Journal of Economic Entomology, 114(2), 2021, 776–783
doi: 10.1093/jee/toaa309
Advance Access Publication Date: 18 January 2021
Research

Forest Entomology

Responses of Native and Non-native Bark and Ambrosia Beetles (Coleoptera: Curculionidae: Scolytinae) to Different Chemical Attractants: Insights From the USDA Forest Service Early Detection and Rapid Response Program Data Analysis

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Subject Editor: Elizabeth McCarty

Received 17 October 2020; Editorial decision 5 December 2020

Abstract

More than 60 non-native bark and ambrosia beetle species (Coleoptera: Curculionidae: Scolytinae) are established in North America and several have had severe negative impacts on ecosystems. Non-native scolytines can introduce fungi which may cause vascular wilts and compete with native fungi and lead to reductions in native species through host reduction. The Early Detection Rapid Response (EDRR) program was created by the USDA Forest Service in 2007 to detect non-native bark and ambrosia beetles and provide a baseline for tracking populations over time. This program has led to new collection records and increased communication among agencies to delimit non-native scolytine populations and perform appropriate management. Although insect responses to different lure types vary, it is unknown how different lures compare in attracting bark and ambrosia beetles. Our goal was to examine how lure combinations used in the EDRR program affect captures of bark and ambrosia beetle communities and to determine the most effective combination of lures for targeting non-native scolytines. The highest proportion of non-native scolytines was captured with ethanol, as was the greatest total number of species, and the most diverse beetle community. Traps with *Ips* (Coleoptera: Curculionidae) lures captured the highest proportion of native scolytines but the lowest total number of total species and was also the least diverse. Communities of scolytines differed significantly among lures, states, and years. While ethanol is an appropriate lure for generalist trapping and targeting a wide range of non-native bark and ambrosia beetles, more targeted lures are needed for monitoring certain species of non-natives.

Key words: early detection, invasive species, monitoring, rapid response, semiochemical

Non-native bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) cause significant global economic and ecological damage, and trends suggest their rates of introduction and establishment will continue to increase (Aukema et al. 2010, Lantschner et al. 2017, Seebens et al. 2017). In North America, non-native bark and ambrosia beetles such as the redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff) and the European elm bark beetle (*Scolytus multistriatus* (Marsham)) have devastated native host tree populations and host tree associates which may have negative ecological consequences, including deleteriously impacting specialist arthropods that feed on host foliage (Brasier and Buck 2001, Riggins et al. 2018). In addition to causing direct mortality, the introduction of non-native vascular wilt fungi into the tree may impact decomposition, nutrient cycling, and other ecosystem processes (Skelton et al. 2020). In the cases of *X. glabratus* and *S. multistriatus*, these fungi cause laurel wilt and Dutch elm disease, respectively, and their presence in a tree nearly always results in tree mortality.

Due to the increasing importance of non-native scolytines, the USDA Forest Service initiated the Early Detection Rapid Response (EDRR) program in 2007 (Rabaglia et al. 2019). Over the last 13 yr, this program has detected eight species new to North America, led to dozens of new collection records for non-native scolytines already established in the United States, and increased communication among local, state, and federal agencies responsible for delimiting non-native species ranges and subsequent control efforts (Rabaglia et al. 2019). Early detection and rapid response to a non-native species is a critical aspect in an invasive species management program (Hulme 2006) and efforts to increase efficacy of such programs, such as examining spatial heterogeneity of landscape types and efficiency of monitoring (e.g., Kaiser and Burnett 2010), are necessary to ensure that time and resources are used in the most efficient manner possible by targeting certain areas and species for monitoring.

Previous analyses of EDRR data indicated that several abiotic (e.g., temperature) and biotic (e.g., native scolytine community diversity) factors are responsible for non-native bark and ambrosia beetle establishment, spread, and subsequent impacts. For example, post-invasion changes to native bark and ambrosia beetle community diversity are primarily due to an overall reduction in species richness rather than non-native species replacing natives, meaning invasion frequently causes a direct reduction in richness and diversity through a variety of direct and indirect mechanisms such as competition and mutualism disruption (e.g., Riggins et al. 2018, McGeoch et al. 2019). Additional geographic factors such as distance to human communities, rainfall, and temperature also impact the process of invasion by different non-native beetle species, their detection rates, and the effects on native beetles (Rassati et al. 2016). Similarly, variations in methodology, including lure combinations used, can drastically change the diversity and abundance of native and non-native bark and woodboring beetles captured in traps (e.g., Aukema et al. 2010, Hofstetter et al. 2007, Dodds et al. 2010, Miller 2020).

In the United States, different lure combinations attract different scolytine species (Miller and Rabaglia 2009, Allison et al. 2013, Miller 2020). The EDRR program uses several lure types and combinations to attract non-native bark and ambrosia beetles as well as native pest beetles. During the initial years, trapping effort varied considerably but was eventually modified to include three traps per site, approximately 12 sites/state, and 9 states per year on a rotational basis (Rabaglia et al. 2019). Several lure combinations were chosen based on their known attractiveness to scolytines (e.g., Dodds et al. 2010). Ethanol (EtOH) ultra-high release rate lures were chosen because trees experiencing physiological stress produce it (Kelsey et al. 2014) and it also acts as a kairomone, attracting a wide variety of beetles (Miller and Rabaglia 2009, Ranger et al. 2016), whereas the combination of ipsdienol, *cis*-verbenol, and methylbutenol (*Ips*) was chosen to target non-native potential pest species such as *Ips typographus* L. (Bakke et al. 1977). The combination of α-pinene + EtOH (PE) was chosen as a generalist attractant for conifer infesting species (Miller and Rabaglia 2009). Several other lure combinations have been also used in the EDRR program.

We currently lack an understanding of how scolytine communities respond to different lure types. Knowing this information will help targeted monitoring programs, such as EDRR, to detect certain non-native species early and identify additional gaps with regards to non-native species monitoring. Many semiochemicals are used by both native and non-native species, and trap catches are often inundated with native species, making it challenging to find the non-natives. Using lures that are more targeted at attracting certain species or groups may help reduce the total number of non-native individuals, thereby reducing the time necessary to process samples. Additionally, quantifying these responses will help in monitoring effects of non-natives on natives as well. While this is not a specified objective of the EDRR program, it highlights how multiple objectives may be achieved through targeted and widespread monitoring of pest species.

To evaluate the effects of lure combinations on captures of native and established non-native scolytines, we compared capture rates of native and non-native bark and ambrosia beetles to traps baited with three lure combinations used in the EDRR program: combination *Ips* lure (*Ips*), combination α-pinene and ethanol (PE), and ethanol alone (EtOH). Specifically, our objectives were to 1) evaluate the effect of lure combination on trap captures of native and non-native beetles, and 2) evaluate species richness and diversity among lure combinations and states. We examined native and non-native scolytine community assemblages in trap catches by lure combinations, states, and years using nonmetric multidimensional scaling (NMS). We hypothesized that: 1) lure combinations would significantly affect the proportions of native and non-native bark and ambrosia beetles, thereby affecting observed diversity metrics (i.e., Shannon index and species richness) and subsequent interpretation of trapping data; and 2) communities of native and non-native scolytines would differ in their response to different lure combinations.

Methods

EDRR data were downloaded on 15 July 2020 (apps.fs.usda.gov/edrr) and included trap collection data for all states, and all sites within states, from 2007 to 2019 (Table 1). For the purposes of this study, only *Ips*, PE, EtOH lures were used for analyses. Captures with all other lures (e.g., Quercivorol) were removed from the dataset due to their limited use. We used scolytine trap capture data obtained for the lower contiguous 48 states and Alaska to maintain consistency of native and non-native communities. Species collected were identified as either 'native' or 'non-native' based on published records (Rabaglia et al. 2019).

None of the data were normally distributed or had equal variances. Because of high within-state site variation, all dependent variables were calculated on a year/state/lure basis; namely, proportions of native and non-native beetles, Shannon index (measurement of diversity and evenness of a sample), and species richness (the number of species in a sample) were calculated. Total number of individuals per state/trap/lure was summed and then proportions of native and non-native beetles were calculated by dividing the number of either native or non-native individuals by this total. To determine the effect of lure combination on proportions of native and non-native beetles, a generalized linear model was created with separate proportions of native and non-native beetles as the dependent variables using the binomial family with a logit link function. A multiple regression model was conducted with lure combination, state, and year, as well as two- and three-way interactions, as fixed-effect variables and Shannon index and species richness as dependent variables.

Trap collections were then split into native and non-native scolytines for community analysis and visualization using NMS ('vegan' package in R; Oksanen et al. 2019). An analysis of variance on NMS was performed using a Gower dissimilarity matrix. R was used for all statistical analyses (R Core Team 2020).

Results

A comprehensive list of non-native species collected, along with new state records, and states where each species is found, is presented in Rabaglia (2019). Native and non-native scolytine communities responded differently to lures both locally and on a continental scale as traps baited with EtOH lures captured a significantly higher proportion of non-native beetles and had higher Shannon indices and species richness compared to *Ips* lures and the PE lure (Tables 2 and 3; Fig. 1). Thirty-five states were surveyed a total of 165 times, with each state varying considerably in trapping effort (Table 1). There was a grand total of 471 observations, with each lure combination associated with 157 total trap collections over the 13-yr trapping period. On a per year/state/lure basis, total number of beetles

Table 1. Total number of sites used (three to four traps per site) in the EDRR program per state per year

State	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
AK	-	7	-	-	-	-	-	6	-	-	-	-	14
AL	-	5	-	-	12	-	-	-	-	-	-	-	-
AR	-	-	6	-	-	-	-	-	-	-	-	12	12
AZ	-	-	8	-	-	-	-	-	-	-	-	-	-
CA	8	8	-	13	12	11	12	10	11	10	14	16	11
CO	8	-	-	-	10	11	-	-	-	-	-	-	-
CT	-	-	-	-	-	12	-	-	-	-	-	-	-
DC	-	-	-	-	-	-	-	-	-	6	-	-	-
DE	-	-	7	-	-	-	-	-	-	-	-	-	-
FL	6	7	-	-	12	12	12	12	12	12	8	12	12
GA	7	-	-	7	12	12	12	13	12	12	16	16	16
ID	-	8	-	-	-	-	-	-	-	-	-	12	-
IL	-	-	13	14	-	-	-	16	-	-	-	-	-
IN	-	10	13	14	-	-	-	12	12	-	-	-	-
KS	-	-	7	-	-	-	-	-	-	-	-	-	-
KY	9	-	-	12	-	12	-	-	-	-	-	-	-
LA	7	-	-	12	-	12	-	-	-	-	14	-	-
MA	-	9	-	12	-	-	-	-	-	-	-	-	-
MD	-	-	-	-	12	-	-	12	12	-	-	-	-
ME	-	-	9	-	-	-	-	-	-	-	-	-	-
MI	9	9	-	-	12	-	-	-	-	12	11	-	-
MN	7	-	-	-	-	-	-	-	-	-	12	12	-
MO	-	10	-	-	-	-	-	12	-	-	-	-	-
MS	-	7	-	-	12	-	-	-	12	-	-	-	-
MT	-	-	-	-	-	-	-	-	-	12	-	-	-
NC	-	8	-	-	12	-	12	-	-	-	-	-	12
ND	-	-	-	-	-	-	-	-	-	-	-	-	12
NE	-	9	-	-	12	-	-	-	-	-	-	-	-
NH	9	-	-	-	-	-	-	-	-	-	-	-	-
NJ	-	9	9	12	12	-	-	-	-	-	-	-	-
NM	-	8	-	-	12	-	-	-	-	-	-	-	-
NV	-	-	9	-	-	-	-	-	-	-	-	-	-
NY	9	9	-	12	12	12	12	12	12	12	12	12	12
OH	9	-	-	12	-	13	-	-	-	-	-	-	-
OK	-	-	-	-	12	-	-	-	-	-	-	-	-
OR	9	-	-	12	15	-	-	12	13	-	-	-	-
PA	-	-	9	12	12	12	12	12	12	12	-	-	12
RI	-	-	7	-	-	-	-	-	-	-	-	-	-
SC	8	-	-	12	-	12	-	-	-	-	-	-	-
SD	-	-	9	-	-	-	-	-	-	-	-	-	-
TN	-	-	7	-	-	-	-	-	-	-	-	-	-
TX	8	-	-	8	9	13	11	10	12	12	16	16	12
UT	32	-	-	-	14	14	-	-	-	-	-	-	-
VA	-	8	-	-	-	-	12	-	-	-	12	-	-
VT	-	-	8	-	-	-	-	-	-	-	-	-	-

Table 1. Continued

State	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
WA	8	-	-	12	-	12	-	-	-	-	-	-	-
WI	-	-	7	-	-	-	-	-	-	-	-	12	-
WV	-	-	9	-	-	-	-	-	-	-	-	-	-
WY	-	-	7	-	-	-	-	-	-	-	-	-	-
Total	153	131	144	176	216	170	95	139	120	100	115	120	125

collected ranged from 6 (2010 KY EtOH) to 41,251 (2017 GA *Ips* lure). Proportion of non-native beetles collected ranged from 0 to 1. Shannon index ranged from an average of 2.89 (± 0.05) (*Ips*) to 3.28 (± 0.06) (PE). Species richness ranged from an average of 80 (± 4.2) (*Ips*) to 118 (± 4.7) (PE).

Proportion of non-native beetles was significantly higher with EtOH lures (0.68 ± 0.33; $Z = 4.53$, $P < 0.0001$) and lowest with *Ips* lures (0.33 ± 0.35; $Z = -7.98$, $P < 0.0001$) with PE combination lures being moderately attractive (0.49 ± 0.32; $Z = -4.78$, $P < 0.0001$; Tables 2 and 3). Alaska had the lowest proportion of non-natives at 0 and Virginia had the highest proportion of non-native beetles at 0.86 (± 0.04) (Table 3). The lowest proportion of non-native scolytines was collected in 2007 (0.44 ± 0.02) and the highest proportion in 2013 (0.66 ± 0.02) (Table 2). Proportions of non-native beetles collected, Shannon index, and species richness were significantly impacted by interactions among lures, states, and years; however, these effects were highly variable (Table 2). The lure:year and state:lure interactions did not significantly affect scolytine captures in predictable ways with one exception: proportions of non-native scolytines captured was predictably greater in coastal states (e.g., VA, PA) compared to interior states (e.g., MO, SD) and also increased in years with higher trapping effort. Native beetles responded more positively to *Ips* lures (0.64 ± 0.002), followed by PE combination lures (0.51 ± 0.002) and finally EtOH lures (0.32 ± 0.002) (Table 4).

Community composition differed significantly at the tribe level among lure types for both native and non-native scolytines ($F_2 = 12.755$, $P < 0.0001$). Invasive communities differed significantly between *Ips* lures and both EtOH ($Z = 6.457$, $P < 0.0001$) and the PE combination ($Z = 3.965$, $P < 0.0001$), but communities captured with EtOH and PE combination lures did not significantly differ from each other ($Z = 1.462$, $P = 0.098$). Native communities differed significantly among all lure types ($F_2 = 13.474$, $P < 0.0001$) and among all pairwise combinations (EtOH:Ips $Z = 7.885$, $P < 0.0001$; EtOH:PE $Z = 4.664$, $P < 0.0001$; Ips:PE $Z = 5.574$, $P < 0.0001$). Native Hylurgini responded more to the PE combination lure while non-native Hylurgini responded more to EtOH lures. Hylesinini also differed in their responses to lure types; native Hylesinini responded more to PE combination lures while non-native Hylesinini, namely *Hylastinus obscurus* (Marsham), the clever root borer, responded to EtOH lures. Both native and non-native Scolytini responded similarly to all lure types.

Discussion

Our results are consistent with other studies that show the addition or subtraction of certain volatiles may increase or decrease captures of native and non-native bark and ambrosia beetles, both in the United States and in countries from which most North American non-native beetles originate (e.g., Iidzuka et al. 2016, Miller 2020). Because trees experiencing physiological stress produce EtOH (Kelsey et al. 2014), which also acts as a kairomone, a wide variety of beetles respond positively to it (Miller and Rabaglia 2009, Ranger et al. 2016). Understanding how EtOH affects tracking of non-native and native bark and ambrosia beetles can help increase the overall efficiency of the EDRR program by validating the use of this generalist plant volatile in early detection trapping.

Recent work has focused on using ecological models to predict future invasive bark and ambrosia beetles (e.g., Lantschner et al. 2017, Yu et al. 2019) and lures targeting these species are necessary in early detection and rapid response activities. While EtOH is attractive to a wide range of non-native scolytines, some invasive species such

Table 2. *F*-values and *P*-values of main effects, state:year, and state:lure interaction on the proportion of non-native, proportion of native beetles, Shannon index, and species richness

	Proportions *F*-value (*P*-value)	Shannon *F*-value (*P*-value)	Richness *F*-value (*P*-value)
Lure	150.9016 (<0.0001)	22.541 (<0.0001)	63.304 (<0.0001)
State	15.1301 (<0.0001)	6.456 (<0.0001)	17.698 (<0.0001)
Year	9.5282 (0.0023)	69.474 (<0.0001)	159.045 (<0.0001)
State:Year	4.2667 (<0.0001)	3.059 (<0.0001)	4.272 (<0.0001)
State:Lure	2.1315 (<0.0001)	1.005 (0.478)	0.641 (0.993)

Table 3. Number of non-native beetles collected per lure type for each state with percent of the total catch reported in parentheses

	Non-native (% total)			
State	EtOH	Ips	PE	Total
AK	0 (0)	0 (0)	0 (0)	0
AL	31 (16.1)	20 (10.4)	37 (19.2)	88
AR	141 (17.2)	117 (14.3)	109 (13.3)	367
AZ	5 (16.1)	4 (12.9)	1 (3.2)	10
CA	195 (11.8)	123 (7.4)	181 (10.9)	499
CO	26 (2.6)	17 (1.7)	21 (2.1)	64
CT	47 (14.8)	37 (11.6)	36 (11.3)	120
DC	33 (22.1)	24 (16.1)	29 (19.4)	86
DE	43 (14.9)	32 (11.1)	39 (13.5)	114
FL	494 (14.6)	175 (5.2)	469 (13.9)	1138
GA	814 (15.8)	634 (12.3)	759 (14.7)	2207
ID	38 (8.3)	33 (7.2)	28 (6.1)	99
IL	47 (16.1)	30 (10.3)	41 (14.0)	118
IN	161 (16.4)	75 (7.6)	131 (13.3)	367
KS	13 (18.3)	7 (9.9)	11 (15.5)	31
KY	95 (15.6)	61 (10.0)	70 (11.5)	226
LA	196 (14.2)	95 (6.9)	159 (11.5)	450
MA	125 (13.2)	98 (10.4)	106 (11.2)	329
MD	223 (19.1)	134 (11.5)	162 (13.9)	519
ME	36 (10.3)	20 (5.7)	32 (9.1)	88
MI	169 (11.0)	95 (6.2)	153 (10.0)	417
MN	10 (1.7)	9 (1.5)	17 (2.8)	36
MO	114 (15.7)	68 (9.3)	99 (13.7)	281
MS	151 (17.3)	65 (7.5)	126 (14.4)	342
MT	5 (1.8)	0 (0)	2 (0.7)	7
NC	296 (15.7)	218 (11.6)	268 (14.2)	782
ND	4 (2.7)	0 (0)	2 (1.4)	6
NE	14 (8.9)	2 (1.3)	13 (8.2)	29
NH	28 (11.7)	7 (2.9)	20 (8.3)	55
NJ	225 (20.6)	119 (10.9)	201 (18.4)	545
NM	7 (16.3)	3 (7.0)	4 (9.3)	14
NV	7 (4.6)	6 (3.9)	6 (3.9)	19
NY	607 (12.2)	409 (8.2)	577 (11.6)	1593
OH	159 (17.2)	98 (10.6)	156 (16.8)	413
OK	10 (17.9)	8 (14.2)	5 (8.9)	23
OR	68 (14.8)	37 (8.0)	47 (10.2)	152
PA	681 (15.9)	485 (11.3)	610 (14.3)	1776
RI	35 (14.6)	16 (6.7)	23 (9.6)	74
SC	200 (15.7)	139 (10.9)	165 (12.9)	504
SD	4 (2.0)	5 (2.5)	4 (2.0)	13
TN	31 (14.8)	16 (7.7)	24 (11.5)	71
TX	493 (15.9)	231 (7.4)	406 (13.1)	1130
UT	110 (20.8)	58 (11.0)	95 (18.0)	263
VA	226 (16.8)	162 (12.0)	164 (12.2)	552
VT	24 (7.5)	14 (4.4)	20 (6.3)	58
WA	75 (20.2)	16 (4.3)	41 (11.0)	132
WI	42 (10.7)	17 (4.3)	45 (11.5)	104
WV	56 (15.4)	37 (10.2)	50 (13.8)	143
WY	3 (7.7)	2 (5.1)	1 (2.6)	6

Table 4. Number of native beetles collected per lure type for each state with percent of the total catch reported in parentheses

	Native			
State	EtOH	Ips	PE	Total
AK	73 (24.5)	76 (25.5)	149 (50.0)	298
AL	32 (16.6)	21 (10.9)	52 (26.9)	105
AR	131 (16.0)	143 (17.5)	178 (21.7)	452
AZ	5 (16.1)	4 (12.9)	12 (38.7)	21
CA	324 (19.5)	378 (22.8)	458 (27.6)	1160
CO	286 (28.4)	328 (32.6)	329 (32.7)	943
CT	62 (19.5)	58 (18.2)	78 (24.5)	198
DC	19 (12.8)	19 (12.8)	25 (16.8)	63
DE	49 (17.0)	54 (18.8)	71 (24.7)	174
FL	721 (21.3)	569 (16.8)	950 (28.1)	2240
GA	912 (17.7)	820 (15.9)	1210 (23.5)	2942
ID	114 (24.9)	104 (22.8)	140 (30.6)	358
IL	53 (18.2)	47 (16.1)	74 (25.3)	174
IN	170 (17.3)	178 (18.1)	267 (27.2)	615
KS	12 (16.9)	9 (12.7)	19 (26.8)	40
KY	108 (17.7)	131 (21.5)	144 (23.6)	383
LA	300 (21.8)	260 (18.9)	367 (26.7)	927
MA	185 (19.6)	185 (19.6)	245 (26.0)	615
MD	177 (15.2)	195 (16.7)	275 (23.6)	647
ME	76 (21.7)	80 (22.9)	106 (30.3)	262
MI	344 (22.5)	335 (21.9)	436 (28.5)	1115
MN	130 (21.5)	179 (29.6)	260 (43.0)	569
MO	164 (22.6)	112 (15.4)	168 (23.1)	444
MS	155 (17.8)	159 (18.2)	216 (24.8)	530
MT	75 (26.9)	79 (28.3)	118 (42.3)	272
NC	330 (17.5)	277 (14.7)	498 (26.4)	1105
ND	39 (26.5)	40 (27.2)	62 (42.2)	141
NE	43 (27.2)	35 (22.2)	51 (32.3)	129
NH	50 (20.8)	45 (18.8)	90 (37.5)	185
NJ	186 (17.0)	98 (9.0)	265 (24.2)	549
NM	6 (14.0)	11 (25.6)	12 (27.9)	29
NV	44 (28.8)	49 (32.0)	41 (26.8)	134
NY	924 (18.5)	1015 (20.3)	1459 (29.2)	3398
OH	147 (15.9)	134 (14.5)	232 (25.1)	513
OK	6 (10.7)	12 (21.4)	15 (26.8)	33
OR	89 (19.3)	77 (16.7)	143 (31.0)	309
PA	752 (17.6)	686 (16.1)	1060 (24.8)	2498
RI	44 (18.4)	48 (20.1)	73 (30.5)	165
SC	220 (17.3)	220 (17.3)	331 (26.0)	771
SD	41 (20.8)	55 (27.9)	88 (44.7)	184
TN	48 (23.0)	29 (13.9)	61 (29.2)	138
TX	547 (17.6)	592 (19.0)	839 (27.0)	1978
UT	52 (9.8)	82 (15.5)	131 (24.8)	265
VA	236 (17.5)	268 (19.9)	290 (21.5)	794
VT	68 (21.3)	76 (23.8)	117 (36.7)	261
WA	68 (18.3)	48 (12.9)	124 (33.3)	240
WI	82 (20.9)	83 (21.1)	124 (31.6)	289
WV	77 (21.2)	56 (15.4)	87 (24.0)	220
WY	10 (25.6)	13 (33.3)	10 (25.6)	33

as the redbay ambrosia beetle and polyphagous shot hole borer do not respond to EtOH (Hanula et al. 2011, Dodge et al. 2017). In certain cases, exemplified by these two detrimental invasives, it is most beneficial to have species or genus-specific lures to target species of interest in detection efforts. Even these specific lures are not a 'silver bullet' because others, including many xyleborines, do not use pheromones and must be attracted to traps by host volatiles (Yang et al. 2018). Without effective lures, targeted monitoring of new introductions and spreading populations is unlikely to succeed.

While there was substantial variation among the lure:year and state:lure interactions, this likely reflects sites within states—and the states sampled—changing from year to year. Additionally, not all states established traps at the same type of site, as some were near lumber yards or ports of entry while others were in relatively isolated state parks and forests. Collectors who chose sites near areas with a high risk of non-native scolytines likely influenced the relative proportions of native and non-native bark and ambrosia beetles. Also, some collectors chose to keep sites the same from year to year while others changed site locations. Individual collectors were given guidance to select sites where non-native beetles were likely to be collected; however, specific site selections were ultimately left to the trap collectors who likely had varying criteria for selecting

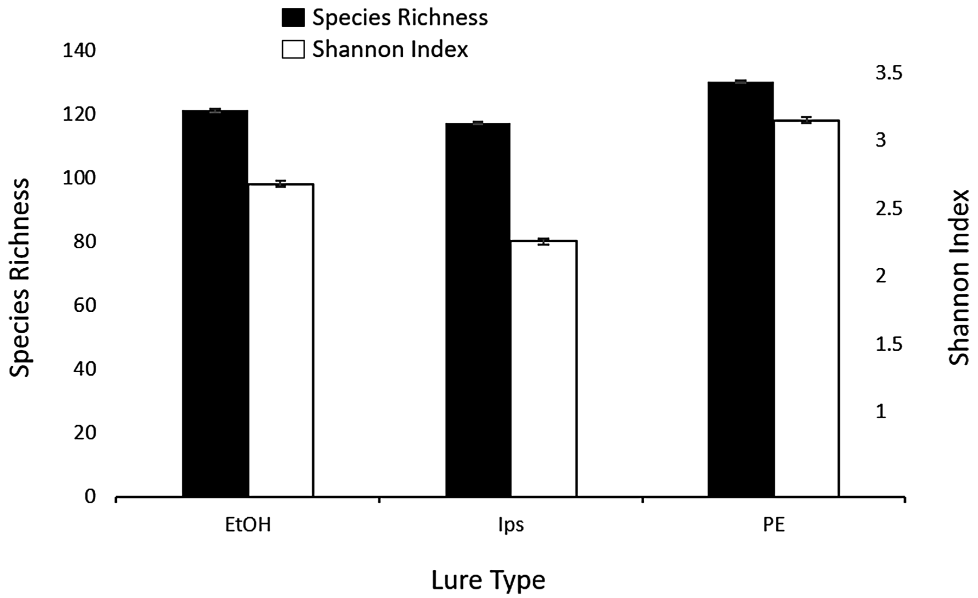

Fig. 1. Shannon indices and species richness per lure type with standard error bars reported.

sites. While we did check for significance among sites, the extreme variation due to these factors likely masked the effect of site on trap catches.

There are limitations to using EDRR data for analyses and generalized management recommendations. Some states are highly represented (e.g., CA, GA) due to their high likelihood of capturing non-native beetles while others are not as well represented (e.g., AK) because they currently have few, or no, recorded non-native scolytines (Rabaglia et al. 2019). Within years, individual states had anywhere from 5 to 13 or more trap sites per state and this number also fluctuated from year to year within, and among, states (Table 1). The EDRR program is meant as an operational working model rather than to be treated as a replicated experiment. But, important information is still captured through the data collected in this program and when appropriate analyses are used—and we consider the results in the greater context of the EDRR program—these data can help us advance our early detection and rapid response capabilities. It is important to note that, even with significant variation in trapping effort, scolytine populations, and lure combinations, we still found significance on a continental scale in terms of scolytine responses to different lures.

Early detection and subsequent rapid response has been termed the second line of defense against invasive species following exclusion tactics, such as port inspections. The success of EDRR programs depends on an understanding of the biology of the target species, potential pathways, and tools for early detection. For some invasive species, such as the emerald ash borer (*Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae)) or Asian longhorned beetle (*Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae)), little was known about their biology or means of detection before they were found in North America, and as a result, early detection has been a challenge. Conversely, the gypsy moth (*Lymantria dispar* L. (Lepidoptera: Erebidae)) has a long history of research and development of traps and lures for detection resulting in successful detection and eradication programs. Early detection of such a large and diverse group of bark and ambrosia beetles has presented challenges. For some genera, such as *Dendroctonus* and *Ips*, there is a solid understanding of their pheromone biology, and traps and lures are readily available for use in detection programs. Other taxa, such as xyleborine ambrosia beetles, may use kairomones, which are less species specific and present challenges for early detection. Large-scale EDRR programs that target several different taxa of bark and ambrosia beetles must select traps and lures for target species based on their availability and efficacy. Utilizing lures for genera-specific targets, such as *Ips*, with kairomone lures (i.e., EtOH or pinene) that attract a broader set of target taxa, including many ambrosia beetles, allows EDRR programs to detect a wide range of potential invasive species before they are well established. The development of additional targeted lures for important scolytines already present (e.g., *Euwallacea* shothole borers or the redbay ambrosia beetle), as well as lures for potential pests not yet present in the United States, such as *Polygraphus proximus* Blandford (Debkov et. al. 2019), *Acanthotomicus suncei* Cognato (Gao and Cognato 2018), and others (Gomez et al. 2020), should be a priority for research programs to support non-native monitoring programs such as EDRR.

Additionally, using a combination of lures allows the EDRR program to achieve multiple objectives in monitoring for non-native species while also tracking native populations of bark and ambrosia beetles. Our results also show that the EDRR program accomplishes other, unstated, objectives, such as tracking native populations in response to the establishment and spread of non-native xyleborines. Care should be used when interpreting large datasets like those provided through the EDRR program—this is, after all, not a large-scale replicated experiment—especially when using these data to examine interactions between insect communities, lures, and their environment. However, this program and the associated data are extremely useful for management and monitoring non-native scolytines in the United States, and have no doubt contributed greatly to our environmental biosecurity.

Acknowledgments

We thank Drs. Kamal Gandhi and Carmen Blubaugh for their thoughtful discussions and comments during various stages of this work. We also thank Dr. Dan Miller and two anonymous reviewers for their thorough reviews of the manuscript.

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