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Woodboring Beetle (Buprestidae, Cerambycidae) Responses to Hurricane Michael in Variously Damaged Southeastern US Pine Plantations

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Abstract

In October 2018, catastrophic Hurricane Michael caused $1.7 billion in damage to standing timber in Florida, USA. To inform recovery efforts, varying levels of damaged (low, moderate, and high) slash pine (*Pinus elliottii* Engelm) stands were sampled for woodboring beetles (Coleoptera: Buprestidae; Cerambycidae). These beetles generally colonize stressed and damaged trees, and their larval tunneling activities reduce the value of timber salvaged post disturbance. From 2019 to 2020, 3,810 adults of 32 species were trapped. *Acanthocinus obsoletus* Olivier and *Monochamus* sp. complex (*M. titillator* Fabricius; *M. carolinensis* Olivier) comprised 86% of all catches. Approximately 50% and 60% more woodborers, especially *Monochamus* sp., were trapped in moderate-damage stands in 2019 than in high- and low-damage stands, respectively. This trend was not present in 2020. From 2019 to 2020, total catches increased by ~29%, reflected by increases in *Monochamus* sp. and *Xylotrechus sagittatus* Germar. In 2019, high-damage stands had the greatest species richness, followed by low- and moderate-damage stands. Species composition in 2019 did not differ among variously damaged stands, but was more heterogeneous in low-damage than high-damage stands in 2020. Results indicate that timely salvage harvesting of moderate- and high-damage stands after catastrophic wind disturbances may lower the economic impacts by subcortical woodboring beetles.

Keywords: community ecology, hurricane, natural resources management, population ecology, subcortical beetles

Study Implications:

Hurricane Michael made landfall in the Florida Panhandle in October 2018, causing catastrophic timber damage. Various damaged pine stands were sampled in 2019 and 2020 for subcortical woodboring beetles, which can exacerbate economic losses via tunneling of wood. Trap catches were highest in moderate-damage stands in 2019 but not in 2020. There were not exponential increases in woodborers, possibly due to rapid breakdown of debris in the hot climatic conditions and higher degree of salvage-logging from 2019 to 2020. Moderately to highly disturbed stands may be scheduled for earlier salvage-logging.

Hurricanes, a type of tropical cyclone, are natural disturbance agents and are critical drivers of forest stand dynamics in the southeastern United States. Hurricanes damage trees due to extreme wind speeds and flooding, resulting in broken, bent, or uprooted stems, broken crowns and branches, root damage, and defoliation (Gresham et al. 1991; Zampieri et al. 2020). Although these disturbance events can injure or kill many trees, they are often crucial to maintaining functional ecosystems. The influx of coarse woody debris and litter caused by wind disturbances leads to increased concentrations and admixing of nutrients in soils, which is critical to the growth of many plant species (Ostertag et al. 2003). Wind disturbances are also important drivers of canopy and gap dynamics (Everham and Brokaw 1996; Mitchell 2013). Changes in stand structure, age distribution, vegetative species composition, and an increase in coarse and fine woody debris in forests affects habitat availability, thus altering population and community dynamics of flora and fauna (Dodds et al. 2019; Gandhi et al. 2007). Although hurricanes are natural disturbance agents, the frequency of hurricanes and other wind disturbances is increasing due to climate change, leading to disturbance regimes outside the historical natural range (Zampieri et al. 2020).

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Responses of subcortical beetles, specifically bark (Curculionidae: Scolytinae) and woodboring (Buprestidae and Cerambycidae) beetles are of particular interest in the interactive contexts of wind disturbance and climate change (Gochnour et al. 2022). Throughout North America and Europe, bark and woodboring beetles can colonize forest stands following windthrow, and populations of subcortical beetles can reach outbreak levels in wind-disturbed forests (Connola et al. 1956; Fettig and Hilszczanski 2015; Gardiner 1975; Gochnour et al. 2022; Kirkendall et al. 2015; Knížek and Beaver 2007; Lieutier et al. 2004; Økland et al. 2016). Loss of branches, bending, snapping, and uprooting make these trees highly susceptible to subcortical beetle infestation (Connola et al. 1956; Gandhi et al. 2007; Gardiner 1975; Nikolov et al. 2014; Zampieri et al. 2020). Additionally, the large numbers of downed trees and the amount of slash generated from wind disturbance can lead to beetle population increases due to the sudden abundance of feeding and brooding resources (Gardiner 1975; Nikolov et al. 2014; Zampieri et al. 2020). These effects may be particularly pronounced in plantation settings due to high concentrations of weakened hosts and the sudden increase in suitable and diverse habitats (Knížek and Beaver 2007).

Buprestid and cerambycid beetles are phloeo-xylophagous borers of living, decaying, or dead wood (Cocquempot and Lindelöw 2010; Evans et al. 2007). These beetles are typically secondary colonizers of stressed, damaged, and dying trees following bark beetle primary colonization (Evans et al. 2007). Adults lay their eggs on trees, and hatched larvae tunnel under the bark and feed on the phloem and xylem layers (Haack et al. 2017). The tunneling activities girdle the tree, contributing to its death and eventual decomposition (Ethington et al. 2018; Gandhi et al. 2007). Populations of woodborers have the potential to quickly increase during periods of extreme disturbance, which results in atypically large amounts of woody debris and standing dead or dying trees (Gandhi et al. 2019). In addition to colonizing stressed or dead trees, overabundant populations of woodborers may be able to colonize adjacent live residual trees, which may exacerbate economic losses for plantation owners (Gandhi 2005). Economic losses from subcortical beetle outbreaks may even exceed losses from wind damage (Nikolov et al. 2014), making subcortical beetle management after wind disturbance a top priority for many landowners and foresters.

Despite the attention paid to subcortical beetle outbreaks in western North America and Europe, far less is known about subcortical beetle population dynamics following catastrophic wind events in the southeastern United States, which constitutes a substantial global source of timber. As of 2017, Alabama, Georgia, and Florida were among the top five southern states for pine (*Pinus* sp.) plantations, with approximately one-third of their timberland classified as planted (Oswalt et al. 2019). Planted pines make up 18% of the forested area in the southern region but account for 67% of the annual growth and 82% of the annual removals of softwood species (Oswalt et al. 2019). Due to the ability to produce high volumes of wood annually, this region has become known as the "wood basket" of the world. As an example of this productivity, in 2013, the forest products industry generated ~$230 billion of the southern US regional economic output (Boby et al. 2014).

The southeastern United States is highly prone to hurricanes in addition to producing a significant proportion of the world's timber. Over the course of a century, the entirety of the North American Coastal Plain region will have experienced at least one category 3 or higher-grade hurricane (Blake et al. 2011; Zampieri et al. 2020). In the past 100 years, the average normalized damage caused by hurricanes was ~$10 billion per year in the continental United States (Lin and Cha 2020; Pielke et al. 2008). Further, rising temperatures due to climate change are expected to stimulate more water vapor in the atmosphere, which will interact with warmer sea surface temperatures to create more intense hurricanes (Emanuel 1987, 2005). North Atlantic hurricanes have increased in intensity since the 1980s, and the frequency of the most destructive storms in this region (category 4 and 5 hurricanes) has also increased (Garfin et al 2014; IPCC 2007; Lin and Cha 2020; Olsen 2015).

With the increase in catastrophic wind disturbance events and more extensive pine plantations, there are no empirical studies on the population dynamics or community responses of woodboring beetles in wind-damaged stands in this region, and very few recent studies elsewhere in the United States (e.g., Dodds et al. 2019; Gandhi et al. 2009). Woodboring beetles contribute to wood degradation and loss of lumber value through larval gallery formations. Knowing populations levels of major species of woodboring beetles following disturbance helps foresters gauge how quickly to salvage for solid wood versus pulpwood in variously damaged stands. An opportunity to understand woodboring beetle responses to wind-damaged stands—information critical to foresters tasked with management of forests post disturbance—was provided by catastrophic Hurricane Michael, a category 5 storm with sustained wind speeds of 259 km/h (Callaghan 2019; Florida Forest Service 2018) that made landfall on October 10, 2018 near Mexico Beach in the Florida Panhandle. The storm system moved north through Georgia, South Carolina, North Carolina, and Virginia before reentering the Atlantic and dissipating, resulting in the loss of 59 lives and $25 billion in damage (Beven et al. 2019). Southern pine plantations experienced cataclysmic damage from Hurricane Michael (Florida Forest Service 2018). Of the total economic losses, $1.7 billion comprised damage to standing timber (Chapman, 2018). Damage to trees was not only from extreme winds but also from prolonged flooding from heavy rains due to the relatively slow-moving storm system (Florida Forest Service 2018).

Foresters were tasked with making rapid decisions about which pine stands to salvage harvest and when to harvest them because of the catastrophic and widespread damage to timberlands and reduced infrastructure following Hurricane Michael. Such catastrophic storm damage causes shortages in harvest and transportation capacities (see Broman et al. 2009). Private foresters posed the following critical management questions posthurricane: (1) Do woodboring beetle numbers vary based on tree damage in pine plantations? (2) Does the level of tree damage affect woodboring beetle species richness? and (3) Will beetle trap catches increase or decrease in the second growing season following the storm? The first question addresses the potential for pestiferous subcortical woodboring insect abundance to spike in more heavily damaged stands following a hurricane, potentially leading to additional economic losses due to the tunnelling activities of these subcortical insects. The second question addresses the identities of the woodboring beetles colonizing dead and dying timber in more- and less-damaged stands, given that management strategies may have species-specific responses (Saint-Germain and Drapeau 2011). The third question addresses time since disturbance and will inform at what point in time stands that experienced different levels of damage may be harvested relative to one another. We also addressed a fourth question: How does the level of forest damage affect woodboring beetle species composition? This question was addressed because we generated these data to address the first three questions, and they provide critical and unique ecological information about forest insect responses following a catastrophic wind disturbance in planted southern US timberlands.

Methods

Study Stands and Sampling Design

Study sites (hereafter "stands") were located on privately managed land (~36,000 ha) in plantations of slash pine (*P. elliotii* Engelm) in the Florida Panhandle. Predominate soil types across all stands include Pelham and Plummer (National Cooperative Soil Survey 2007, 2009). On-site inspections were performed on all planted pine stands in November 2018 by driving accessible roads within and around stands and sometimes walking into the stands. Damage was assessed via visual estimation and measured as rounded percent damage (i.e., percent loss of trees) by assessing the proportion of uprooted trees and broken stems as compared with undamaged trees present in each stand. Estimates were made at multiple points (>3 points) for each stand and were then averaged for the final damage level per stand. Stands that were inaccessible from the ground due to fallen trees blocking the roads were inspected using the latest Google Earth imagery since the hurricane. Similar to the onsite inspections, estimates were made at multiple points (>3 points) for each stand in the imagery and were then averaged to obtain the damage level per stand. These were compared with stands that had been inspected on the ground to assess final percent loss, which was rounded to the nearest tenth and ranged from 20% to 70% (Table 1). These data were collected by the same crew of three personnel to allow consistency in classification of the tree damage classes and comparison.

In spring 2019, seven months after Hurricane Michael made landfall, four plots each of 10 m in radius along a transect were established in 14 affected slash pine stands (figure 1). Plots were placed > 20 m away from each other and > 50 m away from edges and into the damaged stands. Stands were > 20 ha in size and located > 1 km apart to ensure sampling independence. Mature pine stands ranged from 20 to 31 years old, had basal areas ranging from 13.80 to 45.58 m^2/ha (mean = 29.69 m^2/ha), and were unthinned at the time of sampling. Based on percent loss, stands were grouped into three damage categories: low (20% loss), moderate (30%–40% loss), or high (50%–70% loss) (Table 1). These categories were chosen because foresters would be making timely operational decisions (i.e., which ones to salvage and prioritize first) based on these damage levels (Dickens and Moorhead 2016). Control or undisturbed forest stands were not included in the study because the track of Hurricane Michael was very wide (>560 km), and there were no undisturbed stands in or near study sites. Sampling hundreds of miles away would have added the confounding effects of geographical variation on beetle populations and communities.

Table 1. Damage severity assessments for study stands. Percent loss was visually quantified by foresters on the ground. Wind damage categories were assigned to each stand and include low (20% loss), moderate (30%–40% loss), and high (50%–70% loss) categories (for 2019).

Year	[1]Stand	% Loss	Damage Category
2019, 2020	1	40	[2]Moderate/Low
2019, 2020	2	40	[2]Moderate/Low
2019, 2020	3	50	High
2019, 2020	4	50	High
2019, 2020	5	20	Low
2019	6	30	Moderate
2019, 2020	7	20	Low
2019, 2020	8	20	Low
2019, 2020	10	20	Low
2019, 2020	11	60	High
2019	12	70	High
2019, 2020	13	50	High
2019, 2020	14	50	High
2019, 2020	15	50	High

[1]Site 9 was eliminated from both the 2019 and 2020 datasets due to premature harvesting in 2019. Sites 6 and 12 were eliminated from the 2020 dataset due to premature harvesting in 2020.
[2]Stands 1 and 2 were categorized as moderate damage in 2019 and low damage in 2020.

Beetles were sampled in 2019 and 2020 using two flight intercept panel traps baited with standard woodborer lures (Ultra-High Release ethanol and alpha-pinene) and two Lindgren funnel traps baited with *Ips* bark beetle lures ([-]-ipsenol, [+/-]-ipsdienol, and *cis*-verbenol), for a total of four traps per stand (56 traps in total) (all lures are from Synergy Semiochemicals Corp., Canada). Traps with *Ips* lures were intended for the three *Ips* beetle species, but woodboring beetles were also trapped. Traps were placed in each of the plots in the interior of stands and were operated during May (2019) and June (2020), and samples collected every two weeks until August (2019) and September (2020) for a total of 784 trap samples over two growing seasons. The 14 study stands (units of replication) in 2019 comprised four, three, and seven stands in the low-, moderate-, and high-damage categories, respectively. Stand is the experimental unit in this study. Due to premature harvesting, stands 6 and 12 were eliminated from the 2020 dataset, for a total of 12 study stands. Because one of the two stands eliminated from the 2020 dataset had been categorized as moderate damage in 2019, the 2020 dataset was restricted to only two damage categories (low: <50% tree loss; and high: > 50% tree loss). This was accomplished by reassigning stands 1 and 2 as low damage in 2020 (both experienced 40% loss, and in 2019, were categorized as moderate damage) (Table 1). Due to these inconsistencies, the effects of hurricane damage classes on woodborer population and species composition metrics were tested separately for the 2019 and 2020 datasets. To compare beetle responses across sampling years, data from the 12 stands present in both 2019 and 2020 were assessed, and stand-level differences were accounted for using mixed-effects models (see Statistical Analyses section).

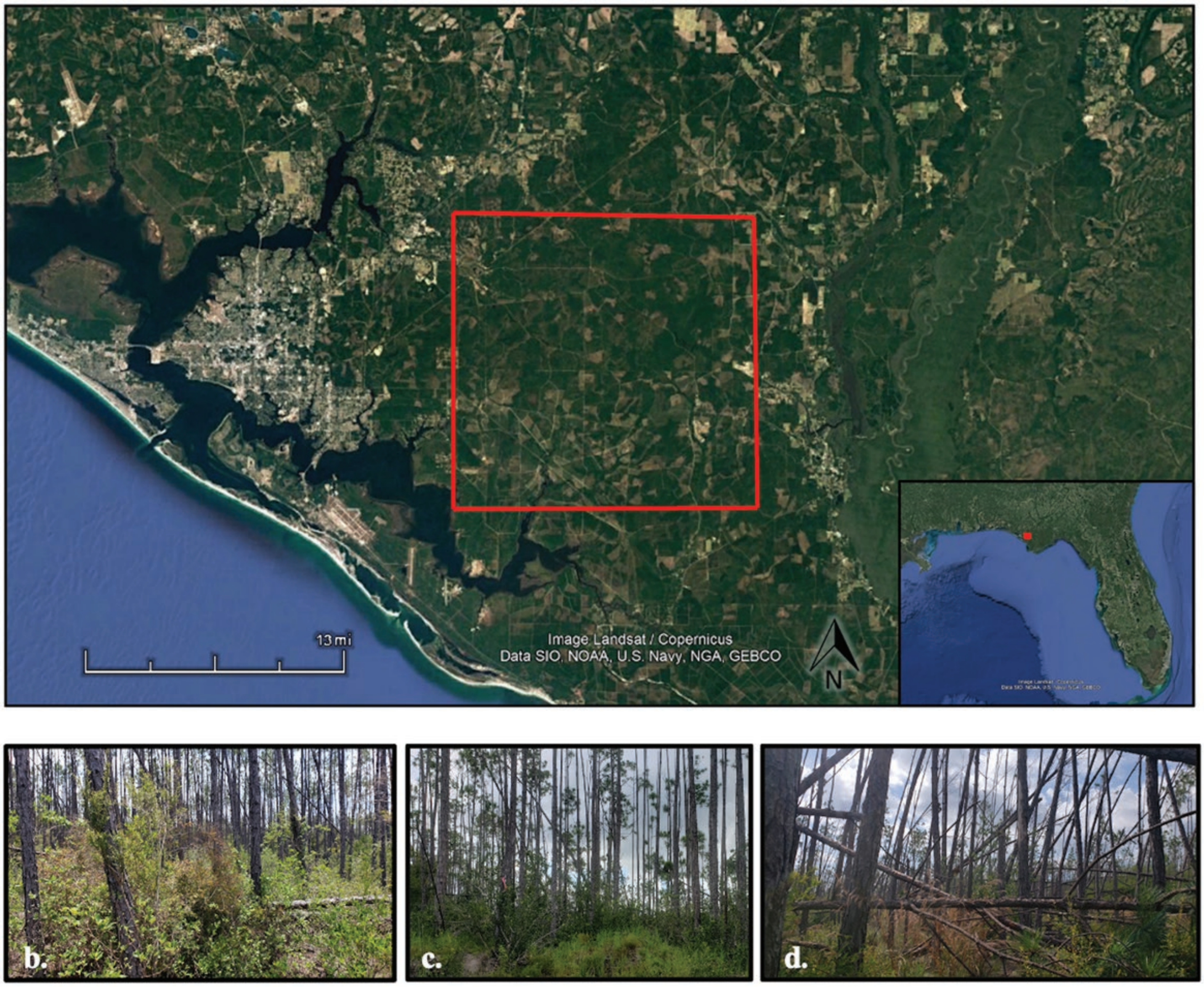

Figure 1 (a) General location of stands within the Florida Panhandle, USA. Exact locations of each stand are not provided as requested by forestry partners. Imagery attained from Google Earth. (b) Example of a low damage stand following Hurricane Michael (>20% loss). (c) Example of a moderate damage stand (30%–40% loss). (d) Example of a high damage stand (50%–70% loss).

Samples were collected in paper funnels and frozen at -16°C. Buprestid and cerambycid adults were sorted from sample bycatch and stored in 70% ethanol in plastic 90 mL specimen cups. Specimens were identified according to Lingafelter (2007), and species identifications were verified by taxonomists at the Georgia Museum of Natural History. The reference collection was also deposited at the museum.

Statistical Analyses

Insect trap catches are an indirect measure of relative abundance: that is, abundance as a function of the activity of a given species or activity-abundance (Apigian et al. 2006a, 2006b; Spence and Niemelä 1994). To account for trap disturbances, woodborer beetle catches from individual traps were averaged to yield mean trap catches per stand per sampling date. These were then standardized to total trap catch in 15 days ([mean trap catch/total number of days that trap was operational] × 15), because traps were emptied approximately every two weeks. These values were averaged per stand across each sampling year to account for lack of independence between sampling dates. After calculating stand averages per year, this yielded a final sample size of 14 replicates in 2019 and twelve in 2020.

Generalized linear models (GLMs) were used to determine whether woodborer beetle trap catches would vary across severity of stand damage following Hurricane Michael. All statistical analyses in this study were performed using the statistical software R (version 1.0.143; R Core Team 2021). GLM response variables included standardized total mean trap catches (hereafter "total catches") and standardized mean trap catches for the three most abundant species (hereafter "catches"). GLMs were performed for each of the four response variables for each year of sampling for a total of eight models (Table 3). Damage category (three levels for 2019, two levels for 2020) was used as the categorical predictor variable in all GLMs. Response variables were continuous and bounded at zero, and raw data distributions and model residuals were evaluated for normality using frequency histograms, density plots, and residual quantile-quantile plots. When data adhered to the assumption of normality, Gaussian GLMs with an identity link function were used. When data did not adhere to the assumption of normality, data were right-skewed with long tails. For response variables that were right-skewed but did not include zeroes (i.e., at least one individual of the target species was captured at every

Table 2. List of woodboring beetle families, subfamilies, genera, and species identified from 14 pine stands in 2019 and 12 stands in 2020 following Hurricane Michael. Damage category (final column header) indicates the damage category or categories in which the species was trapped (H = high, M = moderate, L = low).

Family	Subfamily	Genus	Species	Number trapped 2019	Number trapped 2020	Damage category
Cerambycidae	Cerambycinae	*Aethecerinus*	*Aethecerinus hornii* Lacordaire	1	0	H
		Curius	*Curius dentatus* Newman	0	8	L, M, H
		Eburia	*Eburia quadrigeminata* Say	1	0	H
		Elaphidion	*Elaphidion mucronatum* Say	3	5	M, H
		Knulliana	*Knulliana cincta spinifera* Drury	0	1	M
		Neoclytus	*Neoclytus acuminatus* Fabricius	2	1	H
			Neoclytus scutellaris Olivier	0	3	L, H
		Xylotrechus	*Xylotrechus colonus* Fabricius	1	0	H
			Xylotrechus sagittatus Germar	14	284	L, M, H
	Lamiinae	*Acanthocinus*	*Acanthocinus nodosus* Fabricius	10	43	L, M, H
			Acanthocinus obsoletus Olivier	1,330	694	L, M, H
		Aegomorphus	*Aegomorphus morrisii* Uhler	0	1	L
			Aegomorphus modestus (Gyllenhall)	1	0	L
		Astylopsis	*Astylopsis arcuata* (LeConte)	2	4	M, H
			Astylopsis fascipennis Schiefer	1	0	H
			Astylopsis sexguttata Say	3	11	L, M, H
		Leptostylus	*Leptostylus argentatus* (Miskimen & Bond)	0	6	L, M, H
			Leptostylus transversus Gyllenhal	4	14	L, M, H
		Liopinus	*Liopinus alpha* Say	0	2	L, M
		Monochamus	*Monochamus titillator* Fabricius and *M. carolinensis* Olivier	646	588	L, M, H
	Lepturinae	*Stenelytrana*	*Stenelytrana emarginata* Fabricius	1	0	H
		Strangalia	*Strangalia famelica* Newman	2	0	H
	Prioninae	*Orthosoma*	*Orthosoma brunneum* Forster	0	2	L, M, H
		Prionus	*Prionus pocularis* (Dalman)	4	3	L, M, H
	Spondylidinae	*Arhopalus*	*Arhopalus rusticus* Linnaeus	18	25	L, M, H
Buprestidae	Buprestinae	*Buprestis*	*Buprestis lineata* Fabricius	2	13	L, M, H
			Buprestis maculipennis Gory	7	8	L, M, H
		Chrysobothris	*Chrysobothris dentipes* Germar	2	0	L, M
			Chrysobothris femorata Olivier	0	2	H
	Chrysochroinae	*Chalcophora*	*Chalcophora virginiensis* Drury	12	16	L, M, H
		Dicerca	*Dicerca juncea* Knull	1	3	L
			Dicerca obscura Fabricius	2	3	L, H

stand during the sampling season), GLMs with a Gamma distribution and identity link function were used. For response variables that were semicontinuous (i.e., right-skewed with continuous positive outcomes and exact zeroes arising from no captures of target species at some stands across the sampling season), gamma GLMs were not appropriate because Gamma assumes only positive values and cannot incorporate zeroes. As such, the R package *glmmTMB* was used to specify hurdle-Gamma models, a modified version of the Gamma GLM that combines a binomial component to model the zeroes and a Gamma component to model the continuous positive outcomes (Magnusson et al. 2021). For all GLMs, variable significance was assessed using Wald χ^2 tests (function *Anova* in package *car*; Fox and Weisberg 2019) at $\alpha = 0.05$. For 2019 datasets containing three levels of the predictor variable, Tukey post hoc tests were performed using the *glht* function in the R package *multcomp* (Hothorn et al. 2008).

To determine whether the level of forest damage affected beetle species richness, species rarefaction curves were generated using the *specaccum* function in R package *vegan* (Oksanen et al. 2020). Rarefaction, a technique that calculates species richness based on number of samples, addresses an inherent issue in community sampling: the larger the number of individuals that are sampled, the greater the number of species that will be found. Rarefaction ameliorates this problem by multiple random resampling of the pool of available samples. Rarefaction curves are then plotted against increasing numbers of subsamples or individuals to illustrate the mean species richness present in each sample, that is, the expected number of species in a collection of individuals randomly sampled from the larger available pool (Gotelli and Colwell 2001). Curves were plotted with 95% confidence intervals by accumulating individuals for total catches for both sampling years to illustrate annual differences in species richness and independently for total catches per damage category in 2019 and 2020.

Analysis of similarities (ANOSIM) tests were performed to evaluate whether woodborer species composition was dissimilar among damage categories in 2019 and 2020. ANOSIM is a nonparametric, ANOVA-like test that operates on a ranked dissimilarity matrix (Clark 1993). The woodborer assemblage matrix for each sampling year was composed of catches per stand per date for all species trapped and identified (see Table 3). Prior to performing ANOSIM tests, "null" observations were removed from the dataset (i.e., those in which there were no woodborers trapped), and then dissimilarity matrices were calculated using Bray-Curtis distances [function *vegdist* in package *vegan* (Oksanen et al. 2020)]. Significance of dissimilarity among stands for each sampling year was evaluated at $\alpha < 0.05$. Nonmetric multidimensional scaling (NMDS) was performed using the function *metaMDS* in the R package *vegan* to visualize woodborer beetle assemblage composition among damage categories. NMDS is a means of visualizing similarities among groups within a multivariate dataset by finding a nonparametric, monotonic relationship between the dissimilarity matrix and the Euclidean distances between observed data points and then assigning each a location in reduced-dimensional space (Cox and Cox 2001). NMDS is a robust means of ordination that bypasses the requirement that the data adhere to assumptions of normality by substituting original distances with ranks. Although this approach sacrifices information about the magnitude of distances, it is advantageous for data which do not have an identifiable distribution (Buttigieg and Ramette 2014). Two two-dimensional NMDS models were run on each Bray-Curtis dissimilarity matrix for 2019 and 2020. Models ran for 500 permutations or until a solution was reached.

Linear mixed effects regressions (LMERs) were used to determine whether woodborer beetle catches differed between the first and second years following Hurricane Michael. Response variables again included total catches and catches for the three most abundant species, and individual LMERs were performed for each of the response variables for a total of four models (Table 4). Year (2019, 2020) was used as the categorical fixed effect in all LMERs. Stand was included as a random effect to account for stand-to-stand variability because stands experienced different levels of damage from Hurricane Michael and thus comprised different treatments. Damage category was not included as a fixed or random effect in these models because damage categories differed for 2019 and 2020 due to the loss of two stands between years. For this same reason, LMERs were restricted to only the 12 stands that were present in both 2019 and 2020 (Table 1). LMERs were performed using the R package *lme4* (Bates et al. 2015). Again, variable significance was assessed using Wald χ^2 tests at $a = 0.05$.

Results

In total, 3,810 adult woodborer beetle specimens were identified comprising 32 species, 22 genera, and seven subfamilies within families Buprestidae and Cerambycidae (Table 2). In the 14 stands in 2019, 2,070 adult beetles were trapped. In the 12 stands in 2020, 1,740 adult beetles were trapped. Of the total number of specimens identified from both years, 98.14% were cerambycids and 1.86% were buprestids. The three most abundant taxa, *Acanthocinus obsoletus* Olivier (53.12%) and two *Monochamus* sp. (32.39%), both belonging to Cerambycidae, comprised 85.51% of specimens. Differentiating between *M. titillator* Fabricius and *M. carolinensis* Olivier was challenging, and the two are considered a species-complex. Hence, the counts for these species were pooled together into one taxonomic category. Of the remaining 14.49% of specimens, 7.82% were *Xylotrechus sagittatus* Germar, also a cerambycid. The final 6.67% of specimens were comprised of taxa represented by a single or few individuals of 29 species. Eight species (seven cerambycids and one buprestid) were caught exclusively in 2019, and six species (five cerambycids and one buprestid) were caught exclusively in 2020 (Table 2).

14 species were captured in all three damage categories (11 cerambycids and three buprestids). For the sake of clarity, the qualitative results described in this paragraph adhere to the division of damage categories for the 2019 dataset (i.e., low = 20% loss, moderate = 30%–40% loss, and high = 50%–70% loss). Three species were unique to low-damage stands (*Aegomorphus modestus* Gyllenhall in Schoenherr, *Aegomorphus morrisii* Uhler, and *Dicerca juncea* Knull). One species was unique to moderate-damage stands (*Knulliana cincta spinifera* Drury), and eight species were unique to high-damage stands (*Aethecerinus hornii* Lacordaire, *Astylopsis fascipennis* Schiefer, *Chrysobothris femorata* Olivier, *Eburia quadrigeminata* Say, *Neoclytus acuminatus* Fabricius, *Stenelytrana emarginata* Fabricius, *Strangalia famelica* Newman, and *Xylotrechus colonus* Fabricius). Two species were only found in moderate- and high-damage stands (*Astylopsis arcuaus* LeConte and *Elaphidion mucronatum* Say); two species were only found in low- and high-damage stands (*Dicerca obscura* Fabricius and *Neoclytus scutellaris* Olivier); and two species were only found in low- and moderate-damage stands (*Chrysobothris dentipes* Germar and *Liopinus alpha* Say) (Table 2). The three most abundant species, *A. obsoletus*, *Monochamus* spp., and *X. sagittatus*, were captured in all damage categories.

Total catches were higher in moderate-damage stands in 2019, which contained 50% more woodborers than high-damage stands and 60% more woodborers than low-damage stands ($X^2 = 14.74$, $P < 0.001$; Table 3; figure 2a). High- and low-damage stands did not differ from one another in 2019. In 2020, at $\alpha = 0.01$, high-damage stands had higher total catches than low-damage stands ($X^2 = 2.93$, $P = 0.087$; Table 3; figure 2b). GLMs assessing the effect of damage category on catches of individual taxa yielded mixed results depending on taxa and sampling year. Catches of *A. obsoletus*, the most abundant species in the study, did not differ among damage categories in 2019 ($X^2 = 2.83$, $P = 0.24$; Table 2; figure 3a) or in 2020 ($X^2 = 1.54$, $P = 0.22$; Table 3; figure 3b). Catches of the second most abundant species-group in the study, *Monochamus* sp., were highest in moderate-damage stands in 2019 ($X^2 = 15.32$, $P < 0.001$; Table 3; figure 3c)

Table 3. Results of GLMs[1] and Wald χ^2 significance tests evaluating the effects of stand damage categories on standardized mean trap catches of all woodborers, *Acanthocinus obsoletus*, *Monochamus* sp., and *Xylotrechus sagittatus* for 2019 and 2020. Site damage category (low, moderate, and high for 2019; low and high for 2020) was used as the explanatory variable. Coefficient estimates (Coeff.), standard errors (S.e.), t/z-scores, and *P*-values are included for levels of the explanatory variable. χ^2 test statistics and *P*-values are included for significance of overall models. Asterisks indicate significance at $a < 0.05$.

Standardized mean trap catches	Levels of Damage Category	2019						2020					
		GLM				Significance of overall model		GLM				Significance of overall model	
		Coeff.	S.e.	z/t	*P*	X^2	*P*	Coeff.	S.e.	z/t	*P*	X^2	*P*
Total woodborers	Low/Intercept	16.24	4.35	3.73	0.003*	14.74	<0.001*	26.34	3.68	7.16	<0.001*	2.93	0.09
	Moderate	23.86	6.64	3.59	0.004*			NA					
	High	3.92	5.45	0.72	0.49			8.91	5.20	1.71	0.12		
Monochamus spp.	Low/Intercept	2.07	0.60	3.47	0.005*	15.32	<0.001*	7.24	1.38	5.26	<0.001*	1.75	0.19
	Moderate	9.55	3.91	2.44	0.03*			NA					
	High	2.87	1.23	2.33	0.04*			2.57	1.95	1.32	0.22		
Acanthocinus obsoletus	Low/Intercept	12.16	2.61	4.65	<0.001*	2.83	0.24	8.92	1.59	5.62	<0.001*	1.54	0.22
	Moderate	3.32	4.65	0.71	0.49			NA					
	High	-2.57	3.04	-0.85	0.42			2.78	2.25	1.24	0.24		
Xylotrechus[2] *sagittatus*	Low/Intercept	7.23	2.22	3.28	0.001*	6.48	0.04*	4.55	1.65	2.76	0.02*	0.36	0.55
	Moderate	18.31	11.26	1.62	0.10			NA					
	High	8.71	4.11	2.12	0.03*			-1.21	2.05	-0.59	0.57		

[1]GLMs are gaussian with an identity link function for total woodborers (2019, 2020), *Monochamus* sp. (2020), and *A. obsoletus* (2020); Gamma with an identity link for *Monochamus* sp. (2019), *A. obsoletus* (2019), and *X. sagittatus* (2020); and hurdle-Gamma for *X. sagittatus* (2019).
[2]Summary statistics included for conditional portion of hurdle-Gamma model (2019).

Table 4. Results of LMERs (Fixed effect: year; random effect: stand) and Wald χ^2 significance tests evaluating the change in standardized mean trap catches of all woodborers, *Acanthocinus obsoletus*, *Monochamus* sp., and *Xylotrechus sagittatus* from 2019 to 2020. Coefficient estimates (Coeff.), standard errors (S.e.), and t-scores are included for levels of the fixed effect. χ^2test statistics and *P*-values are included for significance of overall models. Asterisks indicate significance at *a* < 0.05. Random effect variance is included for the effect (stand) and model residuals.

Standardized mean trap catches	LMER Fixed effect				Significance of overall model		Random effect variance	
	Year	Coeff.	S.e.	t	X^2	*P*	Stand	Residuals
Total woodborers	2019/Intercept	23.95	3.31	7.24	3.93	0.047*	60.07	71.4
	2020	6.84	3.45	1.98				
Monochamus sp.	2019/Intercept	5.68	1.18	4.84	9.22	0.002*	11.31	5.25
	2020	2.84	0.94	3.04				
Acanthocinus obsoletus	2019/Intercept	12.04	1.35	8.95	0.82	0.36	0.00[1]	21.72
	2020	-1.72	1.9	-0.91				
Xylotrechus sagittatus	2019/Intercept	0.03	0.73	0.5	14.3	<0.001*	0.01	6.42
	2020	3.91	1.03	3.78				

[1]Singular fit meaning the parameters are on the boundary of the feasible parameter space and the variance of the random effect is close to zero (Bates et al. 2015).

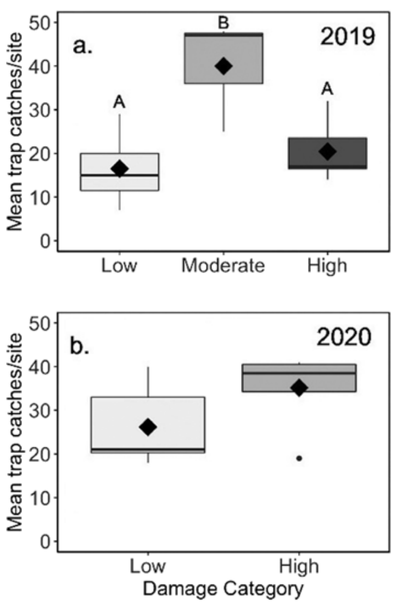

Figure 2 Boxplots depicting differences in means (diamonds), medians (horizontal lines), interquartile ranges (whiskers), and outliers (points) for total standardized mean trap catches across damage categories in (a) 2019 and (b) 2020.

but did not differ among low- and high-damage stands in 2020 (X^2 = 1.75, *P* = 0.19; Table 3; figure 3d). Catches of *X. sagittatus*, the third-most abundant species in the study, were higher in low-damage stands than high-damage stands in 2019 (X^2 = 6.48, *P* = 0.04; Table 3; figure 3e), but also did not differ among damage categories in 2020 (X^2 = 0.36, *P* = 0.55; Table 3; figure 3f).

Species rarefaction curves showed that in 2019, high-damage stands were the most diverse (17 species at 480 individuals), followed by low-damage (12 species at 480 individuals) and moderate-damage (eight species at 480 individuals; figure 4a) stands. Confidence intervals largely overlapped for moderate- and low-damage stands, suggesting that only high-damage stands had meaningfully greater species richness in 2019. Rarefaction curves for 2020 showed little difference in species richness between low- and high-damage stands (approximately 19 to 20 species at 780 individuals; figure 4b). Rarefaction curves per year indicated that 2019 yielded slightly higher species richness than 2020 (23 species versus 17 species at 750 individuals, respectively), but the curves are largely overlapping for all of 2020 (figure 4c).

Two-dimensional NMDS models converged after a maximum of 500 iterations and yielded stress values of 0.089 and 0.146 for 2019 and 2020, respectively. Although these values indicated that the NMDS for 2019 had a better fit than that of 2020, the values of both models fall within the threshold at which NMDS would be considered reliable (i.e., > 0.2; Buttigieg and Ramette 2014). The 2019 NMDS plot depicted largely overlapping groupings of woodborer species among damage categories, and ANOSIM did not detect differences in dissimilarities among groupings of species (*R*-statistic = 0.014, *P* = 0.28; figure 5a). The 2020 NMDS plot also depicted overlapping grouping of species, but ANOSIM indicated more heterogeneity for low- than high-damage stands (*R*-statistic = 0.041, *P* = 0.03; figure 5b). Species groupings for stands with high levels of damage (>50% loss in 2020) were of an intermediate size (e.g., moderately similar) compared with the much broader groupings (e.g., less similar) of stands that had low levels of damage (<50% loss in 2020).

Using the 12 stands present in both 2019 and 2020 and after controlling for the stand-level effects using linear mixed effects regressions, total woodborer catches were higher by 28.6% in 2020 than in 2019 (X^2 = 3.93, *P* = 0.047; figure 6a). Likewise, *Monochamus* and *X. sagittatus* catches were higher by 50% and 11,725%, respectively, in the second year following Hurricane Michael (X^2 = 9.22, *P* = 0.002; figure 6c, and X^2 = 14.3, *P* < 0.001; figure 6d, respectively). The large percent increase in *X. sagittatus* from 2019 to 2020 is due to seven of the 12 stands in 2019 not yielding any individuals, and all stands in 2020 yielding individuals. *Acanthocinus obsoletus* catches did not differ between sampling years (X^2 = 0.82, *P* = 0.36; figure 6b).

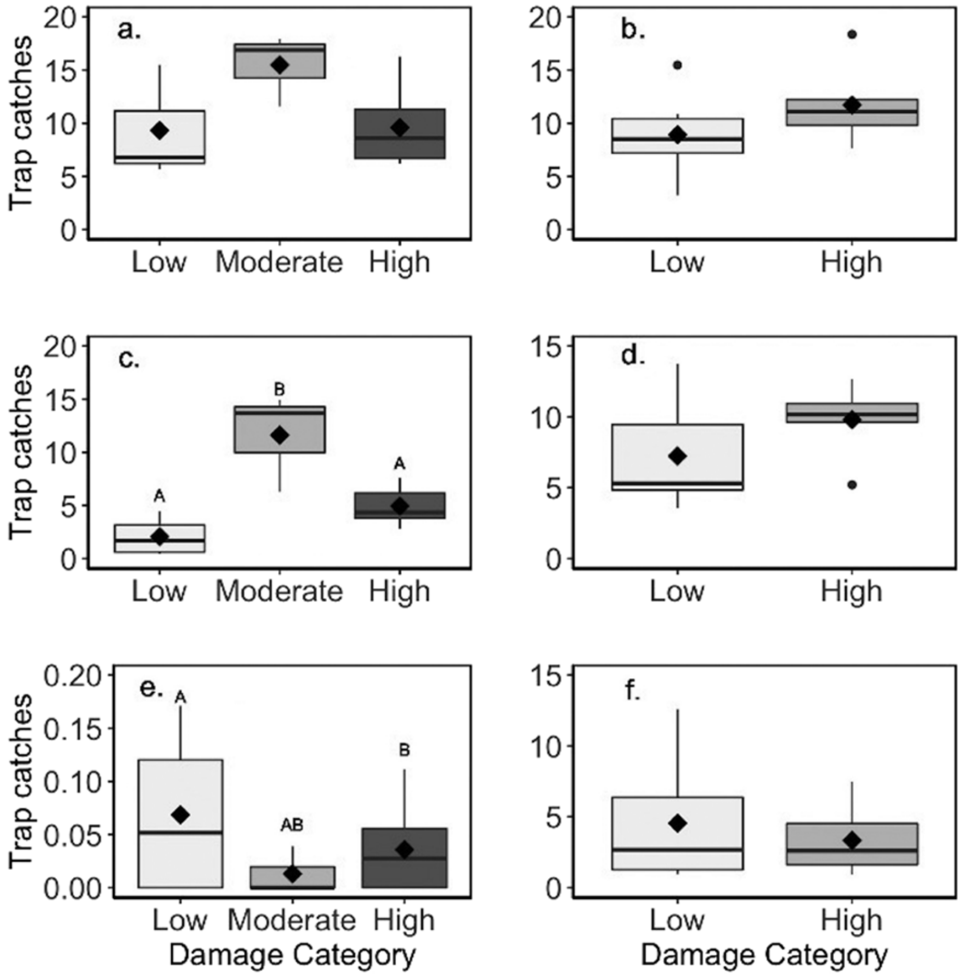

Figure 3 Boxplots depicting differences in means (diamonds), medians (horizontal lines), interquartile ranges (whiskers), and outliers (points) for standardized mean trap catches across damage categories for *Acanthocinus obsoletus* in (a) 2019 and (b) 2020, *Monochamus* spp. in (c) 2019 and (d) 2020, and *Xylotrechus sagittatus* in (e) 2019 and (f) 2020.

Discussion

Wind-disturbed forests may present beneficial environmental conditions and resources to subcortical insects by providing habitats for flowering understory plants, saplings present as advanced regeneration, damaged or stressed boles, and downed branches and twigs. These conditions provide food resources for adult woodborers in the forms of nectar, pollen, and live subcortical tissue for maturation feeding as well as dying woody habitat for breeding, oviposition, and larval development (Lingafelter 2007; Wermelinger et al. 2002). This is the first empirical study that has quantified woodboring beetle populations and assemblages following a catastrophic wind disturbance in southeastern pine forests. We report the following trends: (1) total catches were highest in moderately damaged stands in 2019 but did not differ among variously damaged stands in 2020; (2) catches of the three most-abundant woodborer species had different trends related to stand damage in both years; (3) total woodborer catches and those of *Monochamus* sp. and *X. sagittatus* were higher in 2020 (two years postdisturbance) than in 2019 (one year postdisturbance); (4) woodborer species richness was highest in the high-damage stands in 2019 but did not differ among variously damaged stands in 2020; and (5) woodborer species composition did not differ among variously damaged stands in 2019, but low-damage stands exhibited more heterogenous species groups than high-damage stands in 2020.

Our results bear various implications for the first question posed by forest managers following Hurricane Michael: Do woodboring beetle numbers vary based on tree damage in pine plantations? Total woodborer catches in 2019 were 50% and 60% higher in moderate- than in low- or high-damage pine stands, respectively, and the catches of *Monochamus* sp. (but not *A. obsoletus* or *X. sagittatus*) reflected this pattern. Such trends were not observed in 2020. Hence, in the first year following wind disturbance, the level of woodboring beetle catches depended on the level of tree damage, likely due to a higher habitat diversity but not necessarily quantity present in moderate- than in low- or high-damage stands (or habitat diversity hypothesis), although due to logistical constraints, woody debris could not be measured. Forest damage shortly after major wind disturbances typically results in many green residual trees that are damaged and stressed, resulting in more habitat availability for woodboring beetles, which we expect to be greater in moderately damaged stands in this study. Few studies have assessed the responses of insects to wind damage severity levels. However, in other disturbances such as wildfires, cerambycid beetles (especially *Monochamus* sp.)

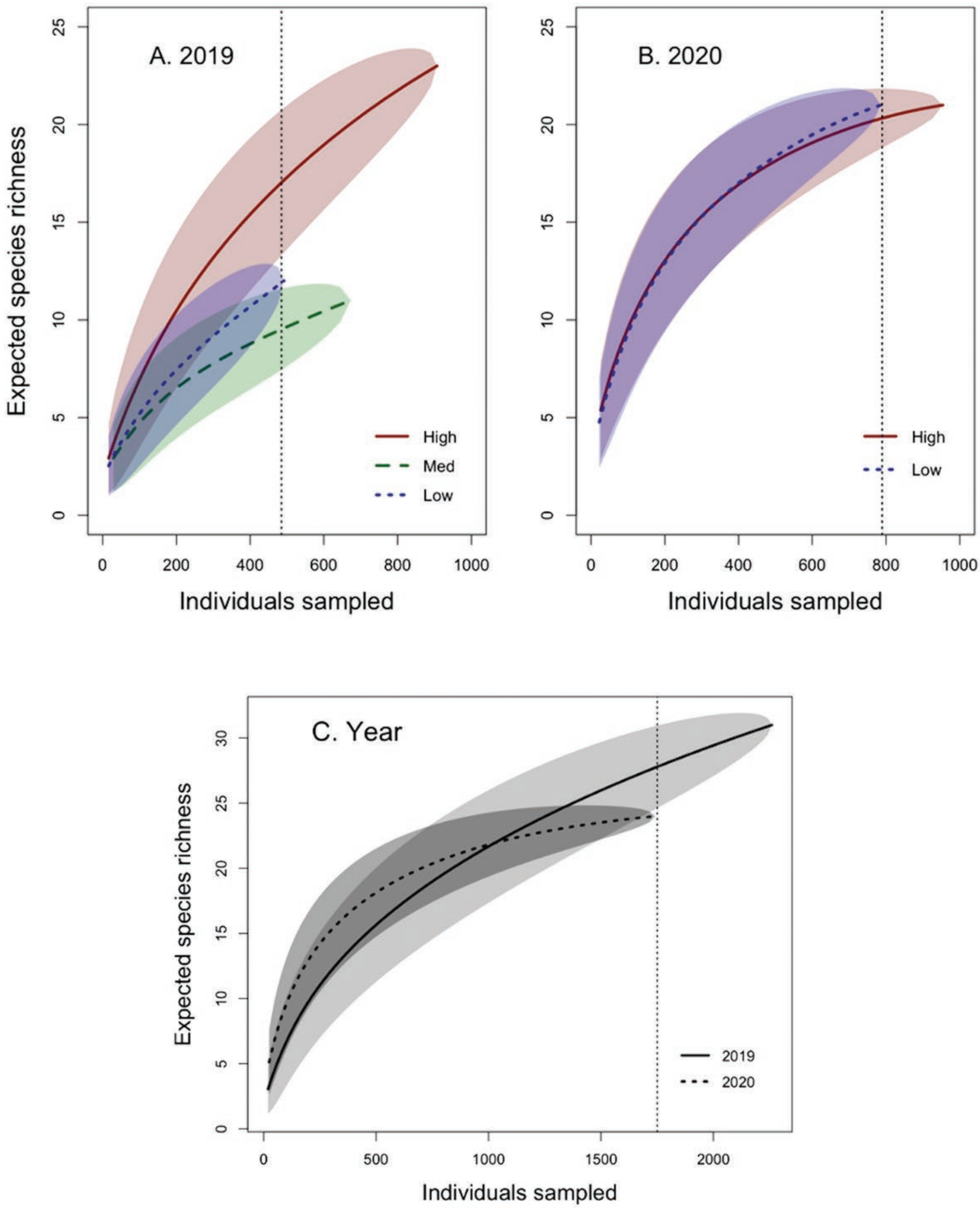

Figure 4 Rarefaction curves across (a) low-, moderate-, and high-damage stands in 2019; (b) low- and high-damage stands in 2020; and (c) sampling year (2019, 2020). Curves depict summed total woodborer trap catches across $n = 14$ stands in 2019 and $n = 12$ stands in 2020, respectively. Plot c depicts overall differences in summed total woodborer trap catches across sampling years, and does not consider damage categories. Shaded areas represent 95% confidence intervals.

were more abundant in low- and moderate-severity levels of burned forests and buprestid beetles in high-severity burned forests in California (Ray et al. 2019). Similarly, *M. alternatus* Hope responded positively to burn severity in *P. densiflora* Siebold & Zucc forests in Korea (Jung et al. 2020). These trends indicate that disturbance severity does appear to matter

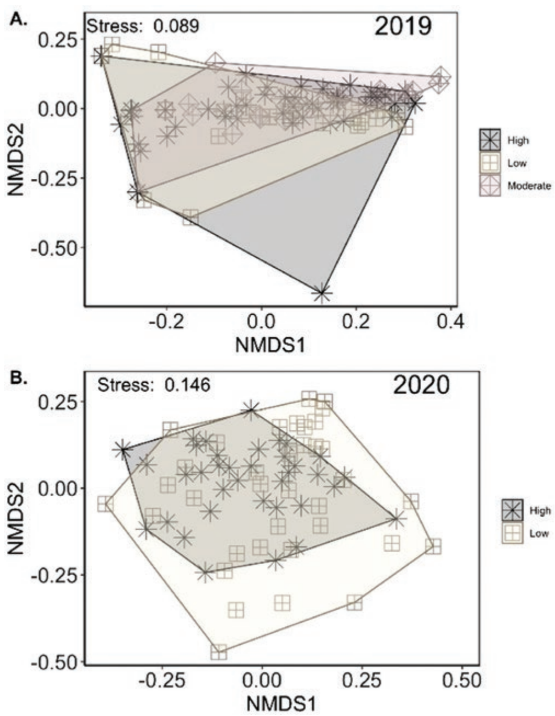

Figure 5 NMDS plots depicting Bray-Curtis dissimilarities in woodborer beetle assemblage composition among stand damage classes in (a) 2019 and (b) 2020.

for woodboring beetles and lends support to monitoring their populations postdisturbance.

In response to the second question posed by foresters—does the level of tree damage affect woodboring beetle species richness?—we found that, in 2019, woodborer species richness was highest in the high-damage stands and was lowest for the moderate-damage stands. This establishes a bimodal relationship between damage severity and species richness (see Moi et al. 2020). Short-term post-hurricane forest conditions, therefore, yielded the greatest numbers of woodborers in moderately damaged stands but the lowest species richness. It is well established that bark beetles and woodborers are the most frequently reported insect taxa in wind-disturbed forests (Connola et al. 1956; Gandhi et al. 2007; Gardiner 1975; Wickman 1965). The increase in woodboring beetle richness in high-damage stands could be due to attractive volatile chemicals (e.g., ethanol and monoterpenes) being released from large numbers of stressed, damaged, and dying trees following the initial influx of volatiles (e.g., ethanol and pinenes) attracting beetles to these areas (Allison et al. 2004; Chénier and Philogene 1989; Gandhi et al. 2007). Eight species in this study were unique to the high-damage stands, including *A. hornii*, *A. fascipennis*, *C. femorata*, *E. quadrigeminata*, *N. acuminatus*, *S. emarginata*, *S. f. famelica*, and *X. colonus*. Not much is known about the ecology of these species, but interestingly, several of them, including *A. hornii*, *A. fascipennis*, *N. acuminatus*, and *S. emarginata*, are known to breed on hardwood trees and are often found on flowers (Lingafelter 2007). Flowering understory plants generally respond positively to the increased light conditions and novel microsites associated with more open canopy conditions (Collins et al. 1985; von Oheimb et al. 2007), which may in turn sustain higher species richness of many woodboring beetles atypical of pine stands.

For the third question posed by forest managers—will beetle catches increase or decrease in the second growing season following the storm?—our results indicated a 28.6% increase in total catches and increases of 50% and 11,725%, respectively, in *Monochamus* sp. and *X. sagittatus* from 2019 to 2020. Differential responses of woodborer numbers to time since forest disturbance have been observed in other North American studies. For example, catches of subcortical insects including woodboring beetles were highest two years following a catastrophic windstorm and declined thereafter in Minnesota (Gandhi et al. 2009). Bark beetles and woodborers increased over a three-year sampling period following an EF1 tornado in Maine (Dodds et al. 2019). In contrast, the total numbers of wood-dwelling beetles in managed bottomland hardwood forests in South Carolina were higher in the center of young artificial gaps (one year) compared to older gaps (six years), likely due to the amount of coarse woody debris present in respective gaps (Ulyshen et al. 2004). Taken together, woodborer numbers may be highest in moderate-damage stands and diversity highest in high-damage stands initially following a catastrophic wind disturbance, but higher levels of diversity (namely, expected richness and assemblage composition) shifted to lower levels of damage, likely due to more trees dying and greater presence of suitable host material with time.

Regarding the fourth research question—does the level of forest damage in pine plantations affect woodboring beetle species composition?—it was found that woodborers responded differently to varying levels of forest damage in 2019 and 2020. Namely, in 2019, ANOSIM did not detect differences in woodborer species composition for high-, moderate-, and low-damage stands. A nonsignificant trend indicated that woodborer species composition in high-damage stands exhibited greater heterogeneity (i.e., less-similar species composition), whereas moderately damaged stands exhibited the greatest homogeneity (i.e., more-similar species composition). These qualitative results align with our findings that moderately damaged stands yielded the greatest trap catches but the lowest species richness in 2019.

As *Monochamus* sp. was the second-most abundant species group in the study, it is likely that some aspect of moderately damaged stands favored significant population increases for these taxa in the short-term following the disturbance. We posit that competitive exclusion by *Monochamus* sp. may explain the simultaneous increase in numbers of these common taxa and the homogenization of overall woodborer assemblages. In stands that experienced low- and high-severities of windthrow, these abundant taxa were favored slightly less, resulting in lower trap catches overall, but also yielding more heterogeneous woodborer species composition, potentially through competitive release. This may explain our finding of a bimodal relationship between expected woodborer species richness and damage severity in the first year following Hurricane Michael. Future studies of *Monochamus* sp. responses to wind disturbances may elucidate the mechanism(s) explaining our observations here.

There are several caveats to this study. Due to the extensive nature of Hurricane Michael, undisturbed stands could not be included in this study as controls to assess how woodboring beetles responded to the wind disturbance per se. Gandhi et al. (2009) reported that *Monochamus* species can increase dramatically (5–6 fold) in stands two to three years following severe wind disturbance as compared to undisturbed areas, and

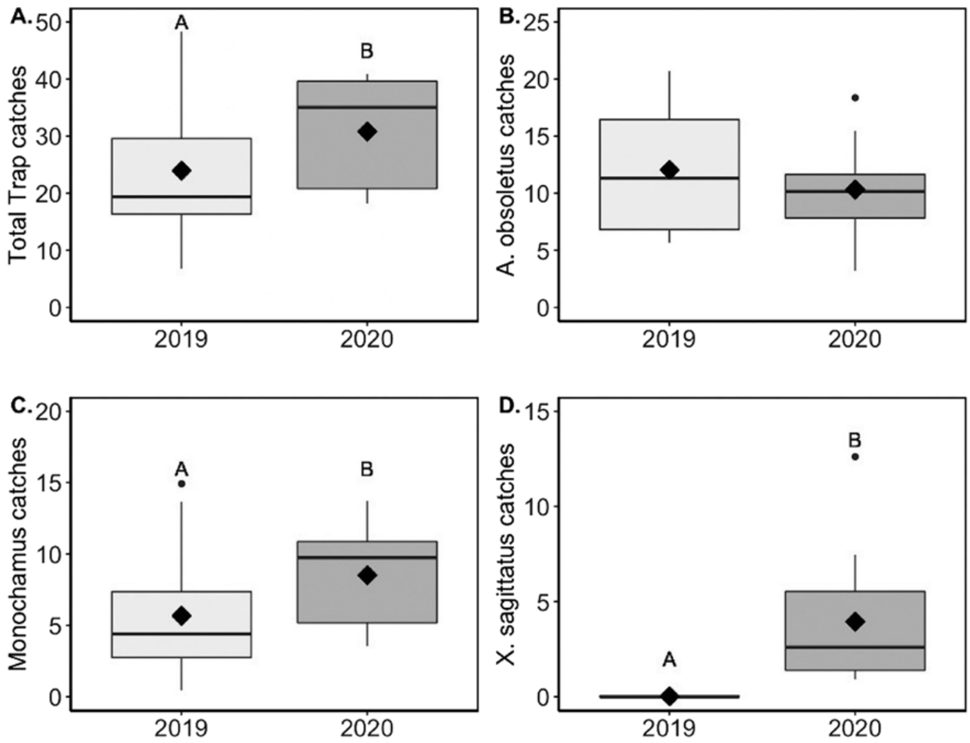

Figure 6 Boxplots depicting differences in means (diamonds), medians (horizontal lines), interquartile ranges (whiskers), and outliers (points) of trap catches for (a) total woodborers, (b) *Acanthocinus obsoletus*, (c) *Monochamus* sp., and (d) *Xylotrechus* in 2019 and 2020 (N = 12 stands for both years).

Bouget (2005) reported that saproxylic beetle assemblages differed and woodborer abundance was higher in short-term comparisons of gap and control plots in windthrown hardwood forests in France. If control stands had been available for our study, they may have indicated that the stands affected by Hurricane Michael would have yielded higher total numbers of woodborers and different community assemblages. Further, this study spanned only two years post disturbance, after which stands were harvested and replanted. This region also experienced an intense wildfire in 2022, thus precluding long-term sampling. We did not measure coarse-woody debris volume in the stands prior to insect sampling, which would have assisted in further refining the damage-level categories. Adult woodboring beetles were trapped using generic baits that largely mimic host volatiles, which likely either underestimated the actual species richness and catches of these taxa or captured species that may not typically colonize pine woody debris. However, long-range pheromones are known for only select cerambycid species and almost none for buprestid beetles (Allison et al. 2004), thus meriting further investigation of their chemical ecology in future studies. Further, trap catch data reflects the activity of beetles in these stands and not necessarily damage per se; however, such correlation studies are lacking, especially in the southeastern US region.

Conclusions

Overall, woodboring beetles exhibited complex and variable responses to a catastrophic hurricane in southeastern US pine plantations. In the first year following the hurricane, total trap catches were highest in the moderately damaged stands, whereas species richness was highest in the high-damage stands. In 2020, neither total catches nor species richness differed between high- and low-damage stands, but woodborer species composition was more diverse in low-damage stands. There was an overall increase of 28.6% in total catches of woodborers from 2019 to 2020, with notable increases in *Monochamus* sp. and *X. sagittatus*. It was not possible to track whether these increases in beetle numbers would have continued linearly or exponentially more than two years after the hurricane, as the study stands were fully harvested by private foresters in 2021, and a wildfire further decimated the stands in 2022. Based on our findings, we advise more timely harvesting of moderate- and high-damage stands after a catastrophic wind disturbance, which may lower additional economic impacts of wood decay due to the tunneling activities of woodboring beetles. As hurricanes continue to become more intense and damaging to forested ecosystems in the southeastern US, similar studies in other forest types (e.g., hardwoods) and ecoregions (e.g., upper Coastal Plains and Piedmont) along with a greater emphasis on other ecologically important insect taxa such as pollinators and ground-dwelling and saproxylic arthropods will be useful for forest recovery and long-term sustainability efforts.

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Conflict of Interest

There is no conflict of interest for this paper.

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