

## Tradeoffs in longleaf pine conservation: Prescribed fire management increases exotic ambrosia beetle abundance in pine-hardwood forests

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### ABSTRACT

Exotic woodboring insects, including some ambrosia beetles (Coleoptera: Curculionidae, Scolytinae, and Platypodidae), are threatening native forests worldwide. Longleaf pine (*Pinus palustris* Mill.) forest is an endangered habitat in the southeastern United States. One of the most important actions necessary for its conservation is prescribed fire, which maintains its savanna structure. However, prescribed fire is a forest disturbance, possibly creating new niches for colonization by exotic insects. The interaction between prescribed fire and exotic ambrosia species is understudied, especially in highly fire-dependent ecosystems. We carried out a two-year experiment in mixed longleaf pine forests in Alabama, USA. We compared ambrosia beetle communities in recently burned and unburned sites. We found that more than 66 % of total individuals in longleaf pine forests, regardless of fire management, were exotic species. Moreover, exotic ambrosia beetles were more abundant in burned stands, whereas native species showed no difference between burned or unburned stands. Fire management influenced stand species composition for native but not exotic ambrosia beetles. These results indicate that trade-offs exist in managing fire-dependent ecosystems, especially in the Anthropocene era, which is associated with rampant biological invasions. Fire is important to preserve the longleaf pine habitat, but it simultaneously acts as a disturbance, increasing the population density of those exotic species taking advantage of the presence of stressed or dying trees.

### 1. Introduction

Woodboring insects, including ambrosia beetles (Coleoptera: Curculionidae, Scolytinae, and Platypodidae), are often unintentionally transported across the globe in lumber and wood-packing materials (Brockhoff and Liebhold, 2017; Lantschner et al., 2020; Meurisse et al., 2019). While most ambrosia beetle species attack dead or dying trees in their native range and are therefore not major pests (Hulcr and Skelton, 2023; Hulcr and Stelinski, 2017), some can become significant threats after introduction in new environments, colonizing and killing healthy trees in conjunction with their symbiotic fungal counterpart (Gugliuzzo et al., 2021; Ploetz et al., 2013). More than 30 exotic ambrosia beetle species are already established in North America, including some important pests (Gomez et al., 2018). Examples include

*Xylosandrus germanus* and *Xylosandrus crassiusculus*, two of the most damaging species in ornamental plant nurseries (Ranger et al., 2016), and the redbay ambrosia beetle *Xyleborus glabratus*, vector of *Harringtonia lauricola*, the causal agent of the lethal laurel wilt disease, which decimated Lauraceae trees in the southeastern United States (Hughes et al., 2017; Kendra et al., 2013; Riggins et al., 2019). The southeastern United States, in particular, hosts a disproportionate concentration of the exotic ambrosia beetle species successfully established in North America due to the warm and humid climate favoring ambrosia beetle establishment and spread (Marini et al., 2011; Rassati et al., 2016). The high proportion of such potential forest pests in this region might threaten the remnant endemic forest patches.

The fire-dependent savannas and woodlands that once covered most of the southeastern United States are an important ecosystem hosting

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many endemic species, and an important component of the North America Coastal Plain (NACP, hereafter) biodiversity hotspot (Noss et al., 2015). The dominant tree species, longleaf pine (*Pinus palustris* Mill.), covered most of the NACP reaching 37 million hectares before European colonization of the region (Frost, 2006). However, only about 2.2 % of the original range of the longleaf pine forests remained by 2005 (Oswalt et al., 2012) because of fire suppression, conversion to other pine species or agriculture, and urbanization (Kirkman and Jack, 2017; Van Lear et al., 2005). Longleaf pine forests are now threatened forest ecosystems and restoration efforts are taking place for conservation purposes. The remaining forests are now dependent on intensive management actions, such as prescribed fire, aimed at restoring natural conditions (Holland et al., 2019). Fire was a fundamental component of pre-colonization longleaf pine forests (Barnett, 1999), with wildfire return intervals every 2–3 years (Oswalt et al., 2012). Prescribed fires allow forest managers to prevent the transition from a longleaf pine savanna to a hardwood-dominated forest, by limiting interspecific competition and sprout potential of hardwood species (Loudermilk et al., 2011). However, fire can also impact the structure and function of non-plant communities and may alter the abundance and distribution of exotic species.

Fire is both a natural disturbance for longleaf pine forests and a habitat perturbation that generates new environmental conditions and leads to ecosystem instability, at least in the short term. On the one hand, fires result in a higher abundance of saproxylic and woodboring insects, such as buprestids, cerambycids, and ambrosia beetles, and this effect increases with fire intensity (Campbell et al., 2008; Catry et al., 2017; Hanula et al., 2002; Sullivan et al., 2003). These insects are relevant components in the forest ecosystem because they play an important role in wood degradation by inoculating bacteria and fungi within deadwood, thus speeding up the decomposition process (Hardersen and Zapponi, 2018; Ulyshen, 2016). On the other hand, forest fires can aid the establishment of exotic species by creating new ecological niches or decreasing competition with native species (Lowry et al., 2013; Lozon and MacIsaac, 1997; Pearson et al., 2018). In pine-hardwood mixed stands, for example, fire can damage hardwood species creating optimal conditions for those ambrosia beetles looking for stressed or dying tree to colonize, including the exotic *Xylosandrus germanus* and *Xylosandrus crassiusculus*, and consequently affecting the structure of the ambrosia beetle community (Catry et al., 2017). Despite several studies have already investigated the effect of wildfire disturbances on woodboring beetles (Campbell et al., 2008; Hanula et al., 2002; Kitchens et al., 2022; Sullivan et al., 2003), only a few investigated the post-fire community dynamics of native and exotic communities of ambrosia beetles (Catry et al., 2017; Palmer et al., 2024).

Here we investigated the effect of prescribed fire management on the communities of exotic and native species of ambrosia beetles in longleaf pine-hardwood forests. Specifically, we tested the hypothesis that prescribed fire can alter woodboring ambrosia beetle communities. We tested the predictions that i) fire would affect ambrosia beetles in terms of the number of individuals (i.e., abundance), species diversity, and species composition; and ii) we tested the null hypothesis that native and exotic species would similarly respond to fire. Finally, we discussed the trade-offs between active conservation management (i.e., fire disturbance) and the expanding pool of exotic forest insects in a highly fire-dependent ecosystem.

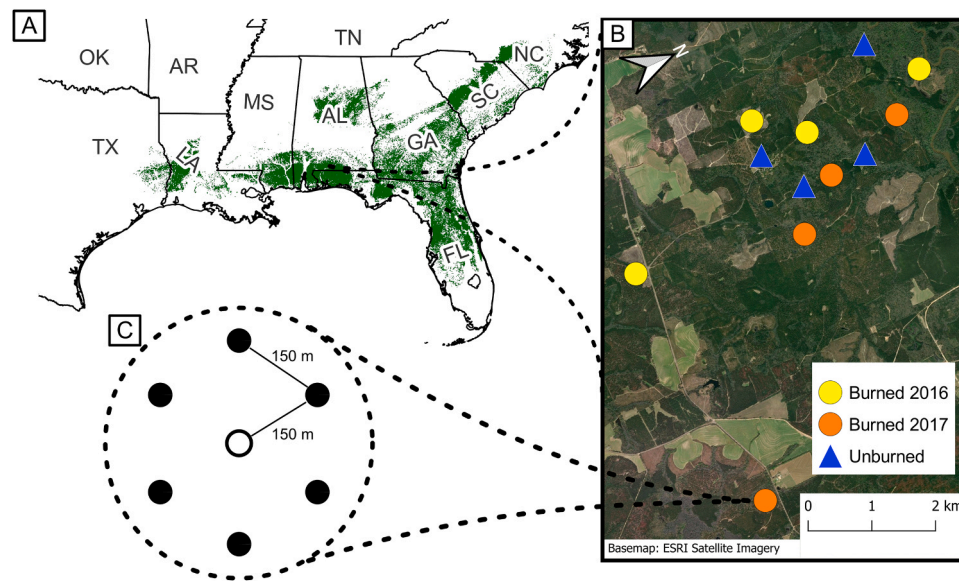
## 2. Materials and methods

### 2.1. Sampling design

To test the impacts of prescribed fire on native and exotic ambrosia beetle communities, in 2016 and 2017 we selected eight mixed pine-hardwood stands in the Auburn University Solon Dixon Research Forest, located in southern Alabama, in Escambia and Covington counties. The area is characterized by a loamy or clayey subsoil with a sandy loam

or loam surface layer (data from: [www.websoilsurvey.nrcs.usda.gov](http://www.websoilsurvey.nrcs.usda.gov)). The primary forest type is a longleaf pine-dominated forest, with the presence of slash pine (*Pinus elliottii*), loblolly pine (*Pinus taeda*) and hardwood species. The hardwood component is particularly numerous in the bottoms and is dominated by oaks (e.g. *Quercus alba*, *Quercus falcata*, *Quercus phellos*). The understory vegetation is characterized by wood bushes, such as *Ilex vomitoria* and *Callicarpa americana*, and small trees, such as *Ilex opaca* and *Ostrya virginiana*. In the first year, we chose four stands that were recently burned (prescribed fire occurred a few months before sampling, during the winter period between January and May on a three-year rotation), and four unburned stands (no records of prescribed fire in the previous 15 years) (Suppl. A, Table A1). All the sites were mixed forests containing both mature pine and hardwood trees. In the second year, we chose four newly burned stands to consistently test the short-term impacts of prescribed fire (i.e., newly selected stands were burned no more than 4 months before the beginning of sampling). However, the same unburned stands were used in both years, as no other forest stands fit the selection criteria.

In each stand, we placed 7 black multi-funnel traps, of which one was placed in the center of the stand (here defined as the “generalist” trap) and the other six (here defined as the “log-baited” traps) in a circle around it (Fig. 1). We used black multi-funnel traps because of their well-recognized efficacy in catching bark and ambrosia beetles (Dodds et al., 2024). The generalist trap located in the center of the stand was baited with both alpha-pinene ultra-high release (UHR) lure and ethanol UHR lure (Synergy Semiochemicals), two stress-related host volatiles commonly used as attractants in ambrosia beetle monitoring programs (Hartshorn et al., 2021; Miller and Rabaglia, 2009; Ranger et al., 2010). The other six log-baited traps (i.e., those located around the generalist trap) (Fig. 1) were baited with one log (or bundle for American beautyberry) 19 cm long and up to 6–7 cm in diameter and fresh foliage of one of the six hardwood species selected among those widely present at the study sites. These species represent a wide taxonomic array of potential hosts for the native and exotic ambrosia beetles known to occur in the Southeastern USA (i.e., American beautyberry (*Callicarpa americana*), American hophornbeam (*Ostrya virginiana*), American holly (*Ilex opaca*), white oak (*Quercus alba*), Southern red oak (*Quercus falcata*), and willow oak (*Quercus phellos*)). These log-baited traps were used to catch ambrosia beetle species primarily attracted by host volatiles (e.g., green leaf volatiles and terpenoids) different than those used to bait the generalist trap (Chen et al., 2021; Kendra et al., 2014; de Groot et al., 2008; Martini et al., 2015). Bait material for log-baited traps was collected from healthy, small-diameter trees present near study sites, but not within experimental stands to minimize disturbance. The logs were wrapped in fine stainless steel mesh (279 microns opening) to prevent insects from boring into the wood and influencing further trap captures via the emission of volatiles by the nutritional symbiotic fungi cultivated by adult females on gallery walls (Diehl et al., 2023; Gugliuzzo et al., 2023). The fresh foliage was collected from each felled tree and placed in plastic mesh produce bags. Logs and foliage were renewed every trap check. Each trap in the 7-trap array was separated by 150 m from each other, and the tree species associated with each log-baited trap at the different sites was ordered and positioned randomly using a random number generator. The possible influence of the generalist trap was equal to all the other tree-baited traps. In each stand, traps were set up in late May and checked every two weeks until mid-July for a total of four collections each year. A solution of propylene glycol (50 %) was used as a preservative. The collected beetles were placed in plastic zip-top bags and refrigerated until returning to the lab, where they were stored in a freezer. Ambrosia beetle specimens were separated from trap catch, counted, identified to species, and stored in 70 % ethanol (Arnett et al., 2002; Atkinson et al., 2013; Hoebeke et al., 2018; Rabaglia et al., 2006; Wood, 1982). Voucher specimens were deposited in the Mississippi Entomological Museum.



**Fig. 1.** Sampling design. A) Location of longleaf pine sites used to evaluate prescribed fire effects on ambrosia beetle populations in southern Alabama (AL). B) Location of stands burned in 2016 (yellow circles) and 2017 (orange circles), and unburned stands (blue triangles). C) Within-stand arrangement of funnel traps baited with logs of various hardwood species (black circles) or lures for generalist ambrosia beetle species (white circles). Satellite base map: Esri World Imagery (sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community).

## 2.2. Data preparation and statistics

A morphospecies (4 individuals) belonging to the genus *Xyleborus* was not identified at the species level. Thus, it was removed from the dataset before statistical analyses because it could not be assigned as native or exotic. To test the efficacy of the trap array in collecting representative communities, we compared individual-based accumulation curves of generalist-only traps vs. the entire array of traps (i.e., pooling the generalist trap and the log-baited traps) using the *iNEXT* 3.0 (Hsieh et al., 2016) package in R 4.3.2 (R Core Team, 2024). Also, we ran a pairwise adonis test using *pairwise.adonis2()* function (Arbizu, 2020) to compare species assemblages of all the different traps. Our explorative analyses showed that the entire trap array helped to retrieve a more representative community of ambrosia beetles (Suppl. B, Fig B1, Table B1). For the subsequent analyses, data were pooled at the site level across the entire trap array, separately for each year. Operatively, we summed all the catches from all the different traps for each stand. Catches belonging to different years were kept separated.

We computed the abundance as the sum of all individuals caught in the stand, and diversity indices as Hill numbers of order 0 (i.e., the effective number of species), order 1 (i.e., “typical” species or exponential of Shannon entropy index), and order 2 (i.e., common species or Simpson index) using the framework proposed by Hill (1973), and finally the community Evenness as Evar index (Smith and Wilson, 1996). To test the effect of fire management (i.e. burned vs. unburned, categorical variable), origin status of beetle species (i.e., native vs. exotic, categorical variable), and their interaction on the abundance, diversity indices, and evenness (i.e., response variables), we used generalized mixed-effect linear models (i.e., GLMM). We used management, origin status, and year as fixed effects, and site as random effect. We tested interactions between pairs of factors. If the interaction effect was not significant, we reran the model without interaction. We used a Gaussian distribution for diversity indices, and a Poisson distribution for abundance data to account for the different data structures. Models were run in R 4.3.2 (R Core Team, 2024), using *LME4* 1.1 (Bates et al., 2015), *LMERTEST* 3.1 (Kuznetsova et al., 2017), *EMMEANS* 1.8 (Lenth et al., 2020), and *EFFECTS* 4.2 (Fox and Weisberg, 2019) packages. The model diagnostic was done using the package *DHARMA* 0.4.6 (Harting, 2021).

To test the effect of fire management (i.e. burned vs. unburned,

categorical variable) on species composition of native and exotic ambrosia beetles, we ran a PERMANOVA using stand management (i.e. burned vs. unburned) and year as the explanatory variable for exotic and native species separately. To measure the distance in species composition between communities, we used Jaccard distance based on the presence/absence matrix to remove the effect of abundance since few abundant species might bias the results. This analysis aims to test the effect of predictors on the whole species assemblage, regardless of abundance. The homogeneity of group variance was tested with the PERMDISP2 procedure (Anderson, 2006). Moreover, we used Dufrene-Legendre Indicator Species Analysis (Dufrene and Legendre, 1997) to determine which species were associated with burned vs unburned stand management based on their abundance. All analyses were done in R 4.3.2 (R Core Team, 2024), and we used *adonis2()* and *betadisper()* functions from package *VEGAN* 2.6 (Oksanen et al., 2020) for PERMANOVA and homogeneity test respectively, and the *indval()* function from package *LABDSV* 2.1 (Roberts, 2023) for Indicator Species analysis.

## 3. Results

### 3.1. General results

Overall, we collected 2523 ambrosia beetles belonging to 29 species, of which 15 are native and 14 are exotic. The abundance of exotic species (1691) was two times the abundance of native species (828). Thus, more than 66 % of our database is constituted of individuals belonging to exotic species.

### 3.2. Effect of fire management on species richness and abundance of native and exotic ambrosia beetles

Regarding the abundance (i.e., the total number of individuals), we found a significant interaction between species origin status (i.e., native and exotic) and fire management (Likelihood ratio test, Chi-square = 67.43, p-value < 0.001), and between fire management and year (Likelihood ratio test, Chi-square = 4.92, p-value = 0.027), but no effects of sampling year (Likelihood ratio test, Chi-square = 1.25, p-value = 0.263). In particular, we found that exotic species were more

**Table 1**

List of ambrosia beetle species collected in a study comparing burned and unburned longleaf pine stands in Alabama, 2016–2017. Host preferences were retrieved by Ruzzier et al. (2023) and [www.barkbeetles.info](http://www.barkbeetles.info) (last accessed on 04/07/2024).

Species	Status	# captured in burned stands	# captured in unburned stands	Hosts
<i>Ambrosiodmus minor</i>	Exotic	17	2	broadleaves
<i>Ambrosiodmus obliquus</i>	Native	2	13	broadleaves
<i>Ambrosiodmus rubricollis</i>	Exotic	14	56	broadleaves
<i>Ambrosiodmus tachygraphus</i>	Native	1	0	broadleaves
<i>Ambrosiophilus atratus</i>	Exotic	12	11	broadleaves
<i>Cnestus mutilatus</i>	Exotic	188	112	broadleaves
<i>Cyclorhipidion bodoanum</i>	Exotic	8	2	broadleaves
<i>Cyclorhipidion</i> sp.	Exotic	2	2	broad spectrum including coniferous, most of the species unknown
<i>Dryoxylon onoharaense</i>	Exotic	210	129	broadleaves
<i>Euplatypus compositus</i>	Native	1	1	broadleaves/ coniferous
<i>Euwallacea interjectus</i>	Exotic	2	4	broadleaves/ coniferous
<i>Gnathotrichus materiarius</i>	Native	6	10	coniferous
<i>Monarthrum fasciatum</i>	Native	5	1	broadleaves/ coniferous
<i>Monarthrum mali</i>	Native	54	48	broadleaves
<i>Myoplatypus flavicornis</i>	Native	4	5	broadleaves/ coniferous
<i>Xyleborinus gracilis</i>	Native	1	8	broadleaves
<i>Xyleborinus octiesdentatus</i>	Exotic	8	7	broadleaves
<i>Xyleborinus saxesenii</i>	Exotic	581	120	broadleaves/ coniferous
<i>Xyleborus affinis</i>	Native	4	8	broadleaves
<i>Xyleborus bispinatus</i>	Native	21	39	broadleaves
<i>Xyleborus ferrugineus</i>	Native	11	15	broadleaves
<i>Xyleborus impressus</i>	Native	63	34	broadleaves
<i>Xyleborus intrusus</i>	Native	1	0	coniferous
<i>Xyleborus pubescens</i>	Native	16	18	coniferous
<i>Xyleborus</i> sp. 1	Exotic (?)	0	4	broad spectrum including coniferous unknown
<i>Xyleborus viduus</i>	Native	3	1	broadleaves/ coniferous
<i>Xylosandrus compactus</i>	Exotic	19	61	broadleaves/ coniferous
<i>Xylosandrus crassiusculus</i>	Exotic	440	114	broadleaves/ coniferous
<i>Xylosandrus germanus</i>	Exotic	1	3	broadleaves/ coniferous

abundant in burned stands than unburned ones (emmeans pairwise comparison,  $p$ -value < 0.001), whereas the abundance of native species was similar in the two management treatments (emmeans pairwise comparison,  $p$ -value = 0.570) (Fig. 2A). The effective species richness (i.e., Hill index of order 0) of exotic species was higher than the richness of native species (F test,  $F = 8.43$ ,  $p$ -value = 0.011) (Fig. 2B). However, the effects of fire management and year were not significant (F test,  $F_{\text{fire}} = 0$ ,  $p$ -value<sub>fire</sub> = 1.00; F test,  $F_{\text{year}} = 0.85$ ,  $p$ -value<sub>year</sub> = 0.37).

Considering the Shannon-based diversity (i.e., Hill index of order 1), we only observed a trend in the fire management suggesting more diversity in the unburned stands, although not significant (F test,  $F_{\text{fire}} = 3.99$ ,  $p$ -value<sub>fire</sub> = 0.07). We did not observe significant patterns for Simpson-based diversity (i.e., Hill index of order 2). Regarding the evenness, we found a trend in the interaction between fire management and the origin status of the species (F test,  $F = 4.18$ ,  $p$ -value = 0.06), with strong effects on the main factors (F test,  $F_{\text{fire}} = 4.91$ ,  $p$ -value<sub>fire</sub> = 0.04; F test,  $F_{\text{status}} = 34.43$ ,  $p$ -value<sub>status</sub> < 0.001). In particular, communities of exotic species showed higher evenness in unburned stands (emmeans pairwise comparison,  $p$ -value = 0.038), whereas no effects for native communities (emmeans pairwise comparison,  $p$ -value = 0.99) (Fig. 2C).

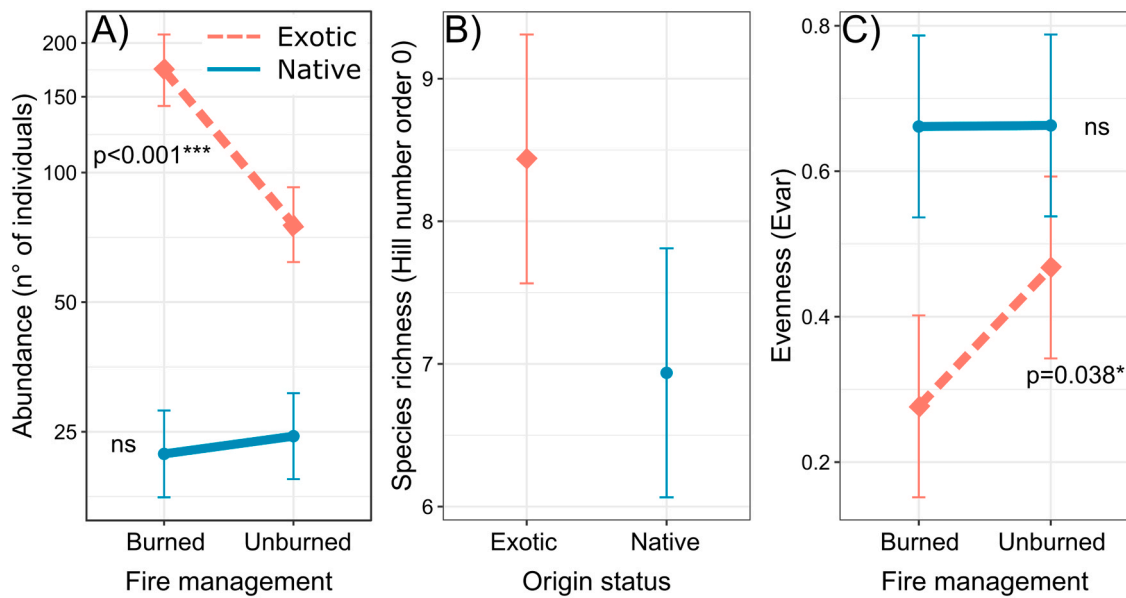
### 3.3. Effect of fire management on composition of native and exotic ambrosia beetle communities

The community composition of exotic species was similar between burned and unburned stands, but different among years accounting for 19 % of the total variance (NDMS tress = 0.13; PERMANOVA,  $F_{\text{fire}} = 1.21$ ,  $p$ -value<sub>fire</sub> = 0.32;  $F_{\text{year}} = 3.37$ ,  $p$ -value<sub>year</sub> = 0.012; Homogeneity test was not significant) (Fig. 3-A). On the contrary, we found opposite trends for native species communities: community composition of native species was different between burned and unburned stands, but similar between years (NDMS tress = 0.18; PERMANOVA,  $F_{\text{fire}} = 2.63$ ,  $p$ -value<sub>fire</sub> = 0.009;  $F_{\text{year}} = 1.29$ ,  $p$ -value<sub>year</sub> = 0.271; Homogeneity test was not significant) (Fig. 3-B). Indicator Species Analysis returned 4 exotic species and 1 native species. For exotic ambrosia beetles, *Xyleborinus saxesenii* (indicator value = 0.83;  $p$ -value = 0.002) and *Xylosandrus crassiusculus* (indicator value = 0.79;  $p$ -value < 0.001) were associated with burned stands, whereas *Ambrosiodmus rubricollis* (indicator value = 0.80;  $p$ -value = 0.023) and *Xylosandrus compactus* (indicator value = 0.76;  $p$ -value = 0.006) were associated with unburned stands. For native ambrosia beetles, there was only one indicator species, *Xyleborinus gracilis* associated with unburned stands (indicator value = 0.67,  $p$ -value = 0.035).

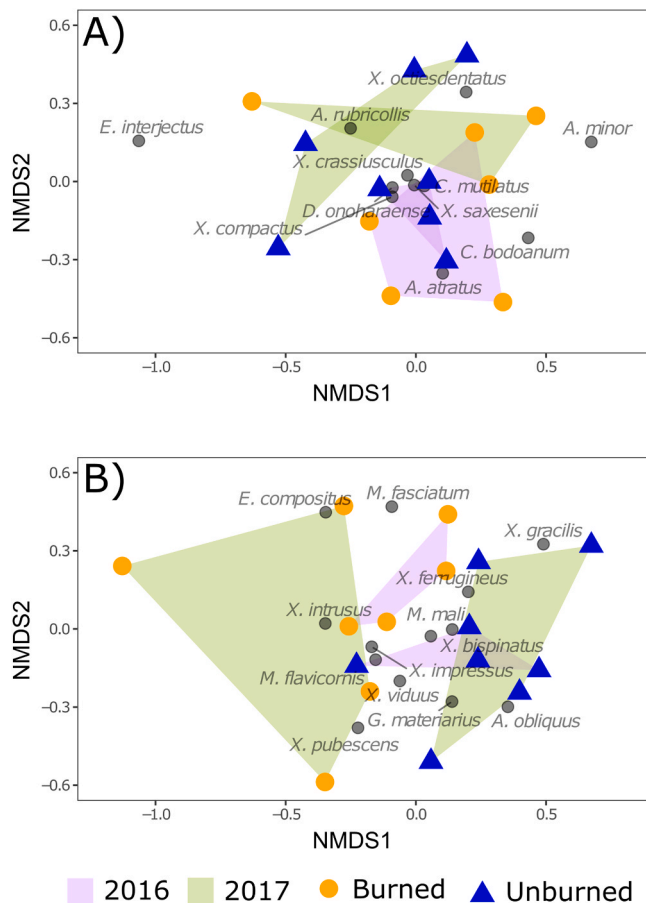
## 4. Discussion

Longleaf pine forests are fire-dependent biodiversity hot spots, and frequent conservation actions, such as prescribed fire, are conducted to maintain the savanna-like structure of longleaf pine forests (Barnett, 1999; Holland et al., 2019). However, a complex relationship between conservation actions and ecological dynamics can exist and disturbances could also facilitate the spread of exotic species due to niche availability at the landscape scale (Hobbs and Huenneke, 1992). In this study, we investigated the role of prescribed fire in shaping communities of native and exotic ambrosia beetles in longleaf pine–hardwood mixed forests. We found that longleaf pine stands harbor significantly more exotic than native ambrosia species and that prescribed fire increases the abundance of exotic ambrosia beetles, at least in the short term. Our results suggest that prescribed fire has important tradeoff effects as a disturbance agent, releasing longleaf pines from competition but also promoting non-native species of ambrosia beetles.

Regardless of the fire management treatment, we found a higher richness and abundance of exotic ambrosia beetle species than native ambrosia beetle species; this is consistent with general continental-scale trends in warm and humid climates, such as the southern USA (Marini et al., 2011). Similar trends have been observed also in other forest ecosystems (Marchioro et al., 2020), even though the abundance of exotic species is generally affected by a disproportionate number of individuals belonging to a few dominant species (Baniszwski et al., 2024; Brockerhoff et al., 2006; Rabaglia et al., 2019; Rassati et al., 2016, 2015). In our study, the community evenness was higher for native species indicating more evenly distributed relative frequencies for native species than exotics. Indeed, 66 % of the collected individuals belonged to two exotic species, *Xyleborinus saxesenii* and *Xylosandrus*



**Fig. 2.** The interaction effect of fire management and origin status on the abundance of ambrosia species is shown in A. The effect of origin status on the species richness is shown in B. The interaction effect of fire management and origin status on the community Evenness (Evar index) is shown in C. Exotic species are shown in orange diamonds and dashed lines, native species in cyan dots and solid lines. Errors bars show 95 % confidence intervals. For interactions (A and C) results of contrasts burned-unburned are reported for each origin status as P-values or “ns” for no-significant effects.



**Fig. 3.** NMDS plots show how the community composition of exotic (A) and native (B) species depends on management type and sampling year: burned (yellow circles) and unburned (blue triangle) stands; purple shade indicates 2016 data, green shade indicates 2017 data. Species centroids are shown as black dots. See Table 1 for names of genera.

*crassiusculus*, which are widespread not only in the USA but also at the global scale (Gugliuzzo et al., 2021; Hulcr and Skelton, 2023; Reed and Muzika, 2010). Similarly, Campbell et al. (2008) showed that individuals of ambrosia beetles belonging to exotic species accounted for 80 % of the total in longleaf pine forests. *Xyleborinus saxesenii* and *Xylosandrus crassiusculus* are two extremely polyphagous species able to attack a very large range of hosts, mainly broadleaves but apparently also some coniferous species (Ruzzier et al., 2023). Also, the richness of exotic species was higher than native species irrespective of the fire management, suggesting that the forests we sampled had all been widely colonized by exotic species. Although most of the exotic species are not considered pests (Hulcr et al., 2021), their effects (and the effects of their fungal symbionts) on the forest ecosystem services and the competition with native species are mostly unknown (Riggins et al., 2019; Skelton et al., 2020). Also, because of their ubiquitous presence, exotic species might rapidly respond to forest dynamics and disturbances, such as prescribed fires. Although we could not evaluate the long-term effect of fire management in pine pure stands, our study supports strong short-term changes in wood-boring insect communities in post-fire conditions in mixed stands. However, the effect of prescribed fire in these stands has not been investigated under the context of biological invasions.

Our results showed that prescribed fire can affect exotic and native communities of ambrosia beetles differently. In particular, post-fire conditions can increase the abundance of exotic species but have a weaker effect on the abundance of native species. Prescribed fire is an environmental perturbation and burned stands can act as a sink for surrounding populations of exotic species, especially in the initial period after burning (Ryan et al., 2013; Sullivan et al., 2003). We found that the structure of communities of exotic species changed after fire disturbance showing low evenness. This uneven partition of species frequencies is mostly driven by some exotic species of primary concern, namely *Xyleborinus saxesenii* and *Xylosandrus crassiusculus*, which were mostly found in the burned stands. Those species are well established in the US and have a high adaptability and wide range of hosts (Gugliuzzo et al., 2021). After fire, stressed trees can release higher amounts of ethanol and volatile terpenes (Bär et al., 2019; Valor et al., 2017), which are known to be key olfactory cues used by both *Xyleborinus saxesenii* and *Xylosandrus crassiusculus* (Cambronero-Heinrichs et al., 2024; Cavaletto

et al., 2021; Rassati et al., 2020) to locate host trees to colonize (Kelsey and Westlind, 2017). Although previous studies found that prescribed burning increased the abundance of bark and ambrosia beetles in longleaf pine forests (Campbell et al., 2008; Sullivan et al., 2003), we showed that these post-disturbance dynamics can differently affect exotic and native ambrosia beetle communities.

However, considering the overall community composition besides a few abundant species, we found that fire impacts the structure of native beetle communities, but not exotic beetle communities. Fire occurrence is a relevant environmental factor affecting species-specific microhabitat availability (Azeria et al., 2012; Saint-Germain et al., 2004). Ambrosia beetles exhibit species-specific responses to prescribed fire depending on different ecology strategies (Hanula et al., 2002). Because of this co-evolution with fire-dependent ecosystems, some native species can show association with fire, such as fire-specific adaptations or saproxylic taxa showing preferential attractiveness for post-fire conditions (Bell, 2023; Boulanger et al., 2010). In the end, this can result in a different species composition between frequently burned and unburned habitats (Hanula et al., 2002; Saint-Germain et al., 2004). Since these represent long-term legacies between co-evolved species and habitats, we did not expect strong temporal dynamics. Indeed, native communities between the two sample years are similar. On the contrary, exotic communities are similar between stands, but different between years. This trend might be due to stochastic differences among the communities monitored in 2016 and 2017, especially in the case of some exotic species with a few individuals, which might influence the community distances. Finally, our results reflect the short-term dynamics of fire management on the exotic species of ambrosia beetles, while prescribed fire can be important for preserving native communities with fire-associated taxa.

As habitats are altered by anthropogenic activities, ecosystem restoration can be an important tool in conserving habitats and increasing biodiversity. However, ecosystem restoration efforts might employ management strategies that can have unintended consequences, such as increasing non-native species (Abella and Chiquoine, 2019). In natural longleaf pine forests, wildfire is a frequent natural disturbance and it is part of the ecosystem dynamics (Frost, 2006; Kirkman and Jack, 2017; Sheehan and Klepzig, 2022). On the one hand, prescribed fire is a commonly used practice to maintain the savanna structure of these forests (Barnett, 1999; Holland et al., 2019). We showed that native communities of ambrosia beetles are shaped by fire management, suggesting that some species are associated with fire-dependent habitats. On the other hand, we found that the abundance of exotic species was higher after the fire. The application of prescribed fire in these mixed stands seems to support larger populations of exotic species, thus facilitating their radiative dispersion across the landscape. This effect suggests a trade-off between conservation goals and prevention measures for the spread of exotic pests. A common paradigm in invasion ecology is that disturbance can facilitate the establishment of exotic species (Lockwood et al., 2013; Zhang et al., 2006). However, these processes are often complicated and involve interactions with many factors, such as the invasion phase (Britton-Simmons and Abbott, 2008), co-occurrence of multiple disturbances (Hobbs and Huenneke, 1992), resource availability (Lear et al., 2020), and taxa-specific traits (Lozon and MacIsaac, 1997). We found a higher abundance of exotic species in the burned stands suggesting that the prescribed fire acts as an environmental perturbation. Moreover, the composition of exotic species did not differ between burned and unburned stands, suggesting a homogeneous distribution of these exotic species, that might potentially over-respond after disturbances, such as prescribed fire. Similar results have already been reported for exotic ants in longleaf pine (Atchison et al., 2018). Overall, our results agreed with the general paradigm stating that disturbance can facilitate the spread of exotic species, thus highlighting an important tradeoff in forest management and conservation under the threat of biological invasions. Managers of highly fire-dependent ecosystems should be aware that while prescribed fire management

activities are necessary to maintain proper ecosystem function, resultant habitat disturbance can potentially increase the availability of niches for exotic forest insect pests across the landscape. Future research should focus on strategies to mitigate this potential negative outcome.

### CRedit authorship contribution statement

**Davide Nardi:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Hannah Bares:** Methodology, Investigation, Data curation, Conceptualization. **Natalie A. Clay:** Writing – original draft, Conceptualization. **Robin Verble:** Writing – original draft, Conceptualization. **Davide Rassati:** Writing – original draft, Formal analysis. **Lorenzo Marini:** Writing – original draft, Formal analysis. **John Thomason:** Writing – original draft, Investigation. **John J. Riggins:** Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data Availability

Data will be made available on request.

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122210.

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