Journal of Insect Conservation (2025) 29:83
https://doi.org/10.1007/s10841-025-00718-z

ORIGINAL PAPER

The potential of semiochemical blends to monitor saproxylic beetle communities

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Received: 26 March 2025 / Accepted: 30 September 2025 / Published online: 22 October 2025

Abstract

The biodiversity of forests is threatened by intensive forestry. Due to a drastic decrease in the supply of dead wood, saproxylic insects constitute a great part of this threatened biodiversity. Their cryptic lifestyles make them hard to find, and we currently lack an effective method for surveying saproxylic insect communities. In this study, we aimed to assess if baited traps can be used to survey saproxylic beetle communities, with a focus on jewel beetles (Buprestidae), longhorn beetles (Cerambycidae), and weevils and bark beetles (Curculionidae). We also asked how sampling efficiency is affected by spatial and temporal factors, and if several blends outperform single-blend surveys. To answer these questions, we used traps baited with three different semiochemical blends aimed at sampling species associated with coniferous wood across three ports and six years. The baited traps managed to capture between 80 and 99% of the previously known saproxylic beetle communities associated with coniferous wood at each port across all years. The efficiency of the baited traps differed between sites, suggesting there are site-specific factors to consider. Sampling across consecutive seasons provided a more comprehensive overview of the total community than single-season surveys. Having multiple blends also increased the proportion of the community sampled, compared to any single blend. To our knowledge, this is the first study evaluating the possibility of using semiochemical blends to sample broad saproxylic beetle communities. We argue that semiochemical blends are an effective addition to conventional sampling schemes when surveying saproxylic beetle communities.

Keywords Saproxylic insects · Sampling · Community composition · Semiochemical blends · Pheromone trapping

Introduction

The biodiversity of forests in large parts of the world is threatened by intensive forestry (Betts et al. 2017). Due to a drastic decrease in the supply of dead wood, saproxylic (wood-dwelling) insects constitute a substantial part of this threatened biodiversity (Seibold et al. 2015; Lachat and Müller 2018; Seibold and Thorn 2018), and many species are red-listed (Stokland et al. 2012). In order to mitigate the problems caused by intensive forestry, many adjustments to forestry practices are made, from setting aside parts of land as nature reserves to retaining dead wood objects at logging sites (Gustafsson and Perhans 2010). However, quantifying the benefit of these mitigations is difficult due to the small size and high mobility of the target species (Martikainen and Kaila 2004; Saint-Germain et al. 2006; Parmain et al. 2013). Currently, there exists no easy or cost-effective method to survey saproxylic insect communities in forests. In this study, we present such a method based on the already widespread concept of traps baited with semiochemical blends.

Semiochemical blends are commonly used to monitor insect pests (Marx 1973; Witzgall et al. 2010; Rizvi et al. 2021), and have constituted an important development in species screening, especially for saproxylic insects (Saint-Germain et al. 2006; Zauli et al. 2014; Fan et al. 2019). Different pheromones and allelochemicals (e.g., kairomones such as plant volatiles) are mixed into a blend, increasing the width of attraction and enabling the sampling of a wide

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array of species (Hanks et al. 2012, 2018; Wong et al. 2012; Rice et al. 2020). As an example, ethanol and α-pinene are commonly used plant volatiles in blends aimed at attracting saproxylic insects (Schroeder and Lindelöw 1989; Miller 2006; Miller and Rabaglia 2009). Blends generally increase the number of species caught, compared to using single semiochemicals (Pajares et al. 2010, 2013; Miller et al. 2016). However, there are also instances where different components in blends have acted antagonistically (Hanks et al. 2018; Millar et al. 2021). In addition to being an effective method to sample species otherwise difficult to find, surveys using baited traps are easy to replicate across space and time and are usually cost-efficient compared to alternative methods (Roques et al. 2023).

Broad-spectrum blends have an important application in monitoring potential introductions of invasive species (Sweeney et al. 2014, 2016; Fan et al. 2019, Hoch et al. 2020; Roques et al. 2023). However, as the spectrum is broad, the probability of also sampling native species should be large, including species of nature conservation concern (Wickham et al. 2021). This means semiochemical blends could potentially be used to map distributions, or assess population sizes, of native saproxylic beetle communities. The concept of using semiochemical blends to sample threatened or difficult-to-sample species has been successfully implemented on several occasions (Musa et al. 2013; Kadej et al. 2015; Harvey et al. 2017; Wickham et al. 2021; Stigenberg et al. 2024). While this potential use of semiochemical blends has not gained much attention yet, baited traps have been shown to be much more effective for sampling certain groups of beetles than more conventional methods, such as direct search or flight-intercept traps (Larsson and Svensson 2009; Larsson 2016). Semiochemical blends might thus prove an effective way of dealing with the Wallacean shortfall, the lack of knowledge on species distributions at large scales (Kadej et al. 2015). Furthermore, insects can be caught alive in traps baited with semiochemicals (Larsson and Svensson 2009), and the release of high amounts of pheromone and allelochemical cues seems to have minimal impacts on long-term behavior and well-being of the insects (Oleander et al. 2015).

This study aimed to assess whether semiochemical blends could be used to sample native saproxylic beetle communities. To achieve this aim, we used six years of trap data collected by the Agricultural Board of Sweden in their monitoring of potential saproxylic beetle introductions through timber import at three ports in southern Sweden, using traps baited with mainly three different semiochemical blends. In short, we were asking four questions:

1. (1) What proportion of native saproxylic insect communities can be sampled by semiochemical blend?
2. (2) Does the effect of the blends depend on the location of sampling?
3. (3) Does one season of sampling provide a good representation of the total community?
4. (4) Do different blends capture different parts of the communities, i.e., should multiple blends be deployed to sample total community assemblages?

Methods

Study site

The dataset used in this study originates from the Swedish Board of Agriculture's survey of the potential introduction of invasive saproxylic beetles at ports in southern Sweden. The survey aims to detect non-native longhorn beetles (Cerambycidae), jewel beetles (Buprestidae), and bark beetles (Scolytinae) as they arrive with timber imports. From 2019 onwards, saproxylic weevils (Curculionidae) that are not bark beetles have also been included in the survey. From here on, any mention of Curculionidae includes bark beetles.

In this study, we used data from three ports surveyed continuously between 2017 and 2023 during May to August, using traps baited with three semiochemical blends. Due to an administrative change in the data repository during 2022, the data for this year was lost. Thus, the following analyses concern data from 2017-2021, and 2023.The three ports are positioned in Gothenburg (57.701627 N, 11.947861 E), Norrköping (58.624924 N, 16.226632 E), and Mönsterås (57.041757 N, 16.448664 E). The ports all lie within the boreonemoral vegetation zone (Hämet-Ahti and Ahti 1969) where forests mainly are dominated by coniferous trees (pine and spruce) with deciduous trees (mainly birch, aspen and southern deciduous trees) intermixed. Also stands dominated by southern deciduous trees (oak, ash, maple, lime etc., and beech in the southernmost parts) are frequent in the region.

Semiochemical blends

Three semiochemical blends were used in the study, hereafter referred to as *Ips*, *Pissodes*, and *Monochamus* based on the target genus of each blend. The blend *Ips* was obtained from Synergy Semiochemicals Corporation (Delta, BC, Canada) and contained two beetle pheromones and three plant volatiles: ipsenol (pheromone) ((50/−50), with a release rate of 0.4 mg per day at 20 °C; ipsdienol (pheromone), with a release rate 0.4 mg per day at 20 °C; 2-methyl-3-buten-2-ol (plant volatile), with a release rate of 11 mg per day at 20 °C; (−) α-pinene (plant volatile), with a release rate of 2 g per day; ethanol (plant volatile), with a release rate of 0.3 mg per day at 25 °C. The blend *Pissodes* was obtained from Synergy Semiochemicals Corporation (Delta, BC, Canada) and contained one beetle pheromone and one plant volatile: ((/−)-pityol (pheromone) with a release rate of 0.2 mg per day at 24 °C; (−)-α-pinene (plant volatile) with a release rate of 150 mg per day at 24 °C. The blend *Monochamus* was obtained from SEDQ (Barcelona, Spain) and contained two beetle pheromones and two plant volatiles: ipsenol (pheromone); 2-undecyloxy-1-ethanol (pheromone); (−)-α-pinene (plant volatile); 2-methyl-3-buten-1-ol (plant volatile). Release rates for this blend are unknown. All mentioned blends are designed to attract saproxylic beetles associated with coniferous trees. See https://semiochemical.com/product-listing/ and https://sedq.es/en/categoria/forestry-and-gardening/ for more information regarding the blends.

Trap design and sampling scheme

We used crosstraps from Econex (CROSSTRAP® Model UIPFETA227) to sample the saproxylic beetles. At the bottom of the trapping funnel was a CROSSTRAP® wet collection cup. The vanes, funnel, and collection cup were treated with a slippery film to increase capture rates by preventing the insects from escaping. The collection cups were filled with ethylene glycol to preserve the trapped insects. The traps were hung in branches at a maximum height of two meters. The blends hung directly on the traps and were exchanged once per sampling season (Appendix 1).

The length of the sampling season and the exact dates for emptying the traps differed between years and ports, with one to two emptying events per month. A full list of start and end dates, bait exchange dates, and trap emptying dates per year and port can be found in Appendix 1. To increase consistency, we use data on trap catches from the first sampling event in May to the last sampling event of August each year, as these months were surveyed across all years. The number of traps also differed between the blends within each port and year (Table 1). The exact location of the traps around the ports has also differed somewhat over the years. However, the differences between trap locations are so small that we regarded the trapping sites as spatially static around each port.

Table 1 The number of baited traps used at each port for each blend, across 2017–2023

Port	Blend	Year	Trap count
Gothenburg	Ips	2017	2
Gothenburg	Ips	2018	3
Gothenburg	Ips	2019–2023	4
Gothenburg	Monochamus	2017–2018	1
Gothenburg	Monochamus	2019–2023	2
Gothenburg	Pissodes	2017–2018	1
Gothenburg	Pissodes	2019–2023	2
Mönsterås	Ips	2017	2
Mönsterås	Ips	2018–2023	3
Mönsterås	Monochamus	2017	1
Mönsterås	Monochamus	2018–2023	2
Mönsterås	Pissodes	2017	1
Mönsterås	Pissodes	2018–2023	2
Norrköping	Ips	2017	2
Norrköping	Ips	2018–2023	3
Norrköping	Monochamus	2017	1
Norrköping	Monochamus	2018–2023	2
Norrköping	Pissodes	2017	1
Norrköping	Pissodes	2018–2023	2

Identification of specimens

The sampled beetles were sent to SLU Uppsala, where they were identified to species level using Spessivtseff (1922), Landin (1971), Bílý (1982), Ehnström and Holmer (2007), Pfeffer (1995) and Rheinheimer & Hassler (2010). Species were designated current valid names as given by Catalogue of Palearctic Coleoptera (Löbl and Smetana 2010, 2011, 2013, 2016). Red-listed species were defined based on the national Swedish Red List (SLU, ArtDatabanken 2020). Due to changes in identification personnel in 2023, *Crypturgus sucribrosus* and *Crypturgus cinereus* were not separated during identification this year. These unidentified individuals have been excluded from analysis. Host tree preferences were assigned according to Ehnström and Axelsson (2002). The raw data can be found in Supplementary Materials.

Comparison of results to publicly available data

To be able to compare trap catches with the known diversity of saproxylic beetles around each port, we used publicly available species records from the Swedish Species Observation System (Artportalen) (SLU ArtDatabanken 2024). It was deemed that these records would give a fair picture of the local fauna, albeit with some limitations and uncertainties (Aceves-Bueno et al. 2017; Johnston et al. 2023). To acquire enough species records for comparisons with trap catches, we recorded all reports of species belonging to Buprestidae, Cerambycidae, and Curculionidae between the years 2017–2023 during May to August within 10 × 10 km square polygons around each harbor. These records included random observations, active searches, and trapping through flight-intercept traps, either as part of surveys or private inventories. Since saproxylic Curculionidae were not recorded in the trap catches before 2019, public reports of these species were only used for the years 2019–2023. While we lack data on trap catches for 2022, it was deemed that data from the previous and following years should hold similar communities. Data from this year could thus be extracted from the Swedish Species Observation System to increase the number of public reports without impairing the comparison with trap catches.

Statistical analysis

Community comparisons

To compare saproxylic beetle catches between blends and ports, we created a matrix defining the number of individuals sampled of each species per unique port-blend-year combination, hereafter referred to as a community. To standardize the communities, we divided the count of individuals for each species found in each community by the total number of individuals across all species found in that community (Jackson 1993). Each community row thus had its species occurrences given as a fraction between 0 and 1, with the sum of all species in that community adding to 1.

To show how species composition differed across blends, years, and ports, we used Non-Metric Multidimensional Scaling (NMDS) through the function metaMDS in the R package *vegan* (Oksanen et al. 2017) in Rstudio (Posit Team 2023) using R version 4.3.0 (R core team 2023) with Bray-Curtis distance, two dimensions, and 1000 random starts. Trapping effort differed between blends but not between ports. This meant temporal community differences within sites and blends could be used to assess the effect of trapping effort on the stability of sampled communities, and trapping effort was subsequently not accounted for in the NMDS model. To ease model fit, all beetle records were pooled per year. To avoid finding a local optimum, the NMDS was rerun once using the previous best score as starting point (Roberts 2020).

To statistically compare community compositions between ports and blends, we performed PERMANOVA analyses using the function *adonis2* from the R package *vegan*, with Bray-Curtis distance and 999 permutations. The model used standardized community compositions as a function of blend, port, and the interaction between these factors, with year included as a random factor. An assessment of homogeneity of variance was conducted for all factors, and none showed significant indications of heterogeneity. We found a significant interaction between blend and port and conducted subsequent pairwise comparisons of both factors using the function *pairwiseadonis* from the R package *pairwiseAdonis* (Martinez Arbizu 2020). To minimize the risk of Type II errors, no p-value corrections were applied. To account for the potential increase in Type I errors, we focus on patterns of significance across comparisons rather than interpreting individual p-values in isolation.

Species-specific comparisons

To compare attraction rates between the blends, we conducted species-specific tests of bait attraction. We chose the 46 species that had been recorded on more than 10 separate occasions and had a minimum of 20 individuals sampled. Exceptions were made if a species was present at only one port or for only a few years, as the number of occasions where the species could have been found was then lower than the total count of occasions across all ports and years. These 46 species were fitted to individual generalized linear mixed models (GLMM: s) via the function *glmmTMB* from the R package *glmmTMB* (Brooks et al. 2017). To ease model fit and remove excess zeros, all years or ports where a species was never recorded were removed from further analysis. The models used the number of individuals sampled as a function of blend and port. To account for yearly differences, a grouping effect of year was added. Due to differences in trapping effort between blends and years, we added an offset term for the number of traps used. The models were fitted with a Poisson distribution and log-link. The possible ecological constraints on Poisson models were accounted for by adding a grouping effect of sample ID to avoid overdispersion, and pooling samples to remove zero-inflation. There was no indication that negative binomial distributions would improve the models. To simplify the models and ease interpretation of outputs, Poisson distributions were therefore chosen. To evaluate the effect of port and blend on the sampled number of individuals for each species, individual type III Wald chisquare tests for analysis of deviance were conducted using the function *Anova* in the R package *car* (Fox & Weisberg 2019). For species with a significant difference in sampled individuals between blends, pairwise comparisons between blends using estimated marginal means were conducted using the function *emmeans* in the R package *emmeans* (Lenth 2024). In instances where one blend had no findings, the other blend was compared against a null hypothesis of no difference from zero by applying a contrast function to the *emmeans* object. If they did differ from zero, they were deemed significantly more attractive than the blend with zero findings. As in the community comparisons, we were not interested in the differences between blends within each species per se, but rather in the overall effectiveness of each blend across species. Since Type I errors would not affect the overall trends, no p-value corrections were applied. Fully reproducible code for all statistical analyses is available in the Supplementary Materials.

Table 2 PERMANOVA evaluating the effect of blend and port, and the interaction between them, on the community composition caught in the traps

Term	df	Sums of Squares	R^2	F-value	*p*-value
Blend	2	2.05	0.136	5.82	**<0.001**
Port	2	3.85	0.255	10.9	**<0.001**
Blend*Port	4	1.26	0.084	1.79	**0.009**

Year is treated as a random effect. For each term the sums of squares, R^2, F-values and p-values are given. Bold p-values denote statistical significance

Table 3 Pairwise comparisons of the community composition caught with each blend for each port

Port	Blend comparison	Sums of Squares	R^2	F-value	*p*-value
Gothenburg					
	Ips-Pissodes	0.912	0.341	5.19	**0.004**
	Ips-Monochamus	0.926	0.328	4.88	**0.006**
	Pissodes-Monochamus	0.542	0.196	2.43	**0.027**
Mönsterås					
	Ips-Pissodes	0.416	0.228	2.95	0.055
	Ips-Monochamus	0.825	0.353	5.46	**0.004**
	Pissodes-Monochamus	0.447	0.197	2.45	**0.034**
Norrköping					
	Ips-Pissodes	0.138	0.0743	0.802	0.59
	Ips-Monochamus	0.507	0.260	3.52	**0.033**
	Pissodes-Monochamus	0.258	0.110	1.24	0.25

All combinations are made on 1 degree of freedom. For each term the sums of squares, R^2, F-values and p-values are given. Bold p-values denote statistical significance

Results

In total, 183,965 individuals belonging to 143 species were included in the study, all previously known from Sweden. The most abundant species was *Ips typographus*, comprising 137,618 individuals or 75% of the total count. Eleven other species were found in between 1000 and 12,000 individuals: *Hylastes attenuatus*, *Crypturgus subcribrosus*, *Hylastes cunicularius*, *Crypturgus cinereus*, *Polygraphus poligraphus*, *Rhagium inquisitor*, *Spondylis buprestoides*, *Pityophthorus pubescens*, *Hylobius abietis*, *Acanthocinus griseus*, and *Tomicus piniperda* (Appendix 2). 33 species were caught on only one occasion, including 29 singletons.

Community comparisons

Overall, traps baited with the different blends caught different communities, but the effect of the blends depended on the port ($p<0.001$; Table 2). Trap catches in traps baited with the blends Ips and Monochamus differed between each other across all ports, trap catches from traps baited with Ips and Pissodes differed only at Gothenburg, and trap catches from traps baited with Pissodes and Monochamus differed at Gothenburg and Mönsterås (Fig. 1; Table 3). Trap catches did not differ within any blend between Mönsterås and Norrköping (Table 4). The trap catches in Gothenburg did, however, differ from trap catches at both other ports across all blends.

Comparisons between known and sampled communities

In total, 785 unique reports of 105 species belonging to the target groups of this study were recorded within 100 km^2 of the three ports between 2017 and 2023 in the Swedish

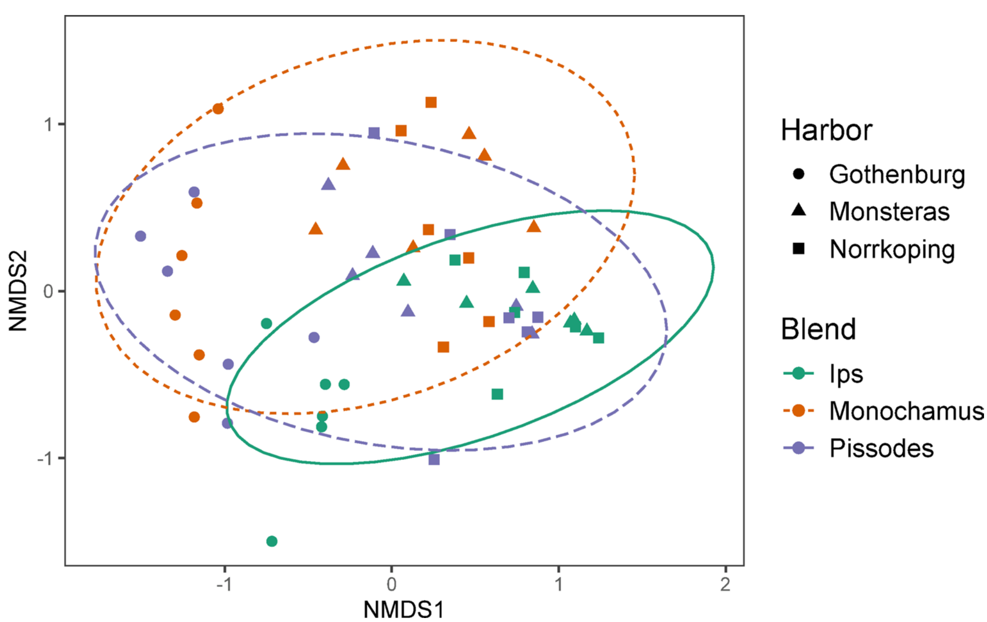

Fig. 1 NMDS plot of the sampled communities of saproxylic jewel beetles (Buprestidae), long-horn beetles (Cerambycidae), and weevils and bark beetles (Curculionidae) caught in baited traps at each of three ports (Gothenburg, Mönsterås and Norrköping) across the three blends (Ips, Monochamus and Pissodes) based on Bray-Curtis dissimilarity of species abundances. Each datapoint represents one year for each port-blend combination. The ellipses show 90% confidence intervals of overall community composition for each blend. Stress = 0.18

Table 4 Pairwise comparisons of the community composition between the ports for each blend

Blend	Port comparison	Sums of Squares	R^2	F-value	*p*-value
Ips					
	Gothenburg-Mönsterås	1.46	0.537	11.6	**0.005**
	Gothenburg-Norrköping	1.51	0.546	12.0	**0.002**
	Mönsterås-Norrköping	0.0614	0.0536	0.566	0.74
Pissodes					
	Gothenburg-Mönsterås	0.744	0.281	3.90	**0.003**
	Gothenburg-Norrköping	1.14	0.339	5.12	**0.002**
	Mönsterås-Norrköping	0.277	0.119	1.36	0.22
Monochamus					
	Gothenburg-Mönsterås	1.16	0.351	5.41	**0.003**
	Gothenburg-Norrköping	1.14	0.353	5.46	**0.003**
	Mönsterås-Norrköping	0.174	0.0854	0.934	0.48

All combinations are made on 1 degree of freedom. For each term the sums of squares, R^2, F-values and p-values are given. Bold p-values denote statistical significance

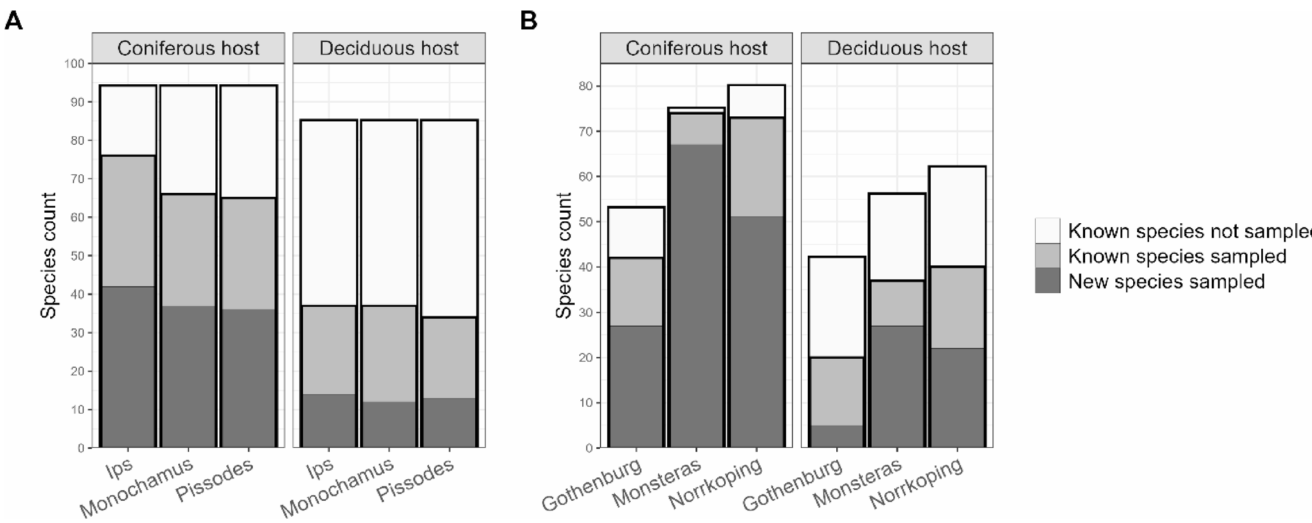

Fig. 2 The total number of saproxylic jewel beetles (Buprestidae), longhorn beetles (Cerambycidae), and weevils and bark beetles (Curculionidae) recorded per port and blend. The species are further classified as living in coniferous or deciduous wood. Species associated with both deciduous and coniferous trees were assigned as coniferous. **A**. The number of species caught per blend across all ports, divided into three groups: (1) Known species not sampled (Species not sampled by the traps that have previously been recorded in the Swedish Species Observation System or in baited traps using any of the other two blends). (2) Known species sampled (species sampled by the traps that have previously been recorded in the Swedish Species Observation System around the ports). (3) New species sampled (species sampled by the traps not previously reported in the Swedish Species Observation System around the ports). **B.** The number of species caught per port across all blends. The division of data is the same as in A, except species counts are instead summed across blends for each port, and *known species sampled* refers to species recorded only in the Swedish Species Observation System around that specific port

Species Observation System. Of these 105 species, 43 were associated with coniferous wood, and 62 with deciduous wood. Since the blends are designed to attract species associated with coniferous wood, species that develop in both deciduous and coniferous wood are assigned as coniferous. 72 of the species reported in the Swedish Species Observation System were also found in the baited traps. The baited traps further added 71 species not reported in the Swedish Species Observation System. The blend Ips sampled the highest proportion of the total community (all recorded species across the Swedish Species Observation System and the baited traps) across all ports and years (63.1%), and Pissodes the lowest proportion (55.3%). Monochamus sampled just above 2% more than Pissodes (57.5%) (Fig. 2A). All blends performed better when considering only species associated with coniferous wood, with Ips sampling 80.9% of those species, Monochamus 70.2%, and Pissodes 69.1%. When considering only species associated with deciduous wood, the proportions of total community sampled were 40.0–43.5% depending on blend.

The 100km^2 area around the port of Gothenburg had 464 reports of 63 species in the Swedish Species Observation System, Mönsterås 119 reports of 37 species, and Norrköping 202 reports of 69 species. The baited traps sampled

47.6%, 45.9%, and 57.9% of these species, respectively. Furthermore, the blends revealed an additional 32 to 94 new species per port (Fig. 2B). The species caught in the baited traps corresponded to 65.2% (Gothenburg), 84.7% (Mönsterås), and 79.6% (Norrköping) of the now known communities within 100 km^2 of each port. When considering only species associated with coniferous wood, the baited traps sampled 79.2% of the known species pool in Gothenburg, 98.7% in Mönsterås, and 91.3% in Norrköping.

The baited traps caught a mean of 56–66% of all sampled species associated with coniferous wood per year, depending on port (Fig. 3; Table 5). Sampling for two consecutive years increased the mean proportion sampled to between 74 and 79%, and sampling for three consecutive years increased the mean proportion sampled to between 85 and 87%. For species associated with deciduous wood the initial numbers were lower (26–37%). However, the increase in proportion sampled when sampling for two or three consecutive years was slightly higher (two years 49–57%; three years 66–74%). A full list of proportions for each port and blend combination can be found in Appendix 3.

Individual species analysis.

Of the 46 species caught frequently enough for individual analysis of blend preference, 27 were caught in similar numbers across all blends. Thirteen of the remaining species had a significantly stronger attraction to a single blend.

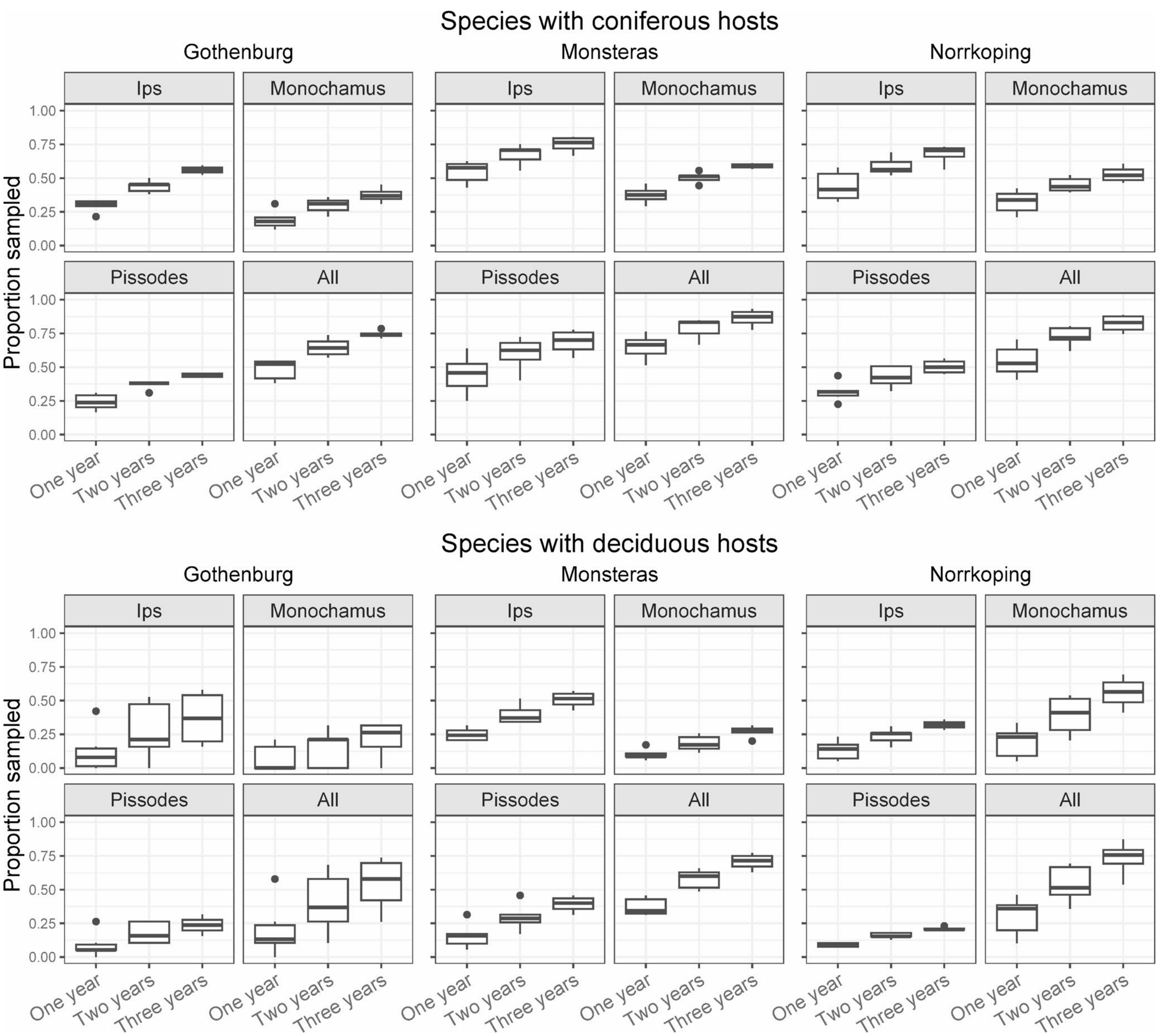

Fig. 3 The proportion of all species sampled by the baited traps caught during one, two, or three consecutive years, divided by port, blend, and tree host preferences. "All" refers to the sum of all three blends (Ips, Monochamus, and Pissodes). Boxplots show the sampled proportion for one year of sampling, for two consecutive years of sampling (i.e., 2017–2018, 2018–2019, 2019–2020…), and for three consecutive years of sampling (i.e., 2017–2019, 2018–2020…)

Table 5 Mean proportions of all sampled species caught during one year of sampling, two consecutive years of sampling, and three consecutive years of sampling, along with standard error, for each Port and host tree

Host tree	Port	Consecutive sampling	Mean	SE	Increase from one year
Coniferous	Gothenburg	One year	0.56	0.03	0
		Two years	0.74	0.03	+0.18
		Three years	0.85	0.01	+0.29
	Mönsterås	One year	0.66	0.04	0
		Two years	0.79	0.04	+0.13
		Three years	0.87	0.03	+0.21
	Norrköping	One year	0.57	0.05	0
		Two years	0.75	0.03	+0.18
		Three years	0.85	0.03	+0.28
Deciduous	Gothenburg	One year	0.26	0.09	0
		Two years	0.49	0.10	+0.23
		Three years	0.66	0.11	+0.40
	Mönsterås	One year	0.37	0.02	0
		Two years	0.57	0.03	+0.20
		Three years	0.70	0.03	+0.33
	Norrköping	One year	0.31	0.05	0
		Two years	0.55	0.06	+0.24
		Three years	0.74	0.06	+0.43

For the last six species, one blend was significantly better at attracting the species compared to one other blend, or one blend was significantly worse at attracting the species compared to both other blends (Table 6). Ips was the most attractive blend in most cases, and the least attractive blend in the fewest cases. A more detailed comparison with predicted counts of individuals per species and blend is found in Appendix 4, and a full list of pairwise analyses is found in Appendix 5. *Pinus sylvestris* was the most common host tree of the 46 species analyzed, with 18 species living solely on *P. sylvestris*, and another fourteen species found on both *P. sylvestris* and *Picea abies* (Table 7). Another eight species had *P. abies* as their only host tree. The remaining six species were associated with deciduous wood.

Red-listed species

In total, 2329 individuals from 21 red-listed species and four species denoted as NE (Not Evaluated) were found in the baited traps. Twelve of the red-listed species were associated with coniferous wood, and nine with deciduous wood. Ips was the most attractive blend in all regards, with 76.5% of all red-listed individuals and 64% of all red-listed species found within traps using this blend (Fig. 4). Traps baited with Monochamus sampled 14.3% of all individuals and 60% of all species, and traps baited with Pissodes sampled 9.2% of all individuals and 56% of all species. 56% of the red-listed species sampled were unique to one blend.

Discussion

This study aimed to investigate whether semiochemical blends can be used to sample native saproxylic beetle communities across space and time, and if different blends sample different portions of these communities. We found that traps baited with the blends caught most of the previously known species associated with coniferous wood at each port, and also sampled many species associated with deciduous wood. Furthermore, the baited traps sampled many previously unrecorded species around each port. The high coverage of known species sampled, the many new species revealed per port, the high diversity sampled across all ports, and the difference in sampled communities between years all suggest that semiochemical blends are indeed a powerful and efficient method to sample native saproxylic beetle communities.

Using baited traps to survey saproxylic beetle communities

The blends combined sampled between ~65–85% of the total known species pool at each port across all years. Furthermore, between 32 and 94 new species records were added per port, even though the search area around the ports for public records was set at 10 × 10 km and included all saproxylic species observed during the months May-August between 2017 and 2023, independent of host tree preferences. The blends are unlikely to attract at such a large spatial scale (Bacca et al. 2006; Schlyter 2009; Adams et al. 2017), and are not designed to attract species associated with deciduous wood. When considering only species associated with coniferous wood, the baited traps sampled between 80 and 99% of all recorded species from the Swedish Species Observation System and trap catches per port. It is thus clear that baited traps have a remarkable effectiveness in sampling saproxylic beetle communities.

The sampled communities differed between the port on the west coast (Gothenburg) and the ports on the east coast (Norrköping and Mönsterås) for all blends in terms of abundances and species composition, while the two east coast locations had similar communities. Such community differences between the coasts have been recorded in previous studies of the saproxylic beetle fauna in southern Sweden (Franc et al. 2007; Jansson et al. 2009; Jonsell et al. 2019). This indicates that each blend can sample a larger community than it did at each site, further adding to proof of their efficiency.

Overall, the baited traps caught a lower proportion of the known community at Gothenburg than at the east coast ports, both per year and across all years. These patterns were similar irrespective of whether the species was associated

Table 6 The attraction to blends for the 46 species that were analyzed individually. Species are ordered systematically after Löbl and Smetana (2010, 2011, 2013, 2016)

Species	Host species	χ^2	*p*-value	Most attractive blend
Phaenops cyanea	*P. sylvestris*	2.46	0.29	No significant difference
Spondylis buprestoides	*P. sylvestris*	19.0	**< 0.001**	Ips
Tetropium castaneum	*P. abies*	2.64	0.27	No significant difference
Tetropium fuscum	*P. abies*	2.78	0.25	No significant difference
Rhagium inquisitor	Conifers	15.6	**< 0.001**	Ips, Monochamus
Rhagium mordax	Deciduous	2.82	0.25	No significant difference
Stictoleptura rubra	*P. sylvestris*	0.0520	0.97	No significant difference
Monochamus galloprovincialis	*P. sylvestris*	6.03	**0.049**	Monochamus
Pogonocherus fasciculatus	Conifers	0.516	0.47	No significant difference
Leiopus linnei	Deciduous	0.379	0.83	No significant difference
Acanthocinus aedilis	Conifers	15.5	**< 0.001**	Ips
Acanthocinus griseus	Conifers	9.49	**< 0.001**	Ips
Platystomos albinus	Deciduous	0.401	0.53	No significant difference
Rhyncolus sculpturatus	Conifers	1.12	0.29	No significant difference
Hylobius abietis	Conifers	6.71	**0.035**	Monochamus
Hylobius pinastri	Conifers	3.94	0.139	No significant difference
Pissodes pini	*P. sylvestris*	1.56	0.46	No significant difference
Pissodes piniphilus	Conifers	2.75	0.25	No significant difference
Hylurgops palliatus	Conifers	14.9	**< 0.001**	Ips
Hylastes attenuatus	*P. sylvestris*	8.39	**0.015**	Ips, Monochamus
Hylastes brunneus	*P. sylvestris*	4.88	0.09	No significant difference
Hylastes cunicularius	*P. abies*	1.03	0.60	No significant difference
Hylastes opacus	*P. sylvestris*	6.21	**0.045**	Ips
Hylesinus varius	Deciduous	0.274	0.87	No significant difference
Tomicus minor	*P. sylvestris*	2.96	0.23	No significant difference
Tomicus piniperda	*P. sylvestris*	55.3	**< 0.001**	Pissodes
Phloeotribus spinulosus	*P. abies*	9.10	**0.011**	Monochamus
Polygraphus poligraphus	Conifers	0.609	0.74	No significant difference
Pityogenes chalcographus	Conifers	0.548	0.76	No significant difference
Pityogenes quadridens	*P. sylvestris*	0.485	0.78	No significant difference
Pityogenes bidentatus	*P. sylvestris*	0.905	0.64	No significant difference
Orthotomicus laricis	Conifers	9.42	**0.009**	Ips
Ips acuminatus	Conifers	62.9	**< 0.001**	Ips
Ips typographus	*P. abies*	36.3	**< 0.001**	Ips (Pissodes)
Dryocoetes autographus	Conifers	3.31	0.19	No significant difference
Crypturgus subcribrosus	Conifers	10.1	**0.006**	Ips
Crypturgus cinereus	Conifers	35.3	**< 0.001**	Ips
Crypturgus pusillus	Conifers	7.02	**0.03**	Ips
Trypodendron lineatum	Conifers	1.74	0.42	No significant difference
Xyloberus monographus	Deciduous	0.346	0.65	No significant difference
Xyloberinus saxesenii	Deciduous.	2.36	0.56	No significant difference
Cryphalus asperatus	*P. abies*	0.563	0.76	No significant difference
Pityophthorus micrographus	*P. abies*	17.7	**< 0.001**	Pissodes
Pityophthorus lichtensteinii	*P. sylvestris*	2.85	0.24	No significant difference
Pityophthorus pubescens	*P. sylvestris*	22.9	**< 0.001**	Pissodes
Pityophthorus glabratus	*P. sylvestris*	3.73	0.15	No significant difference

Tree hosts are according to Ehnström and Axelsson (2002). "Conifers" refers to several coniferous hosts, most often *P. abies* and *P. sylvestris*, and "Deciduous" to species with either one or several deciduous hosts. Chi-square and p-values from the individual GLMM outputs are given for the effect of blend on the number of individuals caught. Significant p-values in bold. For each species, the most attractive blend(s) are given. In cases where two blends had equal attraction and both were significantly more attractive than the third, both are seen as most attractive. If a second blend had an intermediate attraction (i.e., lower attraction than the most attractive blend yet still significantly higher attraction than the least attractive blend), the blend with intermediate attraction is given in brackets. For a full comparison with predicted count of individuals per species and blend, see appendix 4. For more details on the GLMM output, see appendix 5

with coniferous or deciduous wood. Any surveys of saproxylic beetles using semiochemical blends should be aware of such site-specific effects that may affect the efficiency of the baited traps in sampling saproxylic beetle communities.

Most species inventories are conducted during only one season. In this study, a mean of 56–66% of all species associated with coniferous wood were sampled each year, depending on port. For species associated with deciduous wood, the mean proportion was 26–37% for one year of sampling. Species populations usually fluctuate greatly between years (Bouget et al. 2013; Seibold and Thorn 2018), with weather and the amount of available dead wood being important drivers (Jacobs et al. 2007; Seibold and Thorn 2018). In accordance with this, a study on temporal

Table 7 The number of species with a significantly stronger attraction to one blend compared to the other blends, or with no difference in attraction between the blends, per host tree category (Table 6)

Host species	Ips	Pissodes	Monochamus	No difference in attraction
Deciduous	0	0	0	6
Conifers	7	0	2	6
Picea abies	1	1	1	5
Pinus sylvestris	5	2	2	10
Sum	**12**	**3**	**4**	**27**

Note that *R. inquisitor* and *H. attenuatus* had a significantly stronger attraction to both Ips and monochamus compared to Pissodes and are counted for both blends. *Conifers* refers to species associated with both *P. abies* and *P. sylverstris*.

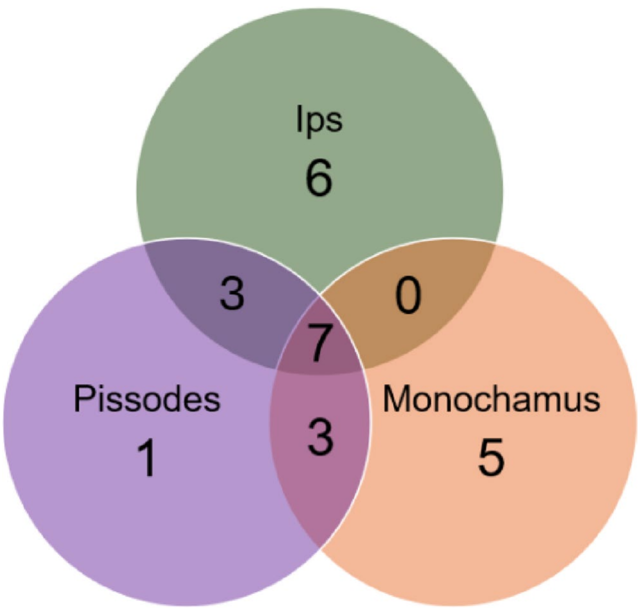

Fig. 4 Number of red-listed species (and species denoted NE) found with each blend across all ports and years. Overlapping areas depict the number of shared species between the overlapping blends. Traps baited with Ips caught 1782 individuals of red-listed species, Monochamus 332 individuals, and Pissodes 215 individuals

variation of saproxylic insect communities by Martikainen and Kaila (2004) found large inter-seasonal variation in trap catches but no long-term trends in community turnover. That roughly a third of all known species caught by the baited traps were not sampled each year is thus not necessarily a sign of low attraction efficiency, but rather reflects the inter-seasonal variability in community composition. Sampling over two consecutive seasons increased the mean proportion of the total community sampled to between 74 and 79% for coniferous species, and 49–57% for deciduous species. For three seasons, the mean proportion further increased to between 85 and 87% for coniferous species, and 66–74% for deciduous species. The increase in proportions of the total community sampled for each consecutive year of sampling match those reported in a similar study on the effect of sampling for several consecutive years by Parmain et al. (2013). Due to the variation in community composition between years within sites and the steep increase in proportion sampled for each consecutive season, we highly recommend that inventories of saproxylic insects relying on baited traps are conducted over the span of at least two consecutive seasons (Martikainen and Kaila 2004; Parmain et al. 2013; Ramírez-Hernández et al. 2014; Seibold et al. 2023). If single-season sampling is the only feasible alternative, the limitations of such a sampling scheme should be considered.

It is also possible that increasing the number of traps could increase the proportion of the total community sampled. However, the blend Ips had twice the number of traps at each site during most years compared to the other blends, yet did not sample a much higher proportion of the community. Thus, increasing the number of traps does not seem to increase community size.

During the six years of sampling, we found 21 red-listed species in the traps. Due to the challenges in finding rare saproxylic species, we risk overestimating the effectiveness of the baited traps if we compared our findings to previous records from around the harbors (Martikainen and Kouki 2003; Martikainen and Kaila 2004; Hedgren & Weslien 2008). It is thus impossible to know what proportion of the total community of red-listed saproxylic beetles the baited traps sampled. However, semiochemical blends are becoming increasingly popular for sampling saproxylic beetles of conservation concern and it is accepted as the best method available for sampling cryptic saproxylic beetles (Musa et al. 2013; Kadej et al. 2015, Larsson 2016; Harvey et al. 2017; Stigenberg et al. 2024). Of the 21 species sampled in this study, 9 were associated with deciduous wood and the rest with coniferous wood. Classic methods aimed at sampling threatened saproxylic beetles are based on tree-host specific trapping techniques, such as pitfall traps in tree hollows or rearing out beetles from logs or branches (Jonsell and Hansson 2007; Chiari et al. 2013). If the aim is to sample the total community of red-listed species present, these techniques would entail high costs and much time. To conclude, we do not know if the baited traps in this study failed to attract some red-listed beetles present around the harbors. However, we still believe that baited traps offer a cost-effective method for sampling red-listed saproxylic beetles. Their usefulness in attracting single species is well documented and semiochemical blends have the ability to attract beetles associated with a broad range of host tree species.

Most species recorded in the Swedish Species Observation System around each port, yet not sampled by the baited traps, were associated with deciduous wood. This is to be expected, as the blends used in this study are designed to attract species associated with coniferous wood. However, the traps also sampled substantial proportions of the deciduous species pools at each port. Notably, six of the 46 most common species sampled were associated with deciduous trees and showed similar catch rates across all blends. General decomposition odors in the semiochemical blends could be a cause of attraction for deciduous species. However, the Pissodes blend caught around as many species associated with deciduous wood as Ips and Monochamus, despite containing only (/−)-pityol and (−)-α-pinene, even though recorded repellent effects of non-host volatiles in some longhorn beetles (Allison et al. 2004) would suggest otherwise. It could be the ethylene glycol used to preserve the insects inside the traps that attracted the deciduous beetles, or the traps themselves. Further studies are required to understand why species associated with deciduous wood are attracted to traps with baits designed to attract species associated with coniferous wood.

A limitation in this study is the lack of comparison to other conventional sampling methods. These methods can be sorted into three groups – rearing techniques (Jonsell and Hansson 2007), active search (Montgomery et al. 2021), and baited or unbaited flight-intercept traps (Bouget et al. 2009; Rodríguez-González et al. 2017; Fan et al. 2019). It is widely accepted that of these methods, flight-intercept traps are the most cost-effective for surveys of broader saproxylic beetle communities (Okland 1996; Wikars et al. 2005, Bouget et al. 2008). Thus, while we have no direct comparison of sampling efficiency between our baited traps and other methods or trap types, we find flight-intercept traps to be the only feasible option for large-scale surveys of saproxylic communities. Furthermore, Bouget et al. (2008) found that crosstraps were the most cost and time efficient flight-intercept traps when sampling saproxylic beetle communities, although window traps sampled a larger proportion of the community. Based on this, we believe that we have used the most efficient sampling method when investigating the possibility of sampling saproxylic beetle communities using semiochemical blends.

Another major methodological limitation of the study is the lack of unbaited control traps. Due to the lack of such control treatment, our data does not allow us to tease apart the attractive effect of the blends from that of the traps themselves. Factors such as trap color (Cavaletto et al. 2020, 2021; Marchioro et al. 2020) and trap height (Graham et al. 2012; Flaherty et al. 2019; Marchioro et al. 2020; Miller et al. 2020) are known to affect community composition in baited traps. However, previous studies on baited traps with unbaited controls have found that semiochemicals indeed increase attraction rates compared to unbaited traps for different types of flight-intercept traps (Bouget et al. 2009; Rodríguez-González et al. 2017; Fan et al. 2019, although see Byers et al. (1989). In this study, the high catch rates of many species, differences in catch rates between blends, and the tendency for species associated with conifers to be more attracted to the traps than species associated with deciduous wood, also indicate that the blends did in fact attract beetles above any baseline effect of the traps. While the traps themselves may have attracted saproxylic beetles, the semiochemical blends clearly diversified the catches and increased species abundances (Table 6).

The effectiveness of using multiple semiochemical blends

The combined catches from all three blends increased the sampled proportion of the full saproxylic community at each port compared to any single blend. The combination of all blends also helped stabilize the proportion of the community sampled at any single year, lowering any interseasonal variability in community composition. This pattern remained consistent when considering multiple years of sampling. Based on these results, we can confidently say that using multiple semiochemical blends outperforms single-blend inventories when sampling saproxylic beetle communities.

When comparing the blends, Ips and Monochamus showed a high degree of complementarity. Pissodes caught mainly a subset of the communities caught with the other blends (Fig. 1; 5). This pattern became even clearer when considering red-listed species, with Pissodes having sampled only one unique, red-listed species compared to six for Ips and five for Monochamus (Fig. 4). 27 of the 46 most frequent species were found in similar numbers across all blends. For the remaining 19 species, Ips showed the strongest attraction rates for most species. Ips also sampled the highest proportion of the total community of species associated with coniferous wood, and Pissodes the lowest. However, this result should be interpreted with caution, as there were also more traps baited with Ips at each site. Despite this caveat, it remains clear that a survey aimed to maximize the number of species sampled using one of these blends should choose Ips. If two blends can be used, Ips should be complemented with Monochamus.

Although Pissodes was the preferred blend for the fewest species, the total number of species caught by Pissodes was only slightly smaller than for the other blends. Furthermore, this blend still attracted some species more efficiently than the other blends. Thus, Pissodes would do a reasonable job in surveying saproxylic beetle communities on its own, and using it to complement the other blends should increase the overall diversity sampled.

In this study, one blend was used for each trap. Previous work has shown that combining several blends on a single trap can increase trap catches compared to the sum of many single-blend traps (Fan et al. 2019). Exchanging many single-blend traps for a few multi-blend traps could potentially be a way to lower the cost and workload of surveys. However, this warrants further research before any definite suggestions can be made.

Conclusions

This study provides the first large-scale evaluation of the use of semiochemical blends to sample native saproxylic beetle communities. We found that traps baited with semiochemical blends were capable of sampling most of the previously known species at a given site and revealed many new species. However, comparisons between sites should be made with caution due to site-specific effects on sampling efficiency. Surveys should aim to sample through several seasons to ensure that any inter-seasonal variation in community composition is accounted for. Using several blends is preferred over single-blend inventories, due to the clear increase in the proportion of the full community sampled with multiple blends, both within and between years. To summarize, using semiochemical blends is an efficient, cost-effective, and easily reproducible method for surveying native saproxylic beetle communities. Future inventories of saproxylic beetle communities are sure to benefit from this sampling method.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-025-00718-z.

Acknowledgements We would like to thank Shermin Eslamifar, Åke Lindelöw, and Tore Dahlberg for their unwavering assistance in identifying the many beetles over the years. Thanks also to all others who assisted during identification, and the field-personnel at the Agricultural Board of Sweden who has maintained the traps over the years. We are thankful to Jozef Rusin for improving the language of the manuscript. We are grateful to the two anonymous reviewers for their pertinent comments.

Author contributions Viktor Gårdman, Mikael Molander and Mats Jonsell developed the theoretical base for the study. Viktor Gårdman conducted the analyses. Viktor Gårdman and Mats Jonsell wrote the main manuscript text. Bo Aulin provided information on the sampling method. Bo Aulin and Mikael Molander helped refine the manuscript.

Funding Open access funding provided by Swedish University of Agricultural Sciences.

Code availability A preprint of the code and data can be found at https://doi.org/10.5878/d84p-5z88.

Declarations

Competing interests The authors declare no competing interests.

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