Invasion of an inconspicuous ambrosia beetle and fungus may alter wood decay in Southeastern North America

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Abstract

Background. Ambrosia beetles include well-known invasive pests, but most species established in non-native areas do not cause any significant impact. Here we report the recent invasion and rapid spread of *Ambrosiodmus minor* in the Southeastern US.

Methods: We used a combination of a multi-year survey, literature data on fungal symbionts from the beetle mycangia and in vitro bioassays of fungal competition, and extensive field observations of wood colonization patterns.

Results. In less than seven years, *A. minor* abundance has increased many-fold in Florida. The beetle is associated with an aggressive wood-rot fungus *Flavodon ambrosius*. Joint colonization of wood by *A. minor* and *F. ambrosius* results in extensive white rot (lignin removal). The invasion of this symbiosis may impact an ecosystem function previously considered not influenced by non-native ambrosia beetles: wood decay. We suggest monitoring of the impact of this invasion on native wood-inhabiting organisms, biomass degradation and the carbon cycle throughout the region.

Introduction

Xyleborine ambrosia beetles (Curculionidae: Scolytinae: Xyleborini) are notorious for invading new regions. There are at least 30 non-native species in the US alone (Gomez et al. 2018). Their capacity to establish and thrive in non-native habitats stems from the combination of the haplo-diploid, inbred reproduction (Jordal et al. 2001) and extensive host ranges, afforded by the

culturing of fungi for nutrition (Fig. 1). The reputation of ambrosia beetles as damaging invasive pests is based on a few species which colonize live tree tissues (Hulcr et al. 2017); these can cause continental-scale destruction of forest habitats (Ploetz et al. 2013) and impact nursery industries (Ranger et al. 2015). Most ambrosia beetle species, however, colonize dead wood, cause no serious damage to living trees, and remain inconspicuous in their newly colonized habitats.

The recent establishment of three Asian *Ambrosiodmus* and two closely related *Ambrosiophilus* species in North America was assumed to fall into the latter category: secondary wood-colonizers with minimal economic and ecological impact. The majority of both native and non-native *Ambrosiodmus* species are uncommon, and typically occur in wood that is already partly decayed. This is an unusual strategy for ambrosia beetles, because most ambrosia fungi require freshly dead wood to proliferate and to supply sufficient nutrients to the vector beetles (Huang et al. 2018). The genus *Ambrosiodmus*, however, is associated with a unique ambrosia fungus in the phylum Basidiomycota: the genus *Flavodon* which is a rapid wood-degrader. In fact, *Flavodon ambrosius* decays lignocellulose faster than most tested fungi, including some widespread wood rot fungi (Kasson et al. 2016). As a result, the *Ambrosiodmus-Flavodon* duo is able to proliferate in substantially degraded wood and dominate large portions of dead trees.

Materials & Methods

Abundances of the three beetle species were derived from catches in traps of the Cooperative Agriculture Pest Survey conducted by the Florida Department of Agriculture and Consumer Services (Figure 2). *Flavodon* was isolated from *Ambrosiodmus* minor using mycangial serial-dilution plating on potato dextrose agar media, and is detailed in our previous publications (Li et al. 2017; Li et al. 2016). The probable second species of *Flavodon* was identified using the amplification and Sanger sequencing of the Internal Transcribed Sequence (the “fungal barcode”) using standard ITS primers (Schoch et al. 2012).

Results

We report the rapidly increasing frequency of an Asian ambrosia beetle species *Ambrosiodmus minor* throughout the state of Florida, and the substantial change this may be causing to the typical wood-decay processes in the regional forests.

Ambrosiodmus minor was first detected in the US in North-East Florida in 2011 (Rabaglia, Okins 2011). Since then, *A. minor* has rapidly spread across the whole of Florida and neighboring states (Figure 2). In the year 2014, our team began to encounter increasing numbers of *A. minor* at our field sites and in traps in North-Central Florida. Recent field collections suggest that beetle communities in most dead branches and trunks now include *A. minor*. Furthermore, this species is often the most abundant species in the material, something not observed with other native or non-native *Ambrosiodmus* species (Fig. 3). During a field sampling

in the spring of 2017, we recovered *A. minor* from 50% of loblolly pine *Pinus taeda* trunks that had been felled 120 days previously. In 2018, the estimated proportion has increased to nearly 100% in hardwoods in an area with extensive post-hurricane tree mortality. While *A. minor* is the latest of the three Asian *Ambrosiodmus* species to have arrived to the US, in just seven years its abundance has far surpassed the earlier two species. *Ambrosiodmus minor* is the only member of its genus that is now routinely found in conifers (specifically *Pinus*) in the region.

All three Asian species of *Ambrosiodmus* in the US have been assumed to be associated with the same species of ambrosia fungus: *Flavodon ambrosius* (Li et al. 2016). This fungal species has been considered identical with the fungal associate of the North American native *Ambrosiodmus* species (Li et al. 2017), but the newly generated DNA sequence data (GenBank accession KR119074) suggest that *Flavodon* associated with the North American *Ambrosiodmus* may be a previously unrecognized separate species. Therefore, *Flavodon ambrosius*, described from *A. minor* only in 2016 (Simmons et al. 2016), may be non-native, as are all its vectors - the introduced Asian *Ambrosiodmus* and *Ambrosiophilus* species.

The key observation is that logs colonized by the *A. minor-F. ambrosius* duo display distinct areas of white rot surrounding the gallery clusters (Fig. 3). *Flavodon* is a very efficient degrader of both cellulose and lignin, and as such leaves behind wood that is of little use to most other organisms (Kasson et al. 2016). An objective quantification of the volume of *Flavodon*-rotted wood in the forests will require systematic sampling. Since no such sampling has been conducted, we instead present photographic documentation of an increasingly common phenomenon: dozens of *A. minor* galleries on a log and a substantial volume of the wood dominated by the *Flavodon* white rot (Figure 4).

Discussion

Most invasion biology studies are focused on species that impact plants that generate biomass and animals that consume them. The opposite process – biomass degradation – is much less frequently the focus of invasion biology studies [exceptions include invasive earthworms (Ashton et al. 2005) or pathogens that exacerbate tree death (Loo 2009)]. Yet biomass degradation is an essential ecological process, and its speed dictates the flow of energy, turnover of nutrients, and carbon release from forests into the atmosphere.

The current situation with *Ambrosiodmus minor-Flavodon ambrosius* colonization of the Southeastern US may not seem to be of concern at this time. What is concerning is the trend of increasing abundance. If the speed of abundance increase continues as it has in the past several years, we may eventually witness a measurable increase in the speed of wood decay in the region. This proportion of decayed wood is at the expense of native biota, which forms a substantial proportion of the native biodiversity, and is already experiencing a landscape-scale decline (Ulyshen 2018).

In addition, the abundance of *A. minor* and its ubiquitous presence in wood results in an increase of its "propagule pressure" making this species a candidate for re-export to additional regions around the world (Storer et al. 2017). The invasion may also eventually spread beyond the subtropical US. While *A. minor* is rare in Asia and recorded mostly from tropical areas [Bangladesh, Bhutan, Burma, India, Nepal, Thailand and Vietnam; (Wood, Bright 1992)], our recent investigation revealed *A. minor* in Nanjing, China. This indicates that this beetle could spread to temperate North America with freezing winters.

Conclusions

The rapidly increasing abundance of *A. minor* in the Southeast United States is of concern because it appears to increase the proportion of dead wood colonized and degraded by the beetle's symbiont, *Flavodon ambrosius*.

In the heavily forested Southeastern US, decaying wood supports myriads of native saproxylic species, ranging from wood boring beetles to termites, to wood rot fungi and their predators and grazers. Ultimately, wood decay is the dominant process of biomass recycling and changes to its rate may have a long-term influence on the time for which carbon is captured in of the region, and its capacity to serve as a carbon sink.

Acknowledgements

Data on trap catches were provided by the Florida Department of Agriculture & Consumer Services, Division of Plant Industry and the Cooperative Agriculture Pest Survey. We thank Lei Gao (Shanghai Academy of Landscape Architecture Science and Planning, China) for aid in Asian beetle collections.

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Figures

Figure 1: *Ambrosiodmus minor* live in *Flavodon*-infested rotten wood. Depicted is the adult mother beetle with her eggs, larvae and one pupa. The white lining on the tunnel wall is the mycelium of *Flavodon ambrosius* which serves as the exclusive food for the beetles.

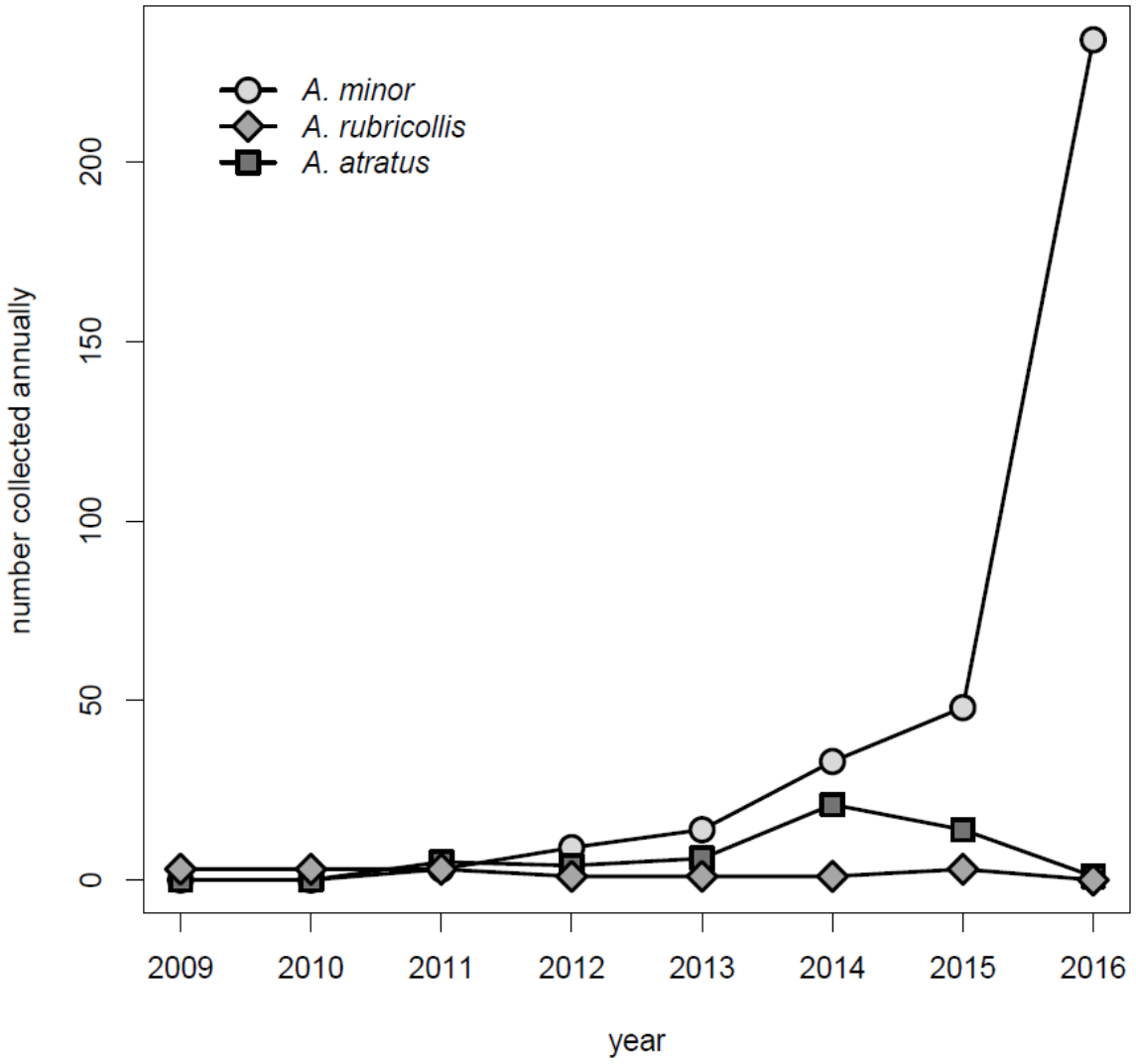

Figure 2: Abundance of *Ambrosiodmus minor*. The abundance of *A. minor* in Florida has rapidly surpassed that of *Ambrosiodmus rubricollis* and *Ambrosiophilus atratus*, the other two exotic vectors of the Asian white-rot fungus *Flavodon ambrosius*. Data represent total catches in traps across Florida by the Cooperative Agricultural Pest Survey (CAPS).

Figure 3: Abundance of *Ambrosiodmus minor* galleries. The density of the galleries of *A. minor* galleries on three randomly selected typical decaying log in North-central Florida in 2018. Each yellow pin is inserted in a separate gallery of *A. minor*. In this case there are 75 in total.

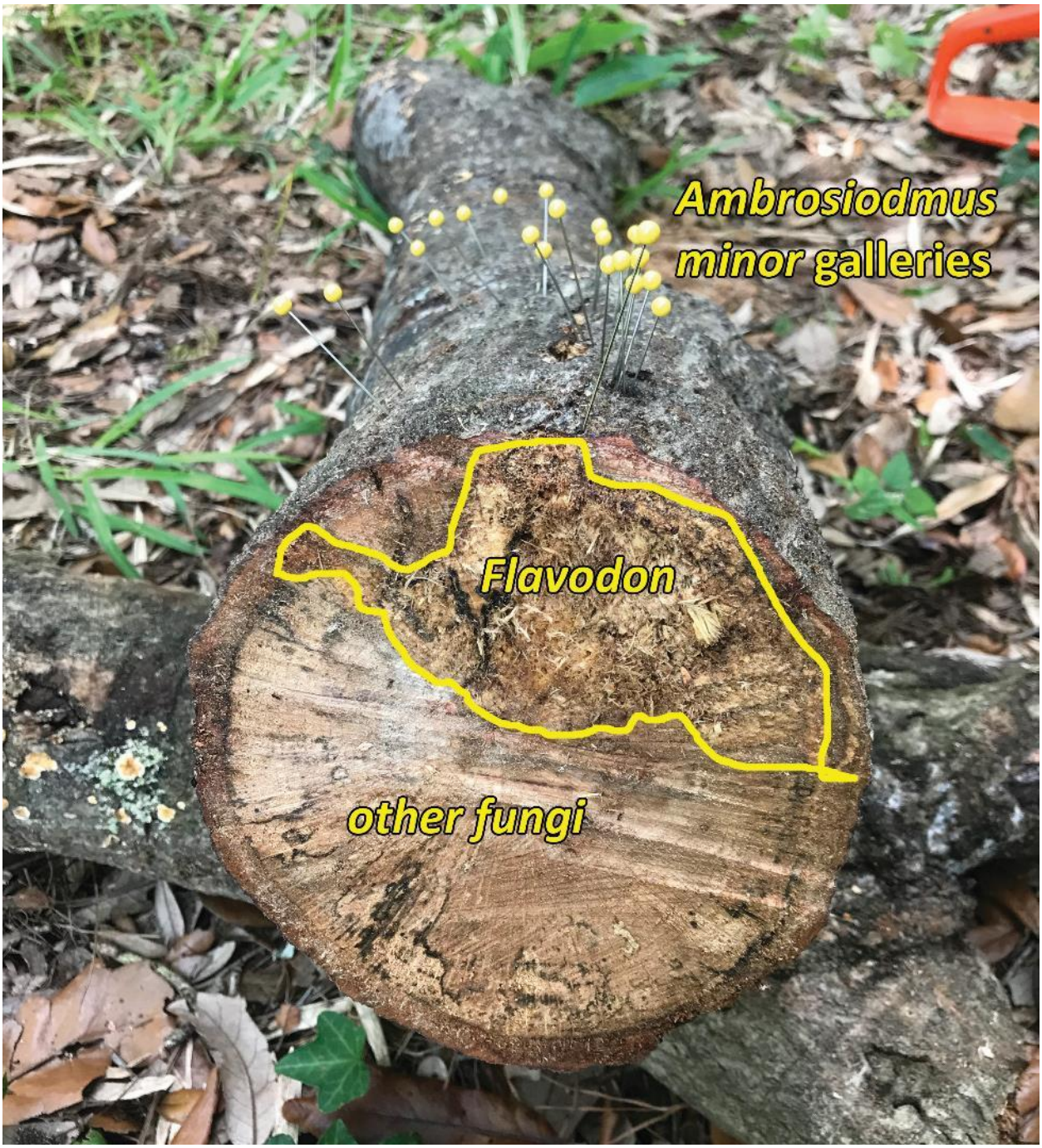

Figure 4: Aggressive colonization of dead wood by the invasive *Flavodon ambrosius*. The prevalence of *Flavodon ambrosius*-dominated wood in a log colonized by *Ambrosiodmus minor*. Illustrated is a cross-section branch from an oak (15 cm diameter) that was broken off approximately half a year earlier. Each pin is inserted into an entrance to a separate gallery of A. minor. In this case, more than 30% of the wood volume is colonized by the ambrosia fungus Flavodon ambrosius. This wood is noticeably more advanced in its decay that the remaining wood, is softer and spongy, and is unavailable to most native wood-degrading organisms.