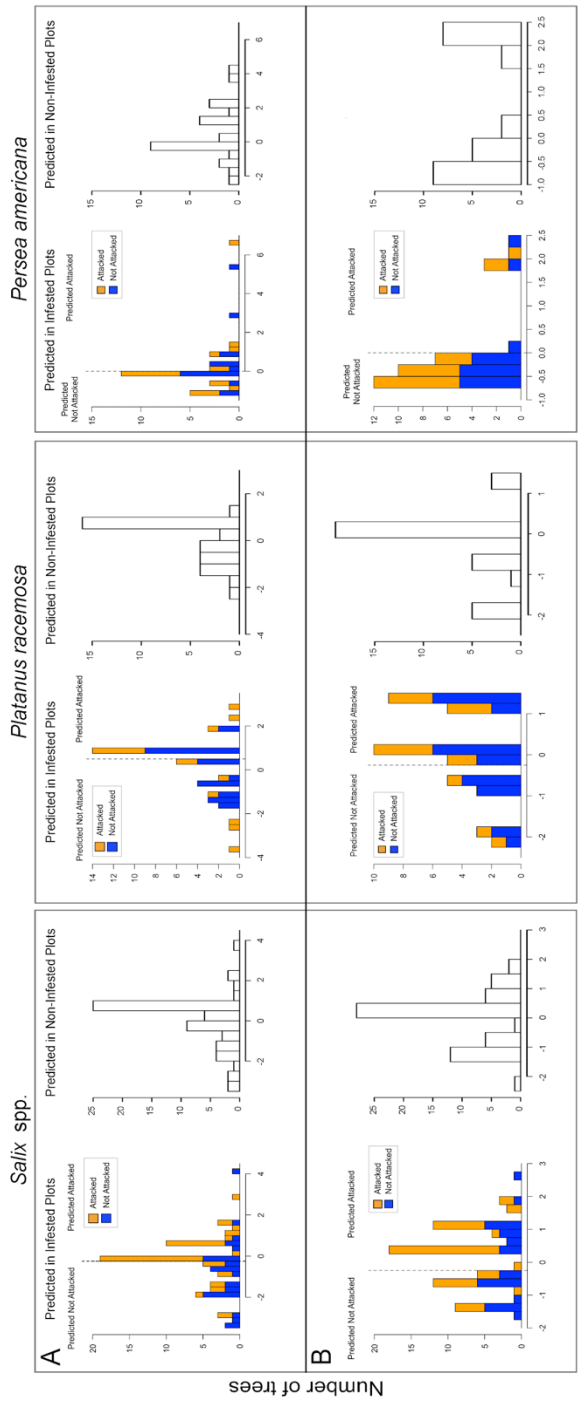
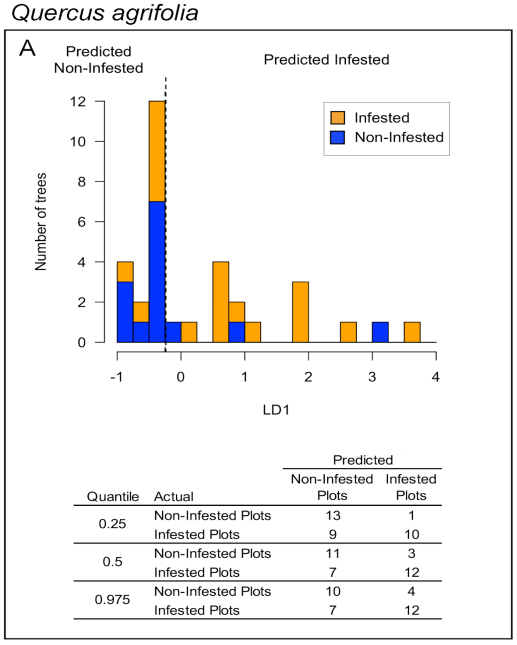
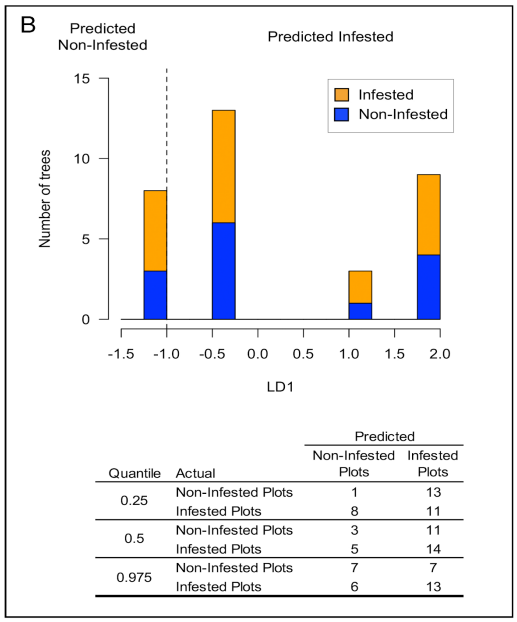


Figure S3. Predicted discriminant scores for testing samples given by the linear discriminant function distinguishing wood endophyte communities among FD-ISHB attacked and not-attacked *Salix, Platanus,* and *Persea* trees within infested plots. Plotted discriminant scores represent models using microbial taxa isolated from **A)** ≥5 trees and **B)** ≥20 trees, and with the median classification accuracy in 100 analytical repetitions. Discriminant score predictions for trees in non-infested plots are also included for each analysis.

Quercus agrifolia



Quantile	Actual	Predicted: Non-Infested Plots	Predicted: Infested Plots
0.25	Non-Infested Plots	13	1
	Infested Plots	9	10
0.5	Non-Infested Plots	11	3
	Infested Plots	7	12
0.975	Non-Infested Plots	10	4
	Infested Plots	7	12



Quantile	Actual	Predicted: Non-Infested Plots	Predicted: Infested Plots
0.25	Non-Infested Plots	1	13
	Infested Plots	8	11
0.5	Non-Infested Plots	3	11
	Infested Plots	5	14
0.975	Non-Infested Plots	7	7
	Infested Plots	6	13

Figure S4. Predicted discriminant scores for testing samples given by the linear discriminant function distinguishing wood endophyte communities in *Quercus* among FD-ISHB infested and non-infested plots. Plotted discriminant scores represent models using microbial taxa isolated from **A)** ≥5 trees and **B)** ≥20 trees, and with the median classification accuracy in 100 analytical repetitions. Test classification of samples in models with classification accuracies at the 0.025, 0.5, and 0.975 quantiles are included for each microbial data set.

Supplementary Methods

Molecular microbial community profiling

DNA extraction

We characterized fungal and bacterial communities from all 1,500 wood core samples collected from the 126 plots. The total genomic DNA from each sample was purified using a Maxwell® RSC instrument. First, 200 mg of lyophilized tissue from each sample were homogenized for 2 min at 6 m/s in 1 mL of lysis buffer (2% CTAB buffer, 2% polyvinylpyrrolidone, 0.02% RNase A [Promega], and 0.04% Proteinase K [Promega]) using lysing matrix D with a FastPrep-24™ 5G Instrument (MP Biomedicals). Suspensions were subsequently incubated for 30 min at 65°C and centrifuged for 30 min at 16,000 x g before transferring 300 µL of the lysate to a Maxwell® RSC PureFood GMO and Authentication Kit reagent cartridge well (Promega, San Luis Obispo, CA, USA). We ran two positive and two negative controls in parallel with collected samples during DNA extraction runs. One positive control included a microbial community standard consisting of eight bacteria (3 Gram-negative and 5 Gram-positive) and 2 yeasts (1.4 x 10^{10} cells/mL) (ZymoBIOMICS™, Irvine, CA, USA). Our second positive control included a fungal mock community (FungalMock) composed of 27 different taxa representing a taxonomic range of fungal species that vary in their GC content and ITS lengths (Table SM1). Mycelia recovered from the above sawdust samples were grown in pure culture and lyophilized tissue of each fungal species was combined with equal mass amounts and processed in lysis buffer as described above. For negative controls, we used autoclaved deionized water and PCR-grade water samples.

Purified gDNA from samples and controls was quantified using a Quantus™ Fluorometer with the QuantiFluor® ONE dsDNA System kit (Promega) prior to HTAS library prep.

DNA community standards

In addition to DNA extraction control samples, we analyzed one bacterial and two fungal mock community samples of known and relevant composition in parallel with field samples to validate/parameterize data processing workflows and account for PCR mismatches and amplification biases, chimera formation, index bleed, and inappropriate sequence clustering parameters (Palmer *et al.* 2018). We used an equimolar synthetic mock community (SynMock) as a standard independent of biological sequences present in the sequencing run that consisted of single-copy non-biological ITS-like sequences cloned in *E. coli* plasmids (Palmer *et al.* 2018). Similarly, we created a biological mock community (BioMock) composed of equimolar amounts of fungal gDNA extracted from pure culture mycelia from the 27 different taxa in Table SM1. Total gDNA was extracted using methods adapted from Cenis (1992), quantified using a Quantus™ Fluorometer with the QuantiFluor® ONE dsDNA System kit (Promega), and combined in equimolar concentration prior to HTAS library prep. For 16S HTAS, we used a patented Microbial Community DNA Standard (10 ng/μL) composed of a mixture of gDNA isolated from pure cultures of the same strains used for DNA extractions (ZymoBIOMICS™, Irvine, CA, USA).

High throughput amplicon sequencing

Sample libraries were prepared, pooled, and sequenced at the Vincent J. Coates Genomics Sequencing Laboratory and Functional Genomics Laboratory at the University of California, Berkeley. Standard sized libraries were prepared using Kapa Biosystems library preparation kits (with covaris/bioruptor shearing for gDNA) and indexes with custom Unique

Dual Indexes. We used the fITS7 and ITS4 primers to amplify the internal transcribed spacer region (nuc rDNA 5.8S-ITS2 [ITS barcode]) for the fungal community (Taylor *et al.* 2016) and the 515F and 806R primers to amplify the 16S rRNA V4 gene region for the bacterial community (Caporaso *et al.* 2012). To suppress plant host plastid and mitochondrial 16S contamination and yield more bacterial 16S rRNA sequence as a fraction of total sequences (Lundberg *et al.* 2013), we added 5μM peptide nucleic acid (PNA) clamp synthetic oligomers to each 16S PCR reaction during HTAS library prep (PNA Bio, Newbury Park, CA, USA). The amplicon, barcoded libraries were individually cleaned using a kit, quantified using a fluorometer with a DNA quantification kit, and combined in equimolar concentration prior to sequencing on a NovaSeq S4 flowcell (paired-end reads, 2 x 250bp) with a target sequencing depth of 50 reads per sample to recover a majority of microbial diversity.

Bioinformatics

The sequences from each NovaSeq run were preprocessed separately, then put together after clustering to enable an inventory of total microbial community membership and evaluation of β-diversity across scales. The NovaSeq sequencing dataset of ITS2 amplicon sequences was analyzed with AMPtk following Palmer et al. (2018). We trimmed reads to 250 bp and discarded any ITS reads shorter than 125 bp; any reads between 125 and 250 bp were padded with N's to improve sequence clustering (Palmer et al., 2018). Samples with fewer than 10,000 reads were dropped before clustering to avoid clustering errors. ITS sequence reads were quality filtered with expected errors less than 1.0 (Edgar & Flyvbjerg, 2015), de-replicated, and clustered at 97% similarity to generate operational taxonomic units (OTUs) using uparse (Edgar, 2013). Following clustering, any padded N's were removed, and the processed ITS sequences were mapped to the OTUs. We clustered the resulting inferred

sequences (iSEQs) into traditional OTUs using uclust and 97% similarity, and the processed sequences were then mapped back to the OTUs. We used the synthetic mock community to account for observed rates of index bleed using the filter module in AMPtk following Palmer et al. (2018). Finally, the OTUs were assigned taxonomic names using the hybrid taxonomy algorithm in AMPtk, and compared to sequences from cultured fungi using a local BLASTn search. All non-fungal OTUs from ITS sequencing were removed prior to statistical analysis.

The 16S NovaSeq reads were de-noised and quality filtered using expected error trimming by the DADA2 algorithm (Callahan et al., 2016) in Quantitative Insights Into Microbial Ecology 2 (Qiime2; (Bolyen *et al.* 2019) to cluster into exact sequence variants (ESV) and assign taxonomic classification to these ESVs.

Table SMI. Fungal species used for the biological mock community (BioMOck) DNA standard in this study.

Species	GC Content	Division	Order	Family
Coprinellus sp.	41.11	Basidiomycota	Agaricales	Agaricaceae
Hannaella oryzae	42.89	Basidiomycota	Tremellales	Incertae sedis
Penicillium sumatrense	60.9	Ascomycota	Eurotiales	Trichocomaceae
Aspergillus sp.	65.8	Ascomycota	Eurotiales	Trichocomaceae
Pleurostoma richardsiae	56.7	Ascomycota	Calosphaeriales	Calosphaeriaceae
Phialemonium sp.	53.8	Ascomycota	Sordariales	Cephalothecaceae
Acrostalagmus luteoalbus	55.5	Ascomycota	Hypocreales	Hypocreaceae
Fusarium euwallaceae	51.2	Ascomycota	Hypocreales	Nectriaceae
Aureobasidium melanogenum	49.95	Ascomycota	Dothideales	Dothioraceae
Aureobasidium pullulans	50.6	Ascomycota	Dothideales	Dothioraceae
Cladosporium cladosporioides	52.3	Ascomycota	Capnodiales	Incertae sedis
Phaeoacremonium angustius	57.89	Ascomycota	Diaporthales	Togniniaceae
Cytospora chrysosperma	52.9	Ascomycota	Diaporthales	Valsaceae
Diaporthe baccae	51.58	Ascomycota	Diaporthales	Diaporthaceae
Arthrinium malaysianum	52.5	Ascomycota	Xylariales	Apiosporaceae
Truncatella angustata	42.77	Ascomycota	Xylariales	Incertae sedis
Botryosphaeria stevensii	53.1	Ascomycota	Botryosphaeriales	Botryosphaeriaceae
Dendrothyrium longisporum	55.86	Ascomycota	Pleosporales	Didymosphaeriaceae
Pseudocamarosporium propinquum	52.68	Ascomycota	Pleosporales	Didymosphaeriaceae
Neocucurbitaria salicis-albae	48.76	Ascomycota	Pleosporales	Cucurbitariaceae
Pyrenochaeta sp.	51.08	Ascomycota	Pleosporales	Cucurbitariaceae
Populocrescentia forlicesenensis	43.97	Ascomycota	Pleosporales	Phaeosphaeriaceae
Alternaria alternata	51.2	Ascomycota	Pleosporales	Pleosporaceae
Pithomyces chartarum	54.29	Ascomycota	Pleosporales	Pleosporaceae
Stemphylium sp.	46.86	Ascomycota	Pleosporales	Pleosporaceae
Pseudopassalora gouriqua	60.38	Ascomycota	Pleosporales	Incertae sedis
Pleiochaeta carotae	47.7	Ascomycota	Incertae sedis	Incertae sedis

Chapter 4

On Collaborative Governance: Building Consensus on Priorities to Manage Invasive Species Through Collective Action

Introduction

The greatest opportunity to effectively manage biological invasions is often at critical early stages. Under these circumstances, politically costly decisions must usually be made at a time with insufficient data about which areas are most vulnerable to an infestation, how the invaders spread across a complex landscape, how severe their impacts might be, and what management approaches are most effective among a variety of land-use jurisdictions (Rotherham & Lambert 2012; Epanchin-Niell *et al.* 2014; Epanchin-Niell & Wilen 2015). As such, important ecological and social considerations, which are often intertwined, create difficulties for effective action. The ecological complexity of the problem also broadens the social context to involve a wider variety of people who have a stake in the outcomes of management decisions (Bodin 2017; Crowley *et al.* 2017). This scenario can be fodder for controversy and social disagreements, posing further challenges to invasive species management (Rotherham & Lambert 2012; Estévez *et al.* 2015; Crowley *et al.* 2017). Moreover, conflicts might escalate or deescalate depending on the characteristics of the introduced species itself (e.g., life history features, charismatic

qualities, economic benefit) and the people, agencies, and institutions involved (Rotherham & Lambert 2012; Estévez *et al.* 2015; Crowley *et al.* 2017).

The emergent tree pest-pathogen complex Fusarium dieback–invasive shot hole borers (FD–ISHB) (Mendel *et al.* 2012; Eskalen *et al.* 2013) is one such biological invasion in Southern California that involves a diversity of stakeholders because of its effect in avocado production and urban-wildland forest systems that confer essential economic benefits and ecosystem services. Indeed, the California avocado industry produces 90% of the United States domestic crop. Urban forests in California remove 567,748 t CO_2 annually, equivalent to the annual output of 120,000 cars (McPherson *et al*. 2016). Additionally, affected riparian forests in California are critical breeding habitat for endangered bird species, help filter pollutants, regenerate groundwater, and enhance recycling of nutrients (Kus 2002). The spread of the introduced beetles and fungi that cause FD–ISHB and the impacts of this invasion across these varied and complex landscapes has led to management challenges of great concern for different entities. FD–ISHB has already resulted in the loss of hundreds of thousands of trees in riparian ecosystems of Southern California (Boland 2016; Parks 2017), and the avocado industry and cities have already spent over $5.5 million to combat the pest-pathogen complex (Parks 2017). For urban forests, initial projections suggest that FD–ISHB has the potential to kill roughly 27 million trees (38%) in Southern California's 10,992-square kilometer urban region (McPherson *et al*. 2016). As such, the FD–ISHB issue is beyond the ability of any single organization to address the full scope of these devastating impacts on the

environment, public health, and economic vitality of diverse social-ecological systems.

Given that invasive pests such as FD–ISHB are characterized by their ability to move across dynamic geographic and social boundaries, a collective action process involving stakeholder groups, policymakers, and researchers is required to address the problem. In contrast to top-down regulatory and technocratic solutions that have proven successful in protecting individual species or solving "end of the pipe" pollution problems, a collaborative governance strategy is often necessary to manage transboundary issues such as source pollution, climate change, and biodiversity protection (Gerlak *et al*. 2012). Indeed, "command-and-control" forms of regulation governing environmental resources face demands by citizens, businesses, and non-profit organizations for more participatory processes and access to public decision making (Ebrahim 2004; Holling and Meffe 1996).

Moreover, transboundary issues need collaborative efforts because one single entity is seldom able to address the full scope of the problem (Bryson *et al.* 2006; Emerson *et al.* 2012). Collaborative governance is part of a worldwide trend pushing toward greater decentralization of environmental governance and is defined as "... a collective decision-making process that allows diverse sets of actors who share an interest or stake in a policy or management issue to work together toward mutually beneficial outcomes (Gerlak *et al*. 2012). This kind of decision-making is particularly applicable in settings involving a "common pool resource" such as fisheries, forests, and water (Wade 1987; Ostrom 1990; Sigurdson *et al.* 2011).

The research I do as a plant disease ecologist to develop the essential building blocks for integrative pest management (IPM) to control FD–ISHB was initiated and informed by informal collaborative governance arrangements with the California Avocado Commission, The Nature Conservancy, the Natural Communities Coalition of Orange County, Irvine Ranch Conservancy, OC Parks, San Diego Association of Governments. These initial arrangements among a collection of industry, governmental, and non-governmental actors evolved into a formal statewide collaborative action effort through new legislation to confront the problem. In 2018, the California Legislature passed, and Governor Brown approved Assembly Bill No. 2470 which authorized the California Invasive Species Council (CISAC) to build a consensus plan "...for the cure or suppression of diseases associated with the spread of Invasive Shot Hole Borers, including, but not limited to the Polyphagous and Kuroshio shot hole borers" and allocated $5 million to execute the plan. The CISAC committee directed the development of the plan that addressed four key elements and corresponding subcommittees: (1) Greenwaste and Firewood as Pathways; (2) Research and Technology Development; (3) Survey, Detection, and Rapid Response; (4) Outreach and Education (Table II).

CISAC's efforts meet the criteria of collaborative governance in that government actors and interested stakeholders from different jurisdictions and organizations came together to address the complex interdependencies emerging at the scale of a specific resource dilemma (e.g., the decimation of endangered wildlife

breeding habitat) and across functional areas (e.g., conserved lands, urban forests, agriculture) (Wondolleck & Yaffee 2000; Mullner *et al.* 2001; Ansell & Gash 2008).

Through consensus-building at formal meetings, all participants engaged directly in the decision-making process to manage the problem (Ansell & Gash 2008). As an appointed co-chair of the Research and Technology Development Sub-committee, I facilitated a public consensus-building process to identify research priorities towards a better understanding of ways to mitigate FD–ISHB.

In this paper, I conduct an empirical study of collaborative governance in action using the statewide collective action effort that prioritized responses to FD–ISHB. My objective is to examine and contextualize the factors and that led to the successful outcomes of the consensus-building process. After describing the FD–ISHB problem in further detail, I first review the literature on collaborative governance and identify elements that might lead to different outcomes of the process. Through participant observation and analyses of other cases of governance involving invasive species, the collaborative governance literature, and CISAC meeting materials, I evaluate how the features of this case study apply to other invasive species cases within a contingency model of collaborative governance developed by Emerson et al. (2012) (Fig. 1; see below). I conclude with a discussion of how collaborative governance can be useful in responding to novel plant pathogen threats, and how an examination of this case study contributes to the collaborative governance literature more broadly.

Pest–pathogen complex– a complex management problem

The avocado industry and land managers of native and urban forest communities in southern California together face the threat of an emergent pest-disease complex: Fusarium dieback–invasive shot hole borers (FD–ISHB) (Mendel *et al.* 2012; Eskalen *et al.* 2013). The dieback is caused by the combined effects of two ambrosia beetle species from Southeast Asia (the polyphagous and Kuroshio shot hole borers; *Euwallacea fornicatus* and *E. kuroshio*), and the specific fungal pathogens each beetle carries (*Fusarium euwallaceae* and *F. kuroshium*) (Freeman *et al.* 2013; Kasson *et al*. 2013; O'Donnell *et al*. 2015; Lynch *et al*. 2016; Gomez *et al.* 2018; Na *et al.* 2018; Smith *et al.* 2019). Over 77 tree species support reproduction of the beetles and their fungi, including 17 tree species native to California, avocado, and ornamental tree species that represent over 25% of all tree individuals planted along streets of southern California (Eskalen *et al*. 2013; https://ucanr.edu/sites/pshb/Map). As such, the pest-pathogen complex produces devastating impacts at various social-ecological scales (Eskalen *et al*. 2013; Lynch et al. *in press*). We continue to confirm regular new infestations in many native riparian, oak woodland, and mixed evergreen forest communities, urban forests, and the main avocado-growing regions of southern California.

In 2003, a single polyphagous shot hole borer (PSHB) beetle was caught in a CDFA trap in Long Beach, California. The beetle species went unnoticed until 2012 when it was found damaging backyard avocado and urban forest trees in the Los

Angeles basin. A rapid monitoring response uncovered the broad host range of the pest-disease complex, but its ability to establish in native vegetation was only gradually recognized (Eskalen *et al*. 2013; Lynch *et al*. 2016). In 2014, a separate introduction of Kuroshio shot hole borer (KSHB) was detected in commercial avocado groves and green spaces of San Diego County. While spreading throughout commercial avocado groves and urban forests, the magnitude of the problem escalated in 2015 after the beetle-pathogen killed an unprecedented number of native willow trees (*Salix lasiolepis* and *S. gooddingii*) in the Tijuana River Valley in San Diego County (Boland 2016). The event quickly prompted local, county, and state land managers and organizations to coordinate and confront the issue. Individual efforts were implemented and loosely coordinated among entities across San Diego, Orange, Ventura, and Los Angeles counties (e.g., Greer *et al*. 2018). Out of these initial efforts emerged the recognition of a need for a cohesive statewide strategy to address the full scope of the problem across different scales. What followed was a lobbying effort facilitated by key natural resource advisors to influence the California state assembly to develop legislation that would provide resources to support a statewide effort to control the spread of the beetle and pathogen to new counties, and to prevent further economic losses and damage to landscapes.

California Invasive Species Council (CISAC)

In 2009, the Invasive Species Council of California (ISCC) was formed by state agencies and approved the California Invasive Species Advisory Committee

Charter (2011) to advise the ISCC on best measures to forestall the ecological and economic harm caused by invasive species "...based on input from and cooperation with other stakeholders and existing organizations." The ISCC is an interagency council chaired by the Secretary of the California Department of Food and Agriculture and vice-chaired by the Secretary of the National Resources Agency (http://www.iscc.ca.gov/). Following established by-laws (ISCC By-Laws), the council is the "highest level of leadership and authority in state government" that helps coordinate and facilitate activities aimed at mitigating invasive species impacts in California (http://www.iscc.ca.gov/). Appointed CISAC members represent the scope of knowledge necessary to address the complex issues concerning invasive species (e.g., biologists, industry representatives, regulators, economists, educators, native people, county agricultural commissioners, researchers, public relations specialists).

In January of 2018 the California Invasive Species Council (CISAC) convened a statewide summit, which initiated the regional collective action process involving collaboration between stakeholder groups, policymakers, and researchers to address the problem. Out of the summit came suggestions that were incorporated into Assembly Bill No. 2470, which was co-authored by Assembly Members Lorena Gonzalez Fletcher and Timothy Grayson representing the 80th and14th Assembly Districts. The Bill allocated $5 million for the execution of a statewide FD–ISHB control strategy and mandated that CISAC build consensus on best measures and funding priorities in cooperation with other stakeholders and existing organizations.

Collaborative governance applied to the FD–ISHB case study

The consensus building mandate to prioritize FD–ISHB control measures fits into a collaborative governance framework because the pest-pathogen complex spreads through many different land-use jurisdictions and involves a complex social network (Table I), as seen with other transboundary environmental problems such as water pollution or habitat degradation (Bryson *et al.* 2006; Kettl 2006; McGuire 2006; Sandström & Carlsson 2008). As such, no single actor in this network is able to develop a comprehensive management plan that will adequately mitigate the threat. The avocado industry in California is governed by the California Avocado Commission, but urban and wildland forests are managed by a conglomerate of stakeholders representing public and private entities. Individual actors thus represent public agency managers, corporations, nonprofits, and policymakers across scales and levels of authority, and share similar backgrounds in biology, agronomy, ecology, and resource management, as well as a shared concern and vested interest in controlling the FD–ISHB problem.

To assess how collaborative governance can be effective in slowing the spread of FD–ISHB and invasive species more broadly, it is important to understand the contextual conditions likely to facilitate or discourage desired outcomes of collaborations.

Collaborative Governance Literature Review

The notion of collaborative governance arises from Ostrom's (1990) theoretical and empirical work that challenges Hardin's (1968) position that individuals using a common resource pool will overuse the commons and become trapped and unable to extricate themselves from the problem. Ostrom shows that without top-down regulation, many are still able to agree on a shared set of rules and avoid this "tragedy of the commons." Through multiple governing authorities at different scales (i.e., polycentric governance), problems with both local and regional effects can be addressed cooperatively and produce globally positive externalities (Ostrom 2010). Collaborative governance is used interchangeably with other terms relating to environmental management such as network governance, participatory management, and adaptive comanagement (Ansell & Gash 2008; Lubell *et al*. 2017; Nourani *et al*. 2018). I prefer the use of collaborative governance as the broader theoretical framework employed across many disciplines; "collaborative" because it indicates a deliberative and consensus-directed process, and "governance" because it includes all aspects of the governing process including management, planning, and policy making (Ansell & Gash 2008).

Governance is distinct from management. Whereas management refers to everyday decision making and practices (e.g., prescribed burns, tree pruning, vegetation rehabilitation), governance "...refers to the decision-making structures, mechanisms, and systems of administration which influence the operation of management systems" (Short & Winter 1999). Ansell and Gash (2008) define

collaborative governance with an emphasis on six criteria: (1) the forum is initiated by public agencies, (2) participants in the forum include non-state actors, (3) participants engage directly in decision making and are not merely 'consulted" by public agencies, (4) the forum is formally organized and meets collectively, (5) the forum aims to make decisions by consensus, and (6) the focus of collaboration is on public policy or public management. Because this approach has been applied and studied across a range of policy contexts, Emerson *et al.* (2012) define collaborative governance more broadly as "the processes and structures of public policy decision making and management that engage people constructively across the boundaries of public agencies, level of government, and/or the public, private and civic spheres in order to carry out a public purpose that could not otherwise be accomplished."

Collaborative governance models in environmental management have mostly been applied in cases of common pool resources (e.g., fisheries, forest, water) (Gerlak *et al*. 2012). These cases primarily concern issues surrounding resource utilization – how resources are or are not utilized and who decides. By contrast, invasive species management involves issues concerning how common resources are affected by a "common enemy." In those cases, a common enemy should drive stakeholders to work together because they have a shared vision for what they would like to achieve through collaboration. In reality, however, management of invasive species can be highly controversial because what constitutes a "common enemy" is hotly contested (Crowley *et al.* 2017). To understand how collaborative governance can be effective

in managing invasive species, it is important to first explore the kinds of conflicts that arise in those cases.

Conflicts in invasive species management

Collaborative governance primarily emerged out of a need to address the rising number and intensity of conflicts over transboundary challenges associated with environmental management that traditional top-down policy solutions could not effectively address (Gerlak *et al*. 2012). The body of research on these intractable "environmental conflicts," which encompass social disputes concerning natural resources, environmental hazards, and biodiversity conservation (Lewicki *et al*. 2002), provides a basis for understanding conflicts associated with invasive species management (Crowley *et al*. 2017). The genesis of these conflicts must be examined to understand the conditions that bear on the success of collaborative governance processes.

My discussion of environmental conflicts in invasive species management will center on two overarching sources adapted from Crowley *et al*. (2017). The first comes from when socio-ecological complexities go unrecognized in making management decisions. The second source comes from how two intertwined components of governance, stakeholder engagement and stakeholder communication, shape the development of conflicts in management. In their review of the literature of highly contested cases surrounding invasive species management, Crowley *et al*. (2017) identify three sources of environmental conflicts: (1) the management context,

(2) management approaches, (3) management communication. To be consistent with the aforementioned definitions of management and governance, I will use the terms "governance approaches" and "communication," which are equivalent to "management approaches" and "management communication". The authors present problems associated with governance approaches (e.g., public education, perfunctory consultation, and internal exclusion) and communications (e.g., unidirectional vs. dialogic exchange, message and tone) as separate factors, but in my view, communication is an intrinsic component of the governance approach.

Socio-ecological complexities of invasive species management include variation in values, attitudes, and perceptions of introduced species and their risks (Rotherham & Lambert 2012; Crowley *et al.* 2017). Not all stakeholders agree that a particular introduced species represents a common enemy, and the terms commonly applied to invasive species (e.g., *native*, *alien*, *exotic*, *invasive*) reflect social constructions of particular understandings of nature (Binimelis *et al.* 2007; Rotherham & Lambert 2012; Ernwein & Fall 2015; Estévez *et al.* 2015). Varied perceptions of the invader can foster social disagreements that sometimes escalate into destructive conflicts within the social-ecological contexts of invasive species management (Crowley *et al*. 2017). In South Africa, for example, removal of the highly invasive black wattle tree (*Acacia mearnsii*) interfered with wood availability for rural livelihoods (de Wit *et al*. 2001). The management efforts led to disputes between local communities and scientists that were rooted in a clash between utilitarian, scientific, and moralistic value systems. In a review of 28 case studies

describing invasive species conflicts, Estévez *et al*. (2015) found that the majority of disputes stemmed from value system disagreements and, secondarily, differences in risk perception between stakeholders and decision makers. Certain kinds of disagreement stem from differences in the desired state of nature, which are based on utilitarian, scientific, moralistic, humanistic, naturalistic, dominionistic, and aesthetic value systems that guide or motivate attitudes or actions (Larson *et al.* 2011; Estévez *et al.* 2015). For instance, invasive *Eucalyptus* spp. trees in ecosystems worldwide generate intractable controversies as all seven value systems confront one another over competing visions of the wildland-urban interface (van Wilgen 2012; Marris 2016). For many, the eucalyptus trees offer recreational value, and their aesthetic beauty represents heritage and a sense of place. For others, the trees represent the destruction of native habitat. Pragmatically, some find tree removal imprudent as a management response because of their importance in carbon sequestration (Gobster 2013; Marris 2016).

Discord among stakeholders additionally comes from perceptions of what constitutes harm from a non-native species, and when/what kind of management is worthwhile. In general, the degree to which a particular threat is understood scientifically or elicits visceral feelings of dread (e.g., "murder hornets"), and the perceived benefits an invasive species or management response might confer to society strongly influence people's aversion, affection, or indifference to an introduced species, and the discrepancies between stakeholder reactions (Slovic 1987; Covello & Sandman 2001). To illustrate, local communities in Monterey and Santa

Cruz counties perceived that possible harm of an emergency response to control a new introduction of the highly invasive and destructive light brown apple moth to be greater than the possible harm posed by the moth itself (Zalom *et al*. 2013). The management actions, which involved aerial applications of a family-specific pheromone, prompted a "...break-down of relations between people living in the affected regions and the agencies involved in enforcing the emergency response" (Zalom *et al*. 2013). Collaborations therefore must be sensitive to the notion that the concerns and perception of risks from invasive species mean different things to different people (Gobster 2013; Simberloff 2013; Estévez *et al.* 2015; Bodin 2017; Crowley *et al*. 2017).

In addition to the management context, governance approaches are another source of conflict. Conflicts arising out of governance approaches can further amplify conflicts coming from the management context. Engagement and communication among stakeholders influence conflict development in governance approaches (Crowley *et al*. 2017), especially when a quick response is required (Chase *et al*. 2004; Bodin 2017). Stakeholder engagement describes who is included in the decision-making process, and how these individuals are included. Transient problems such as novel pests or fire pose a particular type of challenge in that the threat itself often requires a rapid response (Bodin 2017). Because of the urgency for immediate action during an invasion, a common management response is for certain actors to rapidly mobilize coordination efforts without consulting others (Perrings et al. 2002; Bodin 2017). The deliberate exclusion of public participation in the decision-making

process out of an urgent need to act quickly under uncertain circumstances can undermine interpersonal trust that is usually developed through participatory processes (Frentz *et al.* 2000; Chase *et al.* 2004; Davenport *et al.* 2007).

For example, when the highly invasive non-native emerald ash borer (EAB, *Agrilus planipennis*) first emerged attacking ash species in eastern North America, the Canadian Food Inspection Agency (CFIA) was criticized by foresters and conservationists for not responding quickly enough to create an ash-free zone, and were then criticized later by landowners once tree cutting began (Mackenzie & Larson 2010). CIFA engaged landowners through organized town hall meetings after the plan was implemented, but not in the decision-making process. This classic "public education" approach to management, which involves centralized authorities defining the problem and response and then persuading others to accept their decision and supporting evidence (Callon 1999; Crowley *et al*. 2017), was not well received. Landowners felt that "CIFA was insensitive to their concerns and to the emotional impact of the program" by "completely" dismissing their points of view (Mackenzie & Larson 2010). Perrings et al. (2002) argue that managers may use the tradeoff between private losses and large-scale social costs of continued spread to justify exclusion. While this historically adopted DAD approach (Decide-Announce-Defend) (Beecher *et al*. 2005) is accepted by some, *ad hoc* consultations with people who have a stake in the outcome or a strong place-identity can erode in trust, intensify conflicts, and harden stakeholders' perception of risk on all sides (Covello & Sandman 2001; Sandman 1987; Slovic 1993, 1999; Cvetkovich & Winter 2003; Siegrist *et al.* 2008;

Mackenzie & Larson 2010). Ultimately, exclusionary approaches can stymie efforts to appropriately respond to the current problem and leave a legacy of controversy that creates barriers to addressing future unforeseen challenges concerning invasive species (Fig.1).

Finally, communication methods in management activities can either escalate or deescalate conflicts depending on the directionality, content, and the tone of the message (Crowley *et al.* 2017). Public education engagement favors unidirectional over dialogic forms of communication, leaving little opportunity for people to express their concerns, as seen in the EAB and light brown apple moth cases (Mackenzie & Larson 2010; Zalom et al. 2013). Although it may not be the intention of the communicator, "just informing" people about a threat can ignite conflict because it excludes engagement (Visschers *et al*. 2012; Zalom *et al*. 2013).

Collaborative governance efforts show promise in being able to mitigate the variety of ways social disagreements emerge in invasive species management. Proponents of collaborative governance argue that collective action is easier to implement and is more durable than regulation because it enhances social capital, social learning, cooperation, policy learning, innovation, and contributes to democratic principles through transparency and inclusivity (Leach & Sabatier 2005; Bodin 2017). These benefits collectively lead to improved decision-making, sustained policy implementation, and a better ability to deal with change and uncertainty than a more centralized, rigid bureaucracy (Gerlak *et al*. 2013).

However, there are as many examples of failures in collaborative efforts as there are successes, so some caution the use of collaborative governance as a panacea for environmental problems (Huxham 2003; Johnson *et al*. 2003; Bryson *et al*. 2006; Ostrom 2007; Ansell & Gash 2008; Muñoz-Erickson et al. 2010; Bodin 2017). Scholars focusing on collaborative governance have identified key conditions that support or impede successful outcomes of the process.

Collaborative governance models

A large body of literature has been devoted to studying aspects of collaborative governance as it applies to specific cases in many different social environments (e.g., early childhood education policy, green infrastructure development, natural resource management, law enforcement, child and family service delivery, community planning). A number of scholars have interrogated the case study literature in an effort to find a common language for conceptualizing and analyzing collaborative governance in a variety of contexts. Huxham (2003) identified five themes creating pain and reward in collaborative situations: 1) common aims, 2) power, 3) trust, 4) membership structures, 5) leadership. These themes have since been incorporated into more comprehensive and evolving collaborative governance frameworks developed by Bryson *et al*. (2006), Ansell & Gash (2008), and Emerson *et al*. (2013). Whereas Bryson *et al*. (2006) propose a framework based on a literature review, the model developed by Ansell & Gash (2008) is based on an inductive meta-analysis of 137 diverse case studies. Emerson *et*

al. (2012) developed the most comprehensive model based on a synthesis of a wide variety of conceptual frameworks in the literature that were rooted in empirical studies and directly or tangentially related to collaborative governance. None of these frameworks, however, incorporate cases surrounding invasive species management.

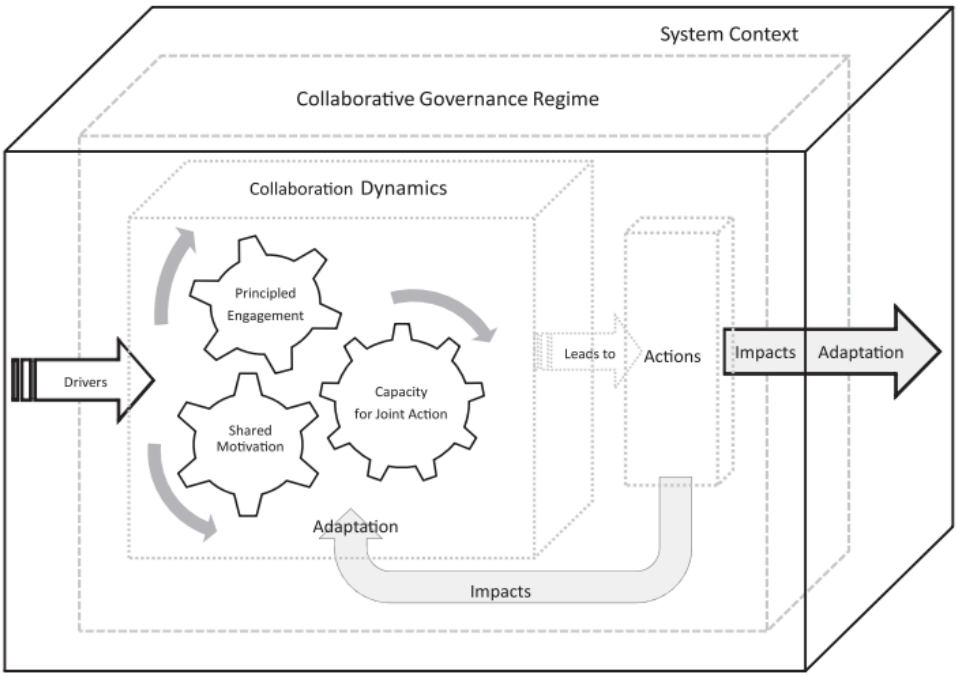


Figure 1. A model of collaborative governance developed by Emmerson *et al*. (2013).

The more comprehensive frameworks are structured by a set of internal and external factors that influence the process in which stakeholders act collaboratively and make and implement decisions. These frameworks suggest causal pathways among different configurations of those key components. Thus, successful outcomes of the collaborative process in all frameworks are contingent on those key internal attributes of the process itself and external factors that influence the process.

Although there are some differences in the ways some elements are configured, there is considerable overlap in how those elements are characterized. The most significant difference is that rather than portraying the outcomes/actions as the endpoint of a linear process, Emerson *et al*. (2013) depict those dimensions as influencers that feed back into collaboration dynamics as actions are adapted and adjusted iteratively through more collaborative processes. I adopt the majority of elements from the most encompassing theoretical framework developed by Emerson *et al*. (2013) as a basis for analysis of collaborative governance in the context of invasive species management (Fig. 1).

Elements in the collaborative governance model

There is general agreement in the literature about which elements are most important to successful collaborations. The model in Emerson *et al*. (2013) is a set of three nested dimensions representing *collaboration dynamics* and *collaborative actions* that are grouped within the *collaborative governance regime* (CGR), which itself is nested within the general *system context* (Fig. 1). *Collaboration dynamics* are initiated by certain *drivers* and refer to three interacting components that work together iteratively to produce *collaborative actions*: *principled engagement*, *shared motivation*, and *capacity for joint action*. *Collaborative actions* lead to *outcomes* and are "the steps taken in order to implement the shared purpose of the CGR" (Emerson *et al*. 2012). Each of the components within *collaboration dynamics* consists of their own specific, self-reinforcing elements.

Worth noting, the contingencies of *leadership*, *interdependence, time,* and *trust* are pervasive, interconnected, influencers in all aspects of collaborative governance models (Ansell & Gash 2008; Emerson *et al*. 2012). Collaborative governance is a time-consuming endeavor that cannot be rushed, especially when trust-building is needed to remedy prior history of conflicts. However, the initial investment in collaborative efforts can save time and efficiency in the long run (Ansell & Gash 2008). Because trust is easier to destroy than create (Slovic 1993), the time spent on bolstering trust through nurturing fair and inclusive participatory processes may also have long term social cost-saving ramifications. Desired outcomes are also maintained over the long term, suggesting that interdependence is important throughout ongoing collaborations (Ansell & Gash 2008). Finally, leadership within the collaboration is considered to be a pervasive influencer of collaborative governance because it "can be an external driver..., an essential ingredient of collaborative governance itself, and a significant outgrowth of collaboration" (Emerson *et al*. 2012).

System context

The system context includes available resources and the policy and legal factors that create opportunities or constraints on processes (Emerson *et al*. 2012), and the role of prior relationships or existing networks. The drivers that initiate collaboration emerge from this context, which is characterized by the socio-ecological and historic preconditions that influence the prevailing mode of cross-

boundary collaborative decision making (Bryson *et al*. 2006; Ansell & Gash 2008; Emerson *et al*. 2012). Collaborative governance is more likely to succeed when existing social networks are already in place (Bryson *et al*. 2006), but the structure of the social network itself (i.e., cohesive, centralized, compartmentalized) (Guerrero *et al.* 2015; Bodin 2017), institutional, political, and regulatory arrangements (Tollefson *et al*. 2012), and prior history of conflict or cooperation among network members also factor into its success (Ansell & Gash 2008).

Drivers

The broader system context of available resources, policy and legal constraints, and social relations "facilitate or discourage cooperation among stakeholders" (Ansell & Gash 2008) and influence the drivers that initiate collaboration (Emerson *et al*. 2012). Drivers are the motivating forces that convene participants and set collaboration dynamics in motion; *leadership* and *consequential incentives* are two key drivers present in all collaborative governance models. *Leadership*, either in the form of a trusted brokering organization or legitimate convener, is widely recognized as crucial to collaborative governance success because mediation and facilitation is key to relationship and trust building. Because participation is voluntary, *consequential incentives* (e.g., financial, interdependence, meeting a threat to a common interest, alternatives to less desirable ways of achieving goals) provide the initiative for leaders and participants to devote their time and

energy to engage collaboratively on salient and timely issues (Brown 2002; Futrell 2003; Ebrahim 2004; Ansell & Gash 2008).

Collaborative governance regime (CGR)

The collaborative governance regime (CGR) "represents the predominant mode for conduct, decision making, and activity" (Emerson *et al*. 2012). The CGR is composed of *collaboration dynamics* and *collaborative actions* that are initially shaped by the drivers that emerge from the system context. These driving forces for collaboration are also essential to the CGR internal processes (Huxham 2003) which in turn are influenced by the CGR over time. *Collaboration dynamics* represent the iterative, self-reinforcing interactions between *principled engagement*, *shared motivation*, and *capacity for joint action* and *collaborative actions* refer to the agreed upon process outcomes emerging from collaboration dynamics (e.g., new management activities, hiring and deploying staff, enacting policy measures). Engagement is principled because it proactively includes fair and civil discourse and open and inclusive communications representing diverse knowledge and interests of all participants (Johnson *et al*. 2003; Emerson *et al*. 2012). Shared motivational benefits (i.e., trust, mutual understanding, internal legitimacy, shared commitment) are the building blocks of social capital (Coleman 1988; Putnam *et al*., 1994; Putnam 2000) and are recognized to be internally reinforced and reciprocally sustain principled engagement in a "virtuous cycle." Finally, the cooperative activities achieved through principled engagement and resulting shared motivational benefits

help to strengthen knowledge, abilities, skills, resources, and group agency, which also improve institutional structures and processes. This new *capacity for joint action* is the potential that empowers collaborative partners to take effective action towards achieving goals in ways that did not exist before, which further bolsters principled engagement and shared motivation, which reinforces or builds new capacity.

Collaborative outcomes: impacts and adaptation

Collaborative outcomes refer to the *impacts* of collaborative actions that change the system context intentionally or unintentionally (e.g., more cost-effective management regimes, added value of a social good, technological innovation) and the *adaptations* in response to impacts on the system context (e.g., improved environmental outcomes; less destructive conflict; new mandates, norms, or institutions) that are prompted through collaborative governance processes (Innes & Booher 1999; Emerson *et al*. 2012). Impacts are expected to have fewer unintended negative consequences and be closer to targeted outcomes in effective collaborative governance, but empirical work is needed to verify these causal links (Thomas & Koontz 2011).

Study Goals

Armed with a theoretical framework for collaborative governance, I explore how it applies to understanding the conditions in cooperative decision-making that

led to a consensus on statewide priorities to control FD–ISHB in California. My purpose in this research is to (1) conduct an empirical study of collaborative governance in action throughout the CISAC-stakeholder consensus building process, and (2) interrogate that case study for its possible theoretical contributions to the literature on collaborative governance in the context of invasive species management. Three previous studies have explicitly explored governance with respect to invasive species management (McAllister *et al*. 2015; Lubell *et al*. 2017; Nourani *et al*. 2018). However, these studies focus on the influence of collaborative network structures on decision making, but not the influence of collaborative processes within those networks. My capacity to document real-time decision-making around the allocation of resources to support regional FD–ISHB management priorities presents a unique opportunity to gain rich insight on collaborative governance in the context of an invasive pest-disease complex across a peri-urban forest-agriculture environment. Specifically, I explore how qualities of the system context, drivers for collaboration, and collaboration dynamics within the collaborative governance regime work together in this case to produce otherwise unattainable actions and forecast how those actions might lead to long-term outcomes (impacts and adaptation). I further explore whether new themes emerge from the process that promote an understanding of collaborative governance more broadly.

Methodology

Drawing from existing theory on collaborative governance, this research was carried out using qualitative methods, through a combination of participant observation and an extensive review of reports, documents, and case study literature, to understand how conditions during consensus-building influence process outcomes on a regional scale to control an emergent pest-pathogen (Stake 1995; Marshall & Rossman 2006; Bernard 2011; Creswell & Creswell 2017; Yin 2017). The overall approach lends itself to an in-depth exploratory analysis embedded with rich and nuanced detail to illustrate broad general themes and informed insights from participants engaged in collective decision-making. Participant observation is a qualitative method with roots in ethnographic research in which "theoretical insights are derived from naturally occurring data rather than through interviews or questionnaires" (Huxham 2003). This approach enabled an analysis of group interactions by examining the "how" and the "what" of members' exchanges. Analysis of documents and meeting minutes helped to establish a link between consensus decisions and process outcomes.

Informed participants in the collaboration represented a broad range of perspectives of individuals directly or indirectly concerned about plant health emergencies. They represented entities from county, state, and federal agencies; academic institutions; environmental organizations; state divisions; and private companies (Table I). For consensus building, each of the four sub-committees (Greenwaste and Firewood as Pathways; Research and Technology Development;

Survey, Detection and Rapid Response; Outreach and Education) held public meetings four times at two-week intervals in March-May 2019, while taking actions between meetings to make progress. As a member of the social community associated with the case, my role as co-chair of the research sub-committee presented a unique opportunity to document the case in real-time as an active participant of the process. My first-hand involvement in all sub-committee and most working-group meetings (see below) naturally placed me in a variety of roles: facilitator, listener, learner, coordinator, science advisor, fact-gatherer. As such, this analysis benefits from an in-depth engagement with stakeholders and deeper understanding of the dynamics and general relationships among them.

Meetings were conducted via a public online GoToWebinar forum (https://www.gotomeeting.com) and the agendas for each meeting providing access information were distributed publicly in several ways: (1) a permanent list of meetings hosted by CISAC on their website: http://www.iscc.ca.gov/cisac_meetings.html; (2) a collaborative tools information sharing system hosted by University of California Agriculture and Natural Resources: http://anrcs.ucanr.edu/Base-New/Information_Technology/Web_Development/tools/ctools/; (3) email notification to roughly 150 actors explicitly requesting they spread the information widely. People were also invited to sign up to receive notices of all the meetings at https://www.cdfa.ca.gov/subscriptions. All public meetings were hosted at the California Department of Food and Agriculture (CDFA) headquarters in Sacramento,

and recorded using the GoToWebinar system for public use. A designated note taker at each meeting distributed the minutes to the subcommittee chairs to send to participants for review and commentary, and the final minutes were approved at the following meeting and then posted on the CDFA and CISAC websites. I documented my observations and personal reflections in field notes after each meeting, and reviewed publicly available recordings and meeting minutes.

Application of a Collaborative Governance Model

I used collaborative governance frameworks (e.g., Fig. 1) as a starting point to identify the prominent conditions influencing the governance processes within the FD–ISHB case and compare it to other cases of governance in the context of pest management (i.e., Mackenzie & Larson 2010; Zalom *et al*. 2013; Petersen & Wellstead 2014). Accordingly, I used NVivo qualitative analysis software (QSR International, v. 1.3.2) to code text from public documents, field notes, and 16 transcribed public recordings that related to those key conditions within the theory of collaborative governance (Bernard 2017). I also used open coding on these text data to uncover potential emergent themes not in the literature, progressively grouped themes, and finally theorized a relationship between these themes (Miles & Huberman 1994). Codes were attributed to speaker identity (e.g., invited participant, sub-committee co-chair, executive committee member, note taker) and affiliation (e.g., state agency, NGO, academia); issues of concern (e.g., firewood movement,

knowledge gaps, identified needs); evidence of prior cooperation or conflict (e.g., explaining previous efforts, sharing learned lessons); engagement activities (e.g., seeking broad participation, sharing knowledge, following up, brainstorming, delegating); intermediate outcomes (e.g., action item, new opportunity, new partnership); expressions raised in conversation (e.g., expressing enthusiasm or understanding); nonverbal characteristics in conversation (e.g., intonation, pacing, sighing, laughing); and patterns of listening (e.g., mirroring, asking questions, summarizing, interrupting, ignoring).

Finally, I used the content from meeting minutes and the *Invasive Shot Hole Borer (ISHB) Strategic Initiative* final report (Lynch 2019) to establish links between collaboration dynamics and process outcomes. The document was reviewed and vetted by executive committee members and selected participants and is publicly available on the ISCC website (www.iscc.ca.gov/ishb.html) for transparency and accountability to legislators who wrote Assembly Bill No. 2470. The report, which details the outcomes of our efforts, has been distributed to over 500 stakeholders using the UC ANR collaborative tools system and used by the CDFA to appropriate the $5 million towards FD–ISHB management priorities. The report was also used by other funding sources (e.g., USDA Forest Service, CAL FIRE) to fund other priorities not covered by AB 2470.

Limitations

While this study benefits from the deep working relationships I developed with members of the social network involved, there are some important limitations to the methodology worth mentioning. Participant observation allowed me to capture the nuances associated with social interactions in this case, but my conclusions rely on verbal and non-verbal communication in participant exchanges. There is a risk that consensus was reached because of "group think," where members in highly cohesive groups reach a premature consensus because they value "harmony and coherence above critical thought" (Janis 1972). The links I make between collaboration dynamics and process outcomes could be strengthened through additional methods, such as pre- and post-collaboration surveys or in-depth interviews, that ask a representative sample of participants direct questions related to enhanced social learning and improved actions as a result of cooperation (Blatner *et al*. 2001). However, because of my position as an insider and participant/leader, it is uncertain whether such data would be subject to response effects that come from respondents "editing" their answers (Bernard 2017). As such, I chose to proceed using naturally occurring data while recognizing those limitations.

Findings and Discussion

Process outcomes– collaborative actions

In theory, collaborative actions refer to the steps taken to "... implement the

shared purpose of the CGR" (Emerson *et al*. 2012). The Invasive Shot Hole Borer Sub-committee of the California Invasive Species Advisory Committee (CISAC) set out to develop essential components of an evolving statewide FD–ISHB Integrated Pest Management (IPM) program and prioritize the use of $5 million to implement the most critical parts of the plan associated with Survey, Detection, and Rapid Response (Survey), Research and Technology Development (Research), Greenwaste and Firewood as Pathways (Pathways) and Outreach and Education (Outreach). After collaborating in corresponding sub-committees to build consensus on priorities and projected budgets for each, participants gathered in a follow-up meeting to decide on priorities for the plan as a whole. Out of this two-month process of highly focused, dynamic collaboration, participants came to a consensus on a comprehensive set of action steps (Table III) and long-term goals that I argue were enhanced by the process, which was supported by the system context, and could not have been attained by any of the organizations acting alone.

Collaborative governance theory promises new innovations to solving old problems through an enhanced generation of new knowledge through social learning that produces new knowledge integrated with insights from different knowledge systems (Gerlak *et al*. 2012; Bodin 2017). However, the direct link between collaboration dynamics and collaborative actions is often difficult to document empirically because key actions take place over time while under the influence of the system context (Conley & Moote 2003; Koontz & Thomas 2006). In this study, it was easier to attribute enhanced actions as products of features of the decision-making

process because decisions were made over a short time frame, and action items were implemented quickly after the process was completed. The connections between dynamics and actions are evident in the way the action items had impacts across sub-committees (Table III). For example, most of the priorities identified by Pathways were addressed through action items prioritized in the other sub-committees. Those priorities included conducting studies on greenwaste post-processing treatments (Research); prioritizing greenwaste facilities, firewood stockpiles, and distribution sites in survey efforts (Survey); and developing paired online-field training programs tailored to target audiences who focus on greenwaste (i.e., "Land Management and Greenwaste") and firewood (i.e., "Campground and Recreation") (Outreach) (Lynch 2019). In another example, the Outreach Sub-committee also "...recognized the imperative need of developing specific printed materials and trainings to be used as an important component of projects identified as priorities by the Survey and Pathways sub-committees" (Lynch 2019, p.7) in their summary of priorities. These cohesive process outcomes were born out of effective principled engagement, participants' deep understanding and appreciation of the system context, and the salient forces of leadership and interdependence baked in throughout the project.

System context and prior histories

Cooperation and conflict

Much of what contributed to the comprehensive set of outcomes with minimal conflict in the FD–ISHB case comes from the conglomerate of many local efforts in

Southern California that catalyzed the endeavor to develop a statewide plan and from a prior history of cooperation and conflict associated with other important pest problems and fire in California and North America over the last 20 years. Examples of novel-pest experiences that participants drew from at various points in different sub-committee discussions include (1) the goldspotted oak borer beetle (GSOB, *Agrilus auroguttatus*) and the pathogen *Phytophthora ramorum* (the cause of sudden oak death, or SOD), which are responsible for widespread oak mortality in Southern and Northern California respectively (Rizzo *et al*. 2002; Coleman *et al*. 2011; Lynch *et al*. 2014); (2) the emerald ash borer beetle (EAB, *Agrilus planipennis*), which has killed hundreds of millions of ash trees in urban forests and wildlands North America; (3) native bark beetles (BB, *Dendroctonus* spp., *Ips* spp.), which have killed billions of pine trees across millions of hectares of forest in North America in association with climate change (Nordhaus *et al*. 2009; Petersen and Wellstead 2014); (4) the Asian citrus psyllid (*Diaphorina citri*) and huanglongbing disease (HLB), which have caused massive citrus decline in Florida and recently established on citrus in Southern California (Warnert 2012); and (5) the glassy-winged sharpshooter, which vectors the bacterial pathogen *Xylella fastidiosa,* causing Pierce's disease on hundreds of important crops and ornamentals in California (Varela *et al*. 2001).

Most of the participants or the organizations they represent were actively involved in those previous efforts or highly familiar with the cases because of their widespread destructive impacts on forests and agriculture. The majority of

stakeholders were particularly close to efforts involving GSOB and BB because of their history in Southern California, where FD–ISHB is having the greatest impact. The BB case involves an interagency collaborative effort, the Mountain Area Taskforce (MAST), that formed after an unprecedented bark beetle outbreak killed over 14 million trees across 70,000 hectares of the San Bernardino National Forest (SBNF) (Merrill 2003; Petersen & Wellstead 2014). This landscape-level outbreak in the early 2000s was induced by drought and a legacy of fire suppression, posing a significant fire threat to local communities. Two other key high-value crop pest cases from Northern California were part of the system context because of the state and federal regulatory agencies involved. These pests include the light brown apple moth (LBAM, *Epiphyas postvittana*), which threatened strawberry, caneberry, and nursery plants in Monterey, Santa Cruz, and San Mateo counties; and the European grapevine moth (EGVM, *Lobesia botrana*), which impacted grapevine in Napa and Sonoma counties (Zalom *et al*. 2013).

Four of the above plant health response cases have been studied to understand which factors contribute to prior histories of conflict (EAB and LBAM) and cooperation (BB and EGVM) in management decisions (Mackenzie & Larson 2010; Zalom *et al*. 2013; Petersen & Wellstead 2014). The cases provide insight into how the system context was used and contributed to successful collaboration in the FD–ISHB case, but there are important similarities and differences among them worth mentioning. The EGVM and BB cases involve a "bottom-up" governance approach, whereas the EAB and LBAM cases represent a "top-down" form of governance.

Interestingly, the LBAM and EGVM cases involve two Lepidoptera species in the Tortricidae family that were introduced to nearby counties in California, but response measures in the LBAM case provoked ire while the EGVM case was considered to be a model response (Zalom *et al.* 2013). Most importantly, the cases concerning EAB, LBAM, and EGVM involve cooperation or conflict between the public and technical and regulatory experts while implementing certain responses to plant health emergencies, whereas the FD–ISHB and BB cases concern cooperation among organizations to address pest management challenges.

Prior history of cooperation over FD–ISHB and GSOB was clearly acknowledged in many discussions throughout the consensus-building process, which contributed to creating essential bonds of shared commitment (Emerson *et al*. 2012) and facilitated efficient and effective decision-making under the given time constraints. As one member of the Executive Committee explained in an Outreach meeting:

> ...there's a lot of folks on this call and a lot of folks that aren't on this call that have been doing a *ton* of outreach and education work with regard to GSOB, firewood, shot hole borers over the last several years. We've been doing it on a shoestring budget basically and it's been an added job to a lot of plates that are already full. And so, I just want for the record that a lot of work has been done, people have been doing tons and tons of work... I mean we've touched millions of people just through state fairs alone and so... everybody ought to be patting themselves on the back for as far as we have come with already full plates and basically almost a zero budget for this.

This deep commitment to engagement entering into the process is recognized to be an important quality in successful collaborative governance (Ansell & Gash 2008) because it is through these prior relationships and networks that "partners judge trustworthiness of other partners and legitimacy of key stakeholders" (Bryson *et al*. 2006, p.46). Meeting minutes from each of the inaugural sub-committee meetings outlined a substantial exchange of ideas, assigned tasks, and designated working groups to drill down on certain issues (Lynch 2019), signifying meaningful progress. At the same time, the overall mood in those meetings was jovial and filled with many moments of levity and laughter. The notable amount of productivity combined with good humor from the start indicated an established sense of trust in existing working relationships, which was maintained and strengthened as the process unfolded. As such, more time could be devoted to getting down to business instead of "remedial trust-building" (Ansell & Gash 2008).

Established capacity for common purpose

Particular institutional and political dimensions of governance that proved effective in addressing previous landscape-level pest problems in California (Petersen & Wellstead 2014) provided a model framework for the ISHB Sub-committee, which in turn supported effective engagement and expedient decision-making once the process launched. The framework can be traced back to when the California Forest Pest Council and CAL FIRE formed the California Oak Mortality Task Force in 2000 to work together on minimizing "the impact and spread of *P. ramorum* on natural,

agricultural, and human communities" in Northern California (COMTF Partners 2020). The structure consists of a core executive committee and sub-committees that reflect a “fluid array of multi-tiered bodies with overlapping and crosscutting jurisdictions, which are typically organized around specific functional tasks” (Tollefson *et al.* 2012, p.6). A similar integrated response materialized two years later with MAST in Southern California, which Petersen & Wellstead (2014) recognized as a "new governance arrangement." The authors reported that the governance structure enabled MAST to achieve short- and long-term goals in protecting mountain communities from looming catastrophic fire threats created from BB outbreaks, and implementation of the plan was well-received by the public.

The ISHB Sub-committee’s institutional arrangements concerning membership and organizational structure (Tables I-II) emulated previous consensus-driven coalitions that promoted diverse representation at every level of the decision-making process and set a precedent for inclusive planning and consultation (Tollefson *et al*. 2012). The sub-committees represented key "functional components" of the statewide plan, allowing participants to "drill down into" various issues, solutions, and opportunities relating to a specific area of concern within a relatively short amount of time. Sub-committee meetings coincided but scheduling times did not overlap to encourage participants to attend all meetings. This overall setup addressed common critical barriers to implementing actions and setting priorities associated with landscape-level pest problems (Petersen & Wellstead 2014).

However, the institutional arrangements also created a unique opportunity for participants to address emerging issues and knowledge gaps at the intersection of the plan's functional components. For example, previous research determined that chipping and solarizing infested wood can kill 99.9% of the beetles and dramatically reduce their risk of long-distance dispersal in plant material if chipped to pieces smaller than 5 cm or solarized for at least six weeks under ideal conditions (Jones & Paine 2015). Therefore, the need for additional research on greenwaste treatments was not recognized until it was discovered through discussions with experts from CalRecycle in the Pathways Sub-committee that these treatments are not an option for many greenwaste processors who do not have chippers and are required to move their greenwaste material within 48 hours. The institutional arrangements consequently contributed to finding better solutions to control FD–ISHB because they created a mechanism to quickly share this new knowledge from unique voices to the people in a position to prioritize more research on greenwaste processing treatments for the state (i.e., the Research Sub-committee).

In addition to membership and organizational structure, the ISHB Sub-committee's institutional arrangements embodied some degree of formality similar to those in MAST. Co-chairs in each sub-committee e-mailed and posted pre-approved agendas at least one week before every meeting. The itinerary on those agendas followed a specific, predictable order but was flexible enough for fluid discussions. Participant roles were clearly defined. Goals, expectations, timelines, and tasks were explicitly stated at relevant points in every meeting. Meeting minutes were approved

following a specific procedure. This level of formality is regarded as a particularly important design feature in governance structures that are facing plant health emergencies because clear, fair, and transparent procedures bring legitimacy to the process so that stakeholders trust that the deliberation has integrity (Fung & Wright 2001, 2003; Imperial 2005; Maldonado & Merrill 2000; Ansell & Gash 2008). Because there was no formal agreement binding participants to the effort, process transparency was critical to ensuring stakeholders' confidence in voluntarily committing to the process.

Finally, the institutional arrangements in the ISHB Sub-committee reflected an understanding of factors that contributed to cooperation and conflict in previous cases. As Crowley *et al*. (2017) predicted, governance approaches were the primary causes of consternation in the EAB and LBAM cases in that management decisions rested with the state and were communicated unidirectionally (Mackenzie & Larson 2010; Zalom *et al*. 2013). Media analysis, focus groups, and in-depth interviews with individuals directly involved in the LBAM (controversial) and EGVM (not-controversial) cases revealed that the biggest difference in the EGVM response was the clear presence of local leadership (e.g., County Agricultural Commissioners, Cooperative Extension) investing early in building strong relationships and support networks with the community (e.g., citizen groups, environmental groups, agricultural industry groups) (Zalom *et al*. 2013). Although public voices were not part of the planning process in the present study, the inclusion of "on the ground" local leadership (Table I) and a stand-alone sub-committee focusing on outreach and

education reflects the inclusive and anticipatory approach adopted in the EGVM case because it established a means for local leadership to discuss information about imminent threats with the public ahead of any decisions. Prior efforts established a robust information sharing system through UC ANR collaborative tools, which served to expedite communication of new knowledge or updates from local leadership to the public. Outreach and education committees were also components in California Oak Mortality Task Force and MAST and provided the apparatus for shared decision-making, critical early face-to-face dialogue, and open, responsive communication between neutral, non-regulatory parties and different groups. This arrangement "enabled MAST representatives to effectively communicate with the public to generate support for forest management actions that prior to the outbreak would not have found support" and "played an important role in moving objectives forward" (Petersen & Wellstead 2014, p.8). The care put into establishing such a system that promotes a well-coordinated emergency response was also linked to decreased pesticide use and, overall, more sustainable pest-management programs (Zalom *et al*. 2013).

Overall, the social mechanisms emerging from the system context created the capacity for participants to achieve a common purpose entering into the FD–ISHB decision-making process. Rather than an outgrowth of principled engagement (Emerson *et al*. 2012), this capacity for joint action formed the essential leadership structure, which together enhanced effective engagement once the FD–ISHB decision-making process mobilized.

Leadership

As expected, leadership was instrumental in promoting the successful outcomes produced by the ISHB Sub-committee. Engagement was driven, maintained, and strengthened by key leadership attributes. Environmental Horticulture Advisor John Kabashima from UC Cooperative Extension took the initiative to mobilize the necessary people to bring the FD–ISHB issue to the legislature and secure funding for a cohesive statewide plan. While he propelled the process into action, the leadership structure set the direction and tone for effective engagement, which was enhanced by the quality of leadership as the process unfolded.

Leadership structure

Given that collaborative governance "requires a commitment to a positive strategy of empowerment and representation" (Ansell & Gash 2008, p.552), perhaps the most important boon that emerged from the system context was a strategic hierarchical leadership structure that distributed power across participants and created opportunities for new leaders to emerge (Table II). Multiple leadership opportunities and roles that reflect various stakeholders' strengths at different points in the CGR are essential to a successful collaborative governance framework (Bryson *et al*. 2006; Emerson *et al*. 2012). The ISHB Sub-committee consisted of multiple types of leaders who participated in every discussion. The CISAC Executive Director, who presided over all ISHB Sub-committee meetings, provided strong facilitative, administrative,

and network leadership and glued all the sub-committee activities together. Executive committee members participated in decision-making and liaised with their respective local, state, and federal entities. Co-chairs led discussions, delegated activities, and shared the workload to conserve one another's time. This collaborative leadership structure created a network of support, a collegial atmosphere, and an added level of accountability, clarity, and procedural transparency and integrity.

The leadership structure also created more opportunities for participants to volunteer for leadership roles as the planning process unfolded and new needs were identified. Volunteers coordinated actions between meetings through smaller working groups within each sub-committee, and these working groups reported back accomplishments and recommendations to the broader sub-committee for discussion and consensus-building. Empowering participants to be part of the decision-making gave stakeholders a sense of ownership of the process, strengthening their trust and commitment to the project (Ansell & Gash 2008; Tollefson *et al*. 2012). Working groups also cultivated new and unique working relationships among diverse stakeholders (e.g., researchers and LEA officers; Disneyland horticulturists and Cooperative Extension Communication Specialists), which generated a collective sense of ownership. This shared theory of action contributed to building new capacity for joint action, which is key to ensuring that collaborative actions are implemented (Emerson *et al*. 2012).

Facilitative leadership

The most common theme that emerged from group interactions was established through critical facilitative leadership – the importance of building and strengthening relationships. In a social network analysis of bottom-up collaborative environmental governance, Guerrero *et al*. (2015) found that self-organized networks would still benefit from some degree of facilitative leadership because social and ecological processes propagate across scales and extend beyond the problem-solving capacity of self-organized networks. A precedent for goodwill was set at the start of the planning process because of the prior history of cooperation among different individual groups. However, leadership was crucial in building and setting the tone for an inclusive group rapport to ensure broad and active participation and productive group dynamics (Lasker & Weiss 2001).

As a facilitator, the CISAC Executive Director (**F**) actively worked to align participants in the same direction to achieve a shared goal. Examples include interjecting to ask a participant to define an acronym they used and ensure a common understanding; fielding questions; following up with participants to verify that questions or honestly expressed disagreements were addressed appropriately; redirecting discussions back to the main topic when they began to drift; soliciting input from silent participants; checking in with the note taker to ensure key points were "captured"; summarizing threads of conversation into opportunities, action items, needs, or solutions with the group to find consensus on next steps; and acknowledging participants' contributions. Co-chairs and working-group coordinators also embodied this style of leadership, creating a culture of inclusive planning and

consultation where participants were regularly told "we need your help" and that their time and energy was "really appreciated."

Facilitative leadership was particularly important in mitigating conflict by allowing participants to express honest disagreements, validating what was shared, and arriving at a mutual understanding to achieve collaborative actions. The following exchange in the second Research Sub-committee meeting illustrates those efforts when a participant (**P65**) raised concerns over creating short- and long-term research categories to prioritize projects:

> …I think one of the things that we do wrong with most of these kind of emerging pest things is that we only concentrate on short-term success. And then you often get also the crazy ideas that where, you know, who knows, maybe it'll work. But uhm, then after a while, it's still the fundamental knowledge that we lack of uh, the biology of these things and the interactions that ultimately is going to result in the solution. And uhm, in the beginning, I think the whole emphasis on this uhm, short-term research for political reasons, it seems to me is, is scientifically not smart.

Here, the Research Co-chair (**RC1**) acknowledges **P65's** concerns and seeks to clarify goals with the help of the facilitator:

RC1: Yeah, I agree. That is, you know, I think the reason for the delineation between those two types of projects is because uh, we would like to see the funding that comes from CISAC, we would like to see results during the three years that the funding will be doled out. And **F**, do you want to speak a little bit more about that?

F: Well, yeah, just, just to that point, that we have the $5 million dollars. So, we're looking for projects that can be funded with a million dollars in the short-term uhm, and they can have a three-year duration to fund those projects. And then simultaneously looking for the more long-term projects....So, the whole kind of goal of this effort is to have a prioritized list that everyone kind of agrees on. So if you, U.S. Forest Service, or CAL FIRE, or uhm you know, Farm Bill Funding comes up with an extra, uhm you know, X amount of dollars, they can just go right down the list uhm, of priority items, because right now it's in difficult for some funders to go "well, there's so many ideas out there," they they're looking for a comprehensive list of uhm, that have been

vetted through a public process so that everyone's kind of on the same page. So, I hope that helps, **P65,** to understand the difference between…

P65: I do understand it, and I still think it's not a smart way of going about it.

Still not seeing eye to eye, the facilitator asks **P65** for more input rather than aiming to convince **P65** to adopt a particular point of view and works to identify points of agreement:

F: What would you propose?

P65: So, I think what we really need to know first is okay, what, what can be an ultimate solution for this problem? Can we see spraying insecticides as being a solution?

F: So, we're with you on that. There has to be some type of uh, solution.

P65: So, I think we just needed to sort of concentrate, let's say, for instance, you know, should we do a lot of monitoring? You know, I think what we need to know is where the bloody thing is, but it would be nice to spend our effort on trying a solution versus saying, "Hey, you guys have this beetle. What are we gonna do about it? Well, we don't know what to do about it." And so, you know, I think we need to put all our eggs, doors, whatever in trying to come up with a solution. And, uhm you know, and sometimes it is, not something that can be arranged in one or two years.

Building off of **P65's** comment, the second Research Co-chair asks additional questions to identify links between the short- and long-term categories:

RC2: Could it be that these are uhm, you know, the the structure of this is short-term funding, but it's kind of like a launchpad to continue doing this research in the long-term as well…to get to continue the work and get it going uhm, until other opportunities come in. So, there you know, there is continuous work on long-term solutions?

P65: Yes, my understanding is it's not what, what is politically savvy in this case.

RC2: Yeah.

F: We just, we're just faced with a pot of money so that we have to get it out the door. Uhm, you know, we're fine with trying to develop long-term solutions. It's just trying to figure out what those mechanisms are and if that is the goal of this exercise

P65: All right, well, let's keep on exercising.

The facilitator followed up on **P65's** concerns later in the meeting when a research need was identified to potentially use available short-term funds towards a particular long-term research project:

> **F:** And I guess the second point would be, to kind of **P65's** point earlier, that **P65**, do you see value in this type of research versus- you were just talking about, you know, trying to develop solutions, right. Isn't this a component that, that, should be part of it?
> **P65:** Oh, definitely. I think it's really important to have these long-term studies to try to determine what goes on. This, this this kind of work is invaluable. And generally, it's not done because it takes too long. Any papers will come up, but it's really important.
> **F:** Okay, thank you.

This frank, open exchange exemplifies how leadership used active listening to facilitate a better group understanding of the importance of how short-term research fits into long-term goals, which was not clear to everyone upfront. Clarity of aims is essential if "joint working partners are to work together to operationalize policies" (Huxham 2003, p.404). This mutual understanding led to participants ranking that particular research project as a top priority in the final meeting, linking process to outcomes.

The pivotal role of leadership in inclusive planning was especially clear when prioritizing actions under an omnipresent awareness of time scarcity. As the CISAC Executive Director put it, "we have some very interested legislators are that are watching this process, and that want us to move forward as quickly as possible, so we don't really have the luxury of additional time, unfortunately." This time constraint sometimes created a palpable

tension between needing to "move on" and ensuring broad participation, but was mitigated by executive leadership.

For example, part of every meeting agenda were introductions at the beginning, when each participant stated their name and affiliation, and public comment at the end to solicit additional participant input. Introductions and public comment each typically took 20-30 minutes because there were many participants. While one co-chair at an inaugural meeting was wrestling with the sincere desire to proceed with introductions but concern it would "take a little bit too much time to go through everyone," the CISAC Executive Director interjected to ensure each participant had the opportunity to introduce themselves. Similarly, the director stepped in when the end of another inaugural meeting approached before getting to public comment, saying, "Well, we need to go through just briefly and make sure we're hearing from folks. That way, we ensure that they contributed." Leaders expressed a genuine interest in stakeholders' opinions regardless of how deeply they were involved in FD-ISHB matters, as highlighted in this example: "And, so **P23**? Your mic's open please…you're in Stanislaus County. We're just reaching out to make sure that we're hearing from you and getting your input on this process." The director's time and care in acknowledging each participant and seeking broad participation demonstrated to everyone that hearing every voice in the room mattered most – even though it meant that every meeting finished 15-20 minutes late. All leaders embodied this commitment to transparent, fair, and inclusive processes that executive leadership modeled, which is linked to nurturing trust (Davenport *et al*. 2007; Leahy & Anderson 2008).

Principled engagement

The direct antecedents of the ISHB Sub-committee planning process set the stage for people with different perspectives, skills, and expertise across institutional, sectoral, and jurisdictional boundaries to deftly build consensus on needs, knowledge gaps, solutions, and action items related to statewide FD–ISHB control priorities. After group introductions, participants naturally stepped through topics following a set of iterative collaborative learning phases (Daniels & Walker 2001), which Emerson *et al*. (2012, p.11) identify as "four process elements: discovery, definition, deliberation, and determination." Briefly, *discovery* refers to identifying the scope of the problem or challenge, determining capacity needs, investigating facts, and determining shared interests, concerns, and values (Ozawa 1991; Ehrmann & Stinson 1999). Participants then *define* their purpose, objectives, criteria, concepts, tasks, and expectations through continuous consensus-building efforts. After *deliberation*, or the "thoughtful examination of issues" through "candid and reasoned communication" (Emerson *et al*. 2012, 12), *determinations* (e.g., procedural decisions, action items) are made.

Together with a commitment to inclusive planning and consultation, this principled engagement created an explicit operating rationale to set shared goals fairly, freely share knowledge and resources, and efficiently achieve durable collective courses of action. As one participant put it, "I just wanted to thank everybody. I thought this was a pretty productive discussion an' kind of focused

everybody in a little bit more on how we can come forward, you know, move the whole process forward."

Process element qualities

The quality of the above process elements observed in the ISHB Sub-committee's participant exchanges reflected the group's commitment to a thoughtfully designed and comprehensive statewide action plan. Collaborative governance literature highlights the importance of actively seeking broad participation in bringing legitimacy to the process and producing successful outcomes (Ansell & Gash 2008), a common behavior that emerged from group interactions in all sub-committee meetings. For example, the ISHB Sub-committee worked to cast a wide net ahead of time and invite as many representative people as possible to the project through various communication channels. Additionally, the initial discovery step in the inaugural sub-committee meetings involved Co-chairs soliciting participants' input on who was missing from the discussion and needed to be recruited – before delving into identifying issues, concerns, and opportunities related to the focus of each sub-committee. This added step of asking participants upfront to be involved in carefully thinking through who needed to be at the table signaled a clear commitment to process transparency and inclusive planning and consultation, which is linked to building trust and a shared commitment to achieving goals (Ansell & Gash 2008; Emerson *et al*. 2012).

Another reliable sign of effective engagement is the acknowledgment of one another's deliberative contributions (Vries *et al*. 2011). Responding directly to a colleague's comment was common throughout the sessions and accompanied by a tone of mutual respect, even when people disagreed. The example from the first Outreach meeting below highlights this observation when a participant raised concern after a long discussion over revamping existing websites:

> **P25:** Um, I'm hoping, I, I think determining what to do with the map and the website is important but I hope we will shortly get to active outreach as opposed to passive outreach- who are we going to target what, what audiences do we think we need to reach other than the discussion we just had about the greenwaste and the chip and mulch users. Um and I think, and I think the legislature might be more impressed by outreach effort, active outreach effort rather than fixing a website.
> **OC1:** Gotcha.
> **P72:** This is **P72**, I agree with **P25**.

The above exchange quickly moved the discussion in a new direction. Participants contributed new ideas such as incorporating FD–ISHB educational materials into K-12 curriculums, reaching out to and working with Homeowners Associations, creating a social media presence, augmenting citizen science programs, and hiring a statewide Outreach and Education Coordinator. The deliberation culminated in a group consensus to create two working groups that drilled down into the details of hiring an Outreach and Education Coordinator and creating a list of existing and needed target audiences (Lynch 2019). Another example includes an exchange that occurred in the third Outreach meeting when the facilitator **(F)** raised the idea of hosting FD–ISHB educational materials on multiple agency websites:

P68: I strongly disagree with that, **F**, for one reason. If we put the materials on all three, then we have to update the materials on all three...

F: No, you just put a link to it. Negative- you just, you just put a link to the materials. So, the material will always be up-updated from the original owner of the document. And then you just put a link to that information. So that's always updated.

P68: Great. Just wanted to clarify that.

F: Sure, yes ma'am, no, I agree. Yeah, that's that's an issue. Yes, no, I would, I was suggesting to just, putting the link to the materials so that when it is updated, they all have the same information.

In most cases, direct acknowledgements came up when participants expressed agreements, such as the following exchange in the third Pathways meeting between a Pathways Co-chair (**PC2**), the notetaker (**N**), **F**, and a participant (**P40**):

PC2: …. One of the composting companies here in Orange County, they produce a product- or it might be wood chips- but they coat it with a substance that makes it less likely to burn so it can be safe for landscaping. And one of the questions I had for research is is can some material be chipped and then coated with something, whether it's a fertilizer or whatever to- maybe that renders it fire, less capable of burn but maybe it also takes care of the shot hole borer too.

N: I got it.

F: Okay, we've captured that.

P40: This is **P40**. I want to support **PC2's** comment because we, we've been focusing mostly on compost. But um, you know, chips are ubiquitous and they're a lot cheaper to produce. So it would be great if we could vet some ideas with regard to chip production and mulch, larger size mulch.

The above exchange led to the group determining an action item for the Research Sub-committee to discuss as a potential research need; the ISHB Sub-committee eventually ranked the idea at the top of the list of research priorities.

Acknowledgments also came in the form of giving credit to other participants' previous efforts and how they contributed to advancing next actions, as revealed by one participant in the third Survey meeting, who volunteered to help develop example survey and rapid response protocols that could be used in the current efforts:

> I just want to acknowledge that I just took a lot of what **SC1** put together an' just kind of reformatted it and took out the actual details on specific uhm trapping uhm methods…. for the interest of, you know, hitting the hot topics, this is what I- this is the excerpted version with most of this credit going to **SC1**…. Similarly to what we did for the visual uhm surveys, I just pulled together what I thought was hitting the topics that we thought were most important. And I want to thank **P46** for uhm, kind of sending along the text for the section on zones with infestation. And I want to take full responsibility for any mistakes I made about the quarantine section because that's something I really don't know anything about so I just did my best with what I had heard from everyone…. So, uhm once again I, I'm hoping that **SC2** and uh **SC1** will spread this to share this with the rest of the group. Uhm, please feel free to edit, add, subtract, delete, whatever and get it back to me as soon as you can and I'll get it back out to everyone before I leave next week incorporating any comments or suggestions.

This example highlights how participants recognized one another's contributions but also demonstrates the important role of interdependence in collaborations and how the collaborative process itself shapes it – a common theme revealed from the group interactions. Ansell & Gash (2008, p.562) explain that "through dialogue with other stakeholders and through achievement of successful intermediate outcomes, they may come to a new understanding of their relationship." In addition to giving credit to others as appropriate, the participant explained her

contribution while recognizing her limitations and the need for more input from other, more knowledgeable group members.

Similarly, in many instances participants who had never before interacted, asked one another questions in many instances and shared what they knew to arrive at a shared understanding of the scope of a problem and appropriate next steps. In the example below, **PC2** starts a discussion in the first Pathways meeting over issues concerning how to track greenwaste material. A participant from CalRecycle (**P12**), who was an expert on all the greenwaste facilities in the state but did not know about the current distribution of shot hole borer around those sites, wanted to understand previous surveying efforts better:

P12: Uhm, **PC2**, do we actually have some trapping that was done that shows, this is **P12** from CalRecycle, that shows, you know, shot hole borer near sites? Is what I'm hearing?

PC2: I'm going to defer to some of the folks in the audience. I know there was a site down in Orange County uh where they had that occur and I believe that is also true in some other counties. Is there somebody? **E3**? **OC1**? That can speak to that or **RC2**?

P67: This is **P67**. We actually trapped around a number of greenwaste facilities in Los Angeles County and detected shot hole borers within about 100 to 200 meters of each locations. That was in 2017.

P12: What kind of facilities were they? Do you know?

P67: Um, they were bio-waste facilities where landscapers would bring all kinds of greenwaste and they chipped on site and then they went either from, the material was either then sold back to landscapers to use as mulch or it was sent to a bioenergy facility.

P12: Okay.

PC2: So I believe there is an opportunity or a need to, perhaps, there's the Survey, the uh Detection and Rapid Response folks that maybe will address putting out traps around greenwaste sites and whatnot. But it is an issue…

In sharing their knowledge and experience with one another, it became clear to the group of the need to monitor greenwaste facilities to understand better the role of greenwaste in FD–ISHB long-distance dispersal. This shared perspective created cohesiveness among those involved, a shared understanding of the problems they collectively faced, and, most importantly, the ability to implement the necessary solutions using the proper mechanisms. Bringing these entities together in the collaborative process opened the door to creating new partnerships between local County Agricultural Commissioners and local enforcement agencies (LEAs), who previously did not cross paths (Table III). Similar to the relationships between CDFA and local County Agricultural Commissioners, who were charged with implementing a trap monitoring program, CalRecycle delegates enforcement authority to local enforcement agencies (LEAs), who have established trusting working relationships with greenwaste processors. Because Agricultural Commissioners did not have a history of working with greenwaste processors, the partnership with LEAs was imperative to facilitate communication between them so they could access their sites and deploy monitoring traps.

In sum, these exchanges demonstrate how the process of principled engagement and a commitment to inclusive planning and consultation allowed the ISHB Sub-committee to leverage knowledge from a range of perspectives and augmented capacity for joint action. Engagement also enhanced group learning, trust, and interdependence, creating the social capital that motivated participants to work together to develop unique and comprehensive collaborative actions.

Contributing to the system context

In this study, the system context influenced collaborative processes in a positive and meaningful way. Most significantly, however, was the revelation that participants were actively aware and appreciative of how the system context contributions and the importance of making decisions that contribute back. The following statement from the Pathways Co-chair in a Survey subcommittee meeting provides a useful example:

> I just want to say that part of this rapid response, idea of rapid response is trying to identify key players, agencies and other groups before the infestations even arrive so you're ready to come up with a rapid response plan. Also, identify issues like where would funding come from to help private property owners, etc. And just a couple examples with goldspotted borer (GSOB) in Riverside County. There had been the Mountain Area Safety Taskforce (MAST) created because of bark beetle kill back in the early 2000s. And when goldspotted borer showed up, they they already had all the agency in there working together– Caltrans, the fire agencies, forest agencies, the public utility companies, and whatnot. They were already used to working together on the fire issue, they immediately turned around and were able to take action on goldspotted borers. So, having that kind of organization up, kind of figured out up front before it actually, the pest actually arrives can be very valuable.

The statement was essentially a call to participants to put systems in place that elicit an effective response to new FD–ISHB introductions, but to also consider that those efforts will have benefits beyond the current system, similar to how MAST efforts benefited the GSOB response. Thinking more broadly was encouraged in many instances. Another example includes a discussion over a statewide Outreach and Education Coordinator position as working group members reported their efforts back to the Outreach Sub-committee:

P31: …one thing that **P69** and I discussed was including room and for other emerging tree pests. So uhm, if we wanted this person to incorporate, or be flexible and adapt information, should another emerging tree pest be found? You know, do we want to coordinate any new messaging with our shot hole borer messaging? So in the beginning, I think, she changed the title of the position a little bit.

P69: Yeah, one, one thing that I wanted to add is going even beyond the position itself. I just strongly encourage this committee to really do some long-term thinking when we do things like establish those social media presence and make sure that are developing something that is sharing a message that this is not just this one pest and when it you know, if...we, you know, solve this problem, the whole concept doesn't go away. So that we're making sure that we're, you know, on message with the Firewood Task Force and that kind of thing that, you know, overall for all tree pests. Think about that so, so when you even then, like your name on Facebook page, Twitter account or something like that, that we don't sort of pigeonhole too much just into shot hole borer.

P40: Yes, thanks. I just want to first thank **P69** for those ideas. I think it's, it's wonderful. And it'll be actually a savings in the long-term to the state and coordination of addressing invasive pests, because it's, what she's suggesting, creates a template. And uhm, and that can be used in and made specific to each species. So thanks, **P69**.

In a Pathways Sub-committee meeting, the *Don't Move Firewood* national campaign manager from The Nature Conservancy raised a similar point:

> I want to bring up an important point which is that ultimately no matter how much we're focusing right now on shot hole borers, you have to look at the issue from the the non-pest-specific perspective as well. And solarization in particular is a, is a really pest-specific treatment because like we just mentioned it only penetrates the outer edges of the wood which may be sufficient for shot hole borers to kill the fungus and to reduce the beetles viability. But goldspotted oak borer, for instance, is far more durable against solarization. So, you may be accidentally rendering the wood more likely to be moved because you haven't communicated that that's not removing the all pest threat. And when you guys talk about these issues in general, you know, I would urge you to not focus on the shot hole borers biology in driving your treatments. In case another pest rears its ugly head that has a more durable biology.

The Executive Committee member representing the U.S. Forest Service also communicated a comparable message to the Research Sub-committee:

> **F** this uh this is **E5** again just, just so the group is aware I dropped off for a little while for a federal call concurrent with the shot hole borer work that y'all are doing. And at the request of APHIS, at least our two contacts at the, at their Washington office level- it's going to be their preference that any Farm Bill proposals, that 2020 proposals that result out of the work of this group for shot hole borer here in California, be vetted here locally, uhm through this this group most likely, and have the support of this group before, if APHIS is really going to look at them at the national level. So, I just wanted to put that on your radar I think it's great that that APHIS is looking for some consensus here locally on what some of the Research and Technology Development needs they might fund for Farm Bill proposals at the national level.

Communicating this message had the added benefit of incentivizing participants to work together because their efforts had long-term advantages by creating new opportunities at the national level.

Finally, a sincere appreciation of the system context and who collaborative decisions impact was revealed in discussions concerning management activities and how to ensure good working relationships with the public. These considerations were particularly clear in discussions over rapid response activities that potentially involve removing high risk, newly infested trees from private properties. In the following example from a Survey meeting, the CISAC Executive Director (**F**) consulted with Survey and Pathways Sub-committee Co-chairs (**SC2** and **PC1-2**; from the Ventura County Agricultural Commissioner's Office and CAL FIRE respectively) over the issue:

I mean the only issue is, say you have a heavily infested tree, without homeowner permission to remove the tree what do we do? Under that scenario and the homeowner says "no, I don't want the tree removed." Um, what's the scenario? How does that play out I guess, I just curious?

After some discussion over who has the authority to remove trees on private property (e.g., CAL FIRE, versus County Agricultural Commissioners) and how the regulatory process works, the group discussed alternative approaches:

PC2: …. I'd like to suggest on the uh tree removal maybe at this stage in the game we should just go with voluntary participation by private property owners at least to get the property to the program off the ground. It may be in year two or three try and go in and take trees if people aren't willing.

SC2: Okay, I think that's a reasonable approach.

F: **SC2,** I just wanted to add a little color to that conversation that we've been very successful working with um, citrus tree owners who refused to remove their trees. We do have the authority to remove their trees. However, we try not to use that and so will triangulate and just sic a bunch of different experts on them. You know, we'll start with our staff or, you know, a master gardener or the county Ag Commissioner or depending on kind of where their issue is you got to figure out the person and it's been really helpful and kind of triangulating and making that person understand that there is a reservoir for the disease and so, you need to remove it. And it usually takes multiple tries but we've been pretty successful. And **SC2**, I know you've had to deal with some of those as well in your county clearly potentially. You know, I think using that model is going to work I guess, you know, without using the hammer. But ultimately, we should explore the hammer but in short term I think it's a path forward. I'm sorry go ahead...

SC2: No I agree with you **F.** Uhm, I I think that most homeowners if given the information that the tree is likely to die and is likely to become a hazard and is likely to become a fire hazard at some point will probably agree to allow the removal of the tree. But I think the biggest problem is is whether they end up paying for that removal or whether um, whether if some of the funds that are available can be used to remove those trees. Um, and if the funds are available to do their tree removal. And probably the best entity to do, to do those removals would be

professional uh tree companies, arborists. You know, professional tree trimming companies and that kind of thing um, under under contract.

PC1: The issue for most home owners is the cost of the tree removal- it is really expensive.

RC2: Yup.

SC2: Absolutely.

This exchange highlights a key similarity between FD–ISHB and the EGVM case, which was considered a model emergency response, and the LBAM and EAB cases, which resulted in law-suits, public outrage, and a loss of institutional trust (Mackenzie & Larson 2010; Zalom *et al*. 2013). Moreover, public pressure resulted in the early termination of LBAM treatment activities. Discussions like the example above led to action items for the Outreach Sub-committee to develop mechanisms for neutral, independent, non-regulatory parties to engage in face-to-face dialogue with the public – before there is even a problem. Interestingly, this strategy was adopted in the EGVM emergency response. Interview respondents involved in both LBAM and EGVM responses "expressed a sense that if the process they had experienced...had been used at the onset of the LBAM emergency that the ultimate outcome would have been different" Zalom *et al*. (2013, p.v). In addition to public engagement, solutions to address the effects of tree removal as a rapid response on low income property owners was taken into consideration:

P40: Yes, I have one thought and it's, it's based on **E3's** comments regarding disadvantaged property owners. I would like to suggest as a possible RFP idea setting up a trust fund or some other allocation at the county or NGO level, which would be more expedient than going through the state as far as qualifying people for assistance and treatments.

F: Yes, you know, I think that's a great idea, this is **F**, like working with like NGOs, giving them a pot of money potentially would be easier to get you know, get the funds out versus us trying to do it. So I think that's a great, there's a lot of good organizations that we've been working with on this process. So, you know, that the Tree People come to mind as well as other NGOs that could help with that. So that's a great point. Thank you.

All the examples above demonstrate how participants of the ISHB Sub-committee carefully thought through how the outcomes of their current efforts will impact the system context and, more importantly, how to ensure long-lasting beneficial outcomes.

Conclusions

It is no surprise that responses to novel landscape-level pest introductions can sometimes be controversial. Making decisions is not an easy enterprise in the face of an unexpected pest arrival with uncertain social and ecological ramifications. Decision-making is further entangled when those introductions result in outbreaks that spread across multiple land-use jurisdictions, rendering any single entity impotent to fully address the scale of the problem. However, the source of friction associated with most pest introduction responses is usually predictable – more often than not, escalated conflicts can be traced back to a top-down governance approach that was communicated either unidirectionally, with an unhelpful tone, or both. This study highlights how using collaborative governance to control a major pest-pathogen complex can lead to thorough and productive pest control strategies and effectively mitigate conflict. Analysis of participant observation and public document data confirmed that the comprehensive set of collaborative actions that emerged from a

statewide deliberative and consensus-directed process to control FD–ISHB spread and impacts were due to conditions identified in theoretical frameworks for collaborative governance (i.e., Emerson *et al*. 2012). This instance represents a model of the "best-case" scenario that could be adapted by other pest and invasive species management cases and help decision-makers prepare for "the next big thing."

The action steps in this case study were enhanced by the structure and quality of principled-engagement process elements and could not have been attained by any organization acting alone. However, these processes greatly benefited from established social mechanisms supplied by the system context that helped to establish process transparency and legitimacy entering into the project. Drawing from prior successful cases (i.e., MAST), institutional arrangements were organized into multiple intersecting "functional components" of the plan that were glued together by an Executive Committee and a facilitative leader: (1) Greenwaste and Firewood as Pathways; (2) Research and Technology Development; (3) Survey, Detection, and (4) Rapid Response; (5) Outreach and Education. This structure allowed participants to drill down deep into certain focus areas while addressing issues and knowledge gaps at the intersection of the plan's functional components. Additionally, embedding outreach into the plan indicated a commitment to anticipatory engagement with the public and other stakeholders and created the apparatus for critical early face-to-face dialogue and shared decision-making between neutral, non-regulatory parties and different groups.

The setup also generated a collaborative leadership structure consisting of multiple leader ship roles and allowed new leadership to emerge, reflecting a shared sense of ownership of the process and a commitment to a positive strategy of empowerment and representation. As a component of the leadership structure, facilitative leadership was instrumental in mitigating conflict, establishing clear expectations, and aligning participants in the same direction to achieve a shared goal. This well-established strategy of inclusive planning and consultation created the capacity for participants to achieve a common purpose entering into the FD–ISHB decision-making process.

A spirit of inclusivity was sustained and strengthened as participants representing different entities engaged in developing new ideas, projects, and partnerships. Members were committed to actively seeing broad participation, and participants' contributions were acknowledged and met with a tone of mutual respect, even when disagreements were expressed. Ultimately, participants in the ISHB Sub-committee devoted their time and energy to a short but intensive planning process resulting in more capacity for joint action, trust, interdependence, and a robust action plan that was quickly implemented.

Essentially, the elements that contributed to productive and rewarding outcomes in this study are consistent with expectations in the literature (Ansell & Gash 2008; Emerson *et al*. 2012). Although this particular pest problem is not shrouded in controversy, the collaborative governance pieces that contributed to a rewarding group effort in this case could still be applied to more thorny situations, with some modifications as appropriate. For

example, high conflict scenarios might require a professional mediator in place of a facilitator to address differences in views or deep resource and power inequities.

Further research will need to determine whether the collaborative actions implemented in this study result in improved environmental outcomes (Gerlak *et al*. 2012) or whether the rewards from the statewide FD–ISHB collaborative efforts are ephemeral. Given that the participants in these efforts were deeply committed to the cause, are highly interdependent, and make conscious decisions to incorporate long-term benefits in short-term planning, I expect that the outcomes identified in this study launched an effective statewide integrated pest management strategy to control FD–ISHB. I expect the strategy also provides a useful template that will help prepare stakeholders' responses to future novel pest introductions. Simply put by one participant at the end of these efforts, "I'm getting really excited about this."

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Table I. Stakeholder actors who share an interest or stake in a statewide management strategy to control the Fusarium dieback–invasive shot hole borers pest–pathogen complex.

	Organization
International	Comisión Nacional Forestal México (CONAFOR)
Academic	CSU Sacramento
	UC Davis
	UC Riverside
	UC Santa Barbara
	UC Santa Cruz
	University of California Cooperative Extension
Federal	United States Department of Agriculture (USDA)
	Forest Service: Fire
	Forest Service: Forest Health Protection (USFS-FHP)
	Plant Protection and Quarantine (USDA-PPQ)
	United States Fish and Wildlife Service (USFWS)
State	California Agricultural Commissioner
	California Board of Forestry and Fire Protection
	California Department of Fish and Wildlife (CDFW)
	California Department of Food and Agriculture (CDFA)
	California Department of Forestry and Fire Protection (CAL FIRE)
	California Department of Resources Recycling and Recovery (CalRecycle)
	State Parks
County	Contra Costa Agricultural Commissioner
	Imperial County Agricultural Commissioner
	Local Enforcement Agencies (LEA)[1]
	Los Angeles County Agricultural Commissioner
	Los Angeles County Botanist
	Orange County Agricultural Commissioner
	Orange County Public Works
	Orange County Waste and Recycling
	San Diego County Agricultural Commissioner
	San Diego County Parks and Recreation
	San Diego County Plant Pathologist
	Santa Barbara County Agricultural Commissioner
	Ventura County Agricultural Commissioner

City	City of San Diego
	Parks and Recreation
	Pest Control Advisor
	Storm Water Division
	San Diego Association of Governments
Non-Profit	Audubon Starr Ranch Sanctuary
	California Association of Resource Conservation District
	San Diego County
	Santa Monica Mountains
	Ventura County
	Center for Invasive Species
	Irvine Ranch Conservancy
	Ojai Valley Land Conservancy
	Southwest Wetlands Interpretive Association
	The Nature Conservancy
	Western Chapter International Society of Arboriculture
	Wildlands Conservancy
Private	Alliance Care Landscaping Company
	Arborjet
	Davey Resource Group
	Disney
	Dudek Environmental
	ICF International
	Private Arborist
	West Coast Arborists

[1]Certificated by CalRecycle to ensure the correct operation and closure of solid waste facilities in the state and guarantee the proper storage and transportation of solid wastes.

Table II. Executive and sub-committee chairs who facilitated collaborative decision making in the present study.

Committee Chair(s)	Title	Affiliation	Code
Executive			
David Pegos	ISCC Agency Liaison; CISAC Executive Director; Special Assistant, Plant Health Division, CDFA	ISCC, CDFA	F
Andy Cline	Entomologist	CDFA	E1
Joe Scheele	Automated Commercial Environment Agent	Department Homeland Security Customs and Border Protection	E2
John Kabashima	Environmental Horticulture Advisor, Emeritus	UC ANR–UC Cooperative Extension	E3
Kyle Beucke	Primary State Entomologist/ Environmental Scientist	CDFA	E4
Sheri Smith	Regional Entomologist	USDA Forest Service Forest Health Protection (FHP)	E5
Subcommittees			
Research and Technology Development			
Stacy Hishinuma	Forest Entomologist	USDA Forest Service, FHP	RC1
Shannon Lynch	Ph.D. Candidate	UC Santa Cruz	RC2

Survey, Detection, and Rapid Response			
Andrea Hefty	Forest Entomologist	USDA Forest Service, FHP	SC1
Ed Williams	Agriculture Commissioner	Ventura County	SC2
Greenwaste and Firewood as Pathways			
Thomas Smith	Forest Pest Management Specialist	CAL FIRE	PC1
Kevin Turner	Southern California Invasive Pest Coordinator	CAL FIRE	PC2
Outreach and Education			
Beatriz Nobua-Behrmann	Urban Forestry and Natural Resources Advisor	UC ANR–UC Cooperative Extension	OC1

Table III. Process outcomes (i.e., collaborative actions) that emerged from sub-committee collaborations.

Category	Action Items	Total Support
Research and Technology Development	Fund research on: • Biocontrol • IPM Efficacy • Epidemiology • Chipping treatments for greenwaste processing • FD–ISHB Economic impacts	$2,057,000 (41%)
Survey, Detection, and Rapid Response	• Hire one centralized trapping/visual survey coordinator and five surveyors • Partner with CAL FIRE to fund hazard tree removal	$2,074,392 (42%)
Outreach and Education	• Hire statewide communications coordinator • Develop training program for new target audiences. • Fund communication operations • Develop Rapid Response Tool-Kit for high-risk counties	$690,000 (14%)
Greenwaste and Firewood as Pathways	• Formalize UC ANR, County Ag Commissioner, and LEA partnerships • Expand relationship, survey, and research capacity	$150,000 (3%)