



# Using semiochemicals to predict biotic resistance and facilitation of introduced species

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**Abstract** Invasive species are leading causes of biodiversity loss and economic damage. Prevention and management of invasions requires risk assessments based on ecological knowledge for species of potential concern. Interactions between introduced species and heterospecifics in the recipient community may affect the likelihood of establishment through biotic resistance and facilitation and are therefore important predictors of invasion risk. Experimentally exposing one species to another to observe their interactions is not always safe or practical, and containment facilities offer artificial environments which may limit the number of species and the types of interactions that may be tested. To predict biotic resistance and facilitation in a more natural setting, we deployed traps with pheromone lures in the field to mimic the presence of two potentially invasive spruce bark beetles, the European *Ips typographus* (tested in eastern Canada), and the North American *Dendroctonus*

*rufipennis* (tested in Norway). We identified and counted possible predators, competitors, and facilitators that were captured in the traps. In eastern Canada, possible predators and competitors responded strongly to *I. typographus* lures, suggesting the potential for considerable biotic resistance. In Norway, *D. rufipennis* lures prompted little response by predators or competitors, suggesting that *D. rufipennis* may experience reduced biotic resistance in Europe. *Dendroctonus rufipennis* was also attracted to *I. typographus* pheromone, which may encourage facilitation between these species through cooperative mass attack on trees. Our findings will inform invasive-species risk assessments for *I. typographus* and *D. rufipennis* and highlight useful methods for predicting interactions between species that rely heavily on semiochemical communication.

**Keywords** Invasive species · Biotic resistance · Facilitation · Semiochemicals · Bark beetles

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## Introduction

Invasive species are a major cause of ecological and economic damage in terrestrial ecosystems and threaten to drive many species to extinction (McNeely 2001). With respect to insects, invasive species management and prevention efforts are largely aimed at taxa that negatively impact agriculture, forestry, or human health. Bark beetles

(Curculionidae: Scolytinae) are one such group, including several species (particularly in the genera *Ips* and *Dendroctonus*) that can cause considerable tree mortality (Bright 1976; Økland et al. 2011). Bark beetles may be transported via plant material and are frequently intercepted at ports around the world (Haack 2006; Kirkendall and Faccoli 2010). Invasive bark beetles may damage or kill host trees, displace native species, introduce pathogens, and reshape the ecology of the recipient community. Furthermore, invading bark beetles may escape predation or encounter naïve host trees that lack co-evolved defenses (Lee et al. 2007; Clark et al. 2014). For example, the red turpentine beetle (*Dendroctonus valens* LeConte) is a minor pest of pines in its native range of North and Central America, but has become invasive in China, where it has caused widespread tree mortality. This has been attributed in part to naïve hosts, a lack of natural enemies, and mutualistic associations with fungal pathogens (Sun et al. 2013).

The European spruce bark beetle, *Ips typographus* L., and the North American spruce beetle, *Dendroctonus rufipennis* Kirby, are particularly noteworthy due to known instances of inadvertent transport and the potential for damaging impacts. These are widely distributed bark beetles in their respective continents that can cause extensive mortality of spruce trees (*Picea* spp.) (Boucher and Mead 2006; Hlásny et al. 2019). While neither has yet established across the Atlantic, they have been intercepted beyond their native ranges (Lieutier 2004; Haack 2006), and *I. typographus* has recently established in England (EPPO 2021).

*Ips typographus* and *D. rufipennis* live in close association with their host trees, where they feed on the phloem tissue. New infestations typically begin in the spring or summer when the adults disperse in search of mates and new host trees. Eggs are laid in galleries in the phloem, and the larvae feed outward from the parental galleries until they pupate. Teneral adults continue to feed until sexually mature and ready to disperse. *Ips typographus* may have multiple generations per year if temperatures are favorable, while adult winter diapause appears to be obligate for *D. rufipennis*, limiting it to one generation per year. Both species prefer to infest stressed or downed trees at low population densities but may attack and kill healthy trees at high densities (Schebeck et al. 2017).

To successfully establish in a new habitat, both *I. typographus* and *D. rufipennis* must find a suitable ecological niche and proliferate despite Allee effects that inhibit population growth at low densities (Taylor and Hastings 2005). This means finding suitable host trees and persisting despite biotic resistance from host defenses, competitors, predators/parasitoids, and pathogens (Mattson et al. 2007). Should they cross the Atlantic, *I. typographus* and *D. rufipennis* appear capable of overcoming at least some of these challenges. Climates appear broadly suitable for both species across the Holarctic (Godefroid et al. 2016; Bentz et al. 2019), and both species can complete their life cycle in non-native spruce species (Økland et al. 2011; Flø et al. 2018, Isitt et al. unpublished data). Understanding how *I. typographus* and *D. rufipennis* may interact with novel heterospecifics (such as predators and competitors) is also crucial for predicting the success of introduced populations, and for obvious reasons this cannot be studied by intentional introductions of the beetles into non-native habitats.

However, chemical communication is ubiquitous among insects and can be used to indirectly assess interactions between non-native species and their novel community. Chemical odors emitted by one individual and responded to by another, known as “semiochemicals”, facilitate many intra- and interspecific interactions. *Ips typographus* and *D. rufipennis* produce aggregation pheromones to attract conspecifics, which allows them to quickly “mass attack” healthy trees, a strategy for exhausting host tree defenses (Krokene 2015). An anti-aggregation pheromone is later produced which discourages the further arrival of beetles and reduces intraspecific competition (Werner and Holsten 1995; Sun et al. 2006). *Dendroctonus rufipennis* appears to locate host trees in part by following the scent of volatile oleoresin components (Pureswaran and Borden 2005), although it is uncertain if *I. typographus* also locates hosts in the same manner (Kalinová et al. 2014). Predators may likewise find their bark beetle prey by cueing on the pheromones (functioning as “kairomones” in this context) produced by *I. typographus* and *D. rufipennis*, or by locating likely host trees by scent (Bakke and Kvamme 1981; Poland and Borden 1997). Additionally, it is possible for multiple species of bark beetle to be cross-attracted to a single pheromone blend, leading to close associations between them

(Gara and Holsten 1975; Smith et al. 1990). Because of the importance of semiochemicals in mediating ecological interactions between insects, we propose that synthetic semiochemicals can be powerful tools for predicting interactions between native and non-native species. By deploying synthetic pheromones to mimic the presence of a non-native species, in this case either *I. typographus* or *D. rufipennis*, we can observe the response of potential predators, competitors, or facilitators. From these observations, we can make more informed predictions about the establishment risk of introduced populations.

Using this approach, we carried out two trapping experiments in the field to quantify the response of ecologically relevant bark beetles and bark beetle predators to the synthetic pheromone blends of *I. typographus* (in North America) and *D. rufipennis* (in Norway), as well as to host tree odors. Beetles caught in traps baited with synthetic pheromone lures and host tree volatiles were identified and counted, and these counts were compared with control treatments to determine if the pheromone lures and/or host odors were attractive to native species. Attraction of a native species to the synthetic pheromone blends of non-native *I. typographus* or *D. rufipennis* was assumed to indicate a likely interaction, resulting in predation, competition, or facilitation depending on the natural history of the species in question. A lack of attraction was assumed to indicate a degree of “semiochemical

inconspicuousness”, making the non-native beetle less apparent to native predators and competitors. We propose that similar methods can be applied beyond our study species, and possibly also to non-insect organisms.

We predict that North American taxa will recognize and respond to *I. typographus* pheromone, because *I. typographus* aggregation pheromone resembles that of many North American *Ips* spp. (Symonds and Elgar 2004). In contrast, we predict that few European taxa will recognize and respond to *D. rufipennis* pheromone because apart from *Den-droctonus micans*, there are no congeners in Europe for *D. rufipennis* (Grégoire 1988). Its aggregation pheromone, therefore, broadly differs from European bark beetle pheromones.

## Materials and methods

We conducted two trapping experiments using synthetic beetle pheromone lures and host odors (Table 1) to quantify responses of predatory beetles, bark beetles, and ambrosia beetles to the simulated presence of non-native spruce bark beetles in Canada and Norway. The experiment in New Brunswick, Canada assessed responses of beetles to Ipslure®, a synthetic analog of the *I. typographus* aggregation pheromone blend. A similar experiment in As,

**Table 1** Technical specifications and suppliers for semiochemical components used in Canada and Norway

Component	Load	Release rate	Purity	Release device	Product	Supplier
(-)- $\alpha$ -pinene	15 mL	120–130 mg/day @ 25 °C	100%	PE bottle	P/N 3153	Synergy Semiochemicals, Burnaby, BC, Canada
Ethanol	8 mL	16 mg/day @ 20 °C	95%	PE pouch	P/N 3344	
Frontalin, racemic	250 $\mu$ L	1.5 mg/day @ 20 °C	97.50%	400 $\mu$ L PE centrifuge tube	P/N 3065	
Seudenol, racemic	250 $\mu$ L	5 mg/day @ 20 °C	$\geq$ 95%	PE bubble cap	P/N 3006	
MCOL, racemic	250 $\mu$ L	5 mg/day @ 20 °C	>95%	PE bubble cap	P/N 3247	
2-methyl-3-buten-2-ol	1500 mg	22 mg/day @20–21 °C *	98%	PE pouch	Ipslure®	KjemiKonsult ANS, Jar, Norway
(S)-cis-verbenol	70 mg	1 mg/day @20–21 °C *	97%			
Ipsdienol, racemic	15 mg	0.22 mg/day @20–21 °C *	98%			

\*Estimated from a total release rate of 22–23 mg/day for three-component Ipslure mixture

PE polyethylene

Norway quantified responses of beetles to a synthetic *D. rufipennis* aggregation pheromone blend. To mimic the odor of trees under attack by beetles, we included synthetic host volatiles (ethanol and (-)- $\alpha$ -pinene) with all pheromone lures. We also included separate host-odor-only (“Host”) treatments to determine if insect response was due solely to the host volatiles. The enantiomeric ratio of  $\alpha$ -pinene is highly variable in white and interior spruce (Grant et al. 2007; Pureswaran et al. 2004), but Norway spruce generally exhibits an excess of (-)- $\alpha$ -pinene (Lindström et al. 1989). Because racemic  $\alpha$ -pinene release devices were not available from our supplier, we chose the (-)-enantiomer as the most suitable host odor for both experiments.

We identified trapped insects of ecological relevance (predatory beetles and bark and ambrosia beetles) to species or sometimes to genus (depending on availability of keys and taxonomic expertise). We counted taxa separately for each individual trap, representing each combination of experimental block and semiochemical treatment. Identification was based on Barr (1962), Bright (1976), Anderson (2002), Opitz (2002), and Majka (2006) for New Brunswick; Duffy (1953), Tottenham (1954), Bakke and Kvamme (1993), Jordal and Knížek (2007), Kvamme and Lindelöv (2014), and Klimaszewski et al. (2018) for Norway; plus local taxonomic expertise and voucher specimens. Uncommon taxa (those with zero median counts across all treatments) were excluded from our results.

#### Ips typographus community response experiment (New Brunswick, Canada)

This experiment took place in Acadia Research Forest, New Brunswick (46.0122°, -66.3254°), in the interior of a mixed red spruce (*Picea rubens* Sargent) and black spruce (*Picea mariana* (Mill.) B.S.P.) forest. We arranged treatments in a randomized block design, with 30 m between adjacent traps. On May 15, 2017, we hung 21 12-funnel Lindgren multiple-funnel traps (Chemtica International, Costa Rica) from rebar poles along two parallel transects, with 12 traps (four blocks) approximately 20 m from and parallel to an access road, and the remaining 9 traps (three blocks) a further 30 m into the forest. This design exceeded the 10–15 m spacing typical of beetle trapping experiments in North America (Borden et al. 1996; Dodds

et al. 2015; Lindgren et al. 2012) and ensured that adjacent traps were suitably independent. The seven blocks each contained one replicate of each of three different treatments: a control (no host odors or pheromone lures), host kairomone (“Host”;  $\alpha$ -pinene and ethanol), and the commercial Ipslure® pheromone lure plus host kairomone (“Ipslure + Host”; methylbutenol, cis-verbenol (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol), ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol),  $\alpha$ -pinene, and ethanol). Semiochemical release devices were hung using twist-ties inside the 6<sup>th</sup> funnel from the top. Collection cups were filled with concentrated sodium chloride solution as a killing agent and preservative, plus a few drops of liquid dish detergent to reduce surface tension. We collected insects from the traps every second week for ~2.5 months, starting on June 1 and ending on August 11. We stored collections at -20° C until they could be processed for identification, and thereafter at room temperature in 75% ethanol.

#### Dendroctonus rufipennis community response experiment (Ås, Norway)

This experiment took place in a private clearcut near Ås, Norway (59.6426°, 10.8003°). We used a clearcut to maintain a forest-free buffer around our traps, preventing beetle attacks from spilling over into nearby standing trees. Spillover attacks were a greater concern in Norway than in Canada because the experiment in Norway was carried out in a privately owned forest. Forty “BEKA” free-standing 10-funnel traps (NoveFella, Norway) were arranged into 10 experimental blocks placed along a transect running parallel to the forest edge, with four traps in the corners of each 10×10 m block. We were constrained by the size of the clearcut but considered 10 m separation between traps to be adequate given that the effective attraction radius for *I. typographus* to its aggregation pheromone blend is 3–10 m (Schlyter 1992). Block centers were separated from each other and from the forest edge by 30 m. We randomized the treatment placement within block 1 and rotated this arrangement clockwise by 90 degrees for each subsequent block. The four treatments were the same as the *I. typographus* experiment (controls, “Host”, and “Ipslure + Host”), plus a combination of *D. rufipennis* pheromone lure and host kairomone (“DRlure + Host”; frontalinal

(1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane), seudanol (3-methyl-2-cyclohexen-1-ol), MCOL (1-methyl-2-cyclohexen-1-ol),  $\alpha$ -pinene, and ethanol). The *D. rufipennis* lure was a combination of the “Atlantic” spruce beetle lure and MCOL release devices (Synergy Semiochemicals Corp., Burnaby, BC, Canada). We chose the Atlantic lure to complement the sister experiment in New Brunswick and added MCOL to account for recent characterizations of eastern *D. rufipennis* pheromone blends (Isitt et al. 2020). The Ipslure+Host treatment was included as a positive control to ensure the arrival of native bark beetles and predators to at least one treatment combination. Semiochemical release devices were hung approximately 30 cm down into the perforated central support columns of the traps.

To prevent predation and escape, we modified the BEKA trap cups to allow the use of 200 mL of concentrated propylene glycol as a killing agent and preservative. The experiment was set up on May 11, 2018. We initially collected catches twice a week, then slowed to once every two weeks. However, due to the large volume of insects captured, particularly of *I. typographus*, we sorted and counted only catches for May 14, May 17, and June 5. Catches were preserved and stored as for the New Brunswick experiment.

### Statistical analyses

For each experiment, we compared community composition (counts of ecologically relevant taxa summed across collection dates) among semiochemical treatments using permutational multivariate analysis of variance (PERMANOVA; Anderson 2017) with 9999 permutations, including block as a random factor. If PERMANOVA showed a significant difference among treatments, we used multiple two-way ANOVAs (type I SS) to test for effects of the semiochemical treatment (fixed factor) and block number (random factor) on the counts of individual taxa. The ANOVA model was  $Y_{ij} = \mu + \tau_i + \beta_j + \varepsilon_{ij}$ , where  $Y_{ij}$  is the taxon count in treatment  $i$  and block  $j$ ,  $\mu$  is the grand mean,  $\tau_i$  is the  $i^{\text{th}}$  treatment effect,  $\beta_j$  is the  $j^{\text{th}}$  block effect, and  $\varepsilon_{ij}$  is the random error. Taxa counts were square-root transformed prior to ANOVA to improve residual normality. We corrected for multiple comparisons using the Holm-Bonferroni method. For taxon-specific ANOVAs that showed a significant

effect of treatment, we used Tukey’s post-hoc tests ( $\alpha=0.05$ ) to compare counts between all pairwise treatment combinations. All statistical analyses were performed in R 4.1.0 (R Core Team 2021) using *vegan* 2.5–7 (Oksanen et al. 2020) and *emmeans* 1.6.1 (Lenth et al. 2021).

## Results

### Ips typographus community response experiment (New Brunswick, Canada)

From New Brunswick collections we quantified four predatory clerid beetles, one possibly predatory nitidulid beetle, and 10 spruce-inhabiting bark and ambrosia beetles. Community composition varied significantly among semiochemical treatments (PERMANOVA, Pseudo- $F_{(2, 18)} = 10$ ,  $P < 0.001$ ). Twelve of 15 taxa showed differences in abundance among treatments (taxon-specific ANOVAs; Table 2).

Among predators, the clerids *Madoniella dislocata* Say and *Thanasimus dubius* F. responded significantly to the combination of Ipslure® and host kairomone relative to the host kairomone alone, and we saw the same result for the possibly predatory nitidulid *Epuraea*. The clerids *Thanasimus undatulus* Say responded equally to both treatments that included the host kairomone, while *Zenodosus sanguineus* Say responded equally to all treatments including controls (Fig. 1).

The bark beetles *D. rufipennis*, *Dryocoetes affaber* Mannerheim, *Ips borealis* Swaine, and *Orthotomicus caelatus* Eichhoff responded significantly to the Ipslure+Host treatment above all others. *Cryphalus ruficollis* Hopkins and *Crypturgus borealis* Swaine showed the same pattern, but the greater response to the Ipslure+Host treatment was not statistically significant. The ambrosia beetles *Gnathotrichus materiarius* Fitch and *Trypodendron lineatum* Olivier were also caught in greater numbers in traps amended with Ipslure® versus the host kairomone alone, but this was statistically significant only for *T. lineatum*. The bark beetle *Dryocoetes autographus* Ratzeburg responded significantly to the host kairomone, whereas the addition of Ipslure® seemed to suppress this attraction. *Polygraphus rufipennis* Kirby responded similarly to *D. autographus*, but the pattern was not statistically significant (Fig. 1).



**Table 2** Results of taxon-specific ANOVAs testing for an effect of three semiochemical treatments on the counts of spruce-associated bark and ambrosia beetles (Curculionidae) and bark beetle predators (Cleridae, Nitidulidae) captured in multiple-funnel traps in Canada (n=7 for each treatment)

Family	Species	Ecological role	$F_{(2,12)}$	$P$
Cleridae	<i>Madoniella dislocata</i>	Predator (Majka 2006)	24.2	<0.001
	<i>Thanasimus dubius</i>		85.9	<0.001
	<i>Thanasimus undatulus</i>		104	<0.001
	<i>Zenodosus sanguineus</i>		1.3	0.31
Nitidulidae	<i>Eपुरaea</i> spp.	Possible predator (Kenis et al. 2004)	51.5	<0.001
Curculionidae	<i>Cryphalus ruficollis</i>	Bark beetle (Bright 1976)	52	<0.001
	<i>Crypturgus borealis</i>		3.23	0.15
	<i>Dendroctonus rufipennis</i>		174	<0.001
	<i>Dryocoetes affaber</i>		26.1	<0.001
	<i>Dryocoetes autographus</i>		10.6	0.011
	<i>Ips borealis</i>		257	<0.001
	<i>Orthotomicus caelatus</i>		100	<0.001
	<i>Polygraphus rufipennis</i>		5.76	0.053
	Curculionidae		<i>Gnathotrichus materiarius</i>	Ambrosia beetle (Bright 1976)
<i>Trypodendron lineatum</i>		36	<0.001	

The semiochemical treatments consisted of: “Control” (no semiochemical amendment), “Host” (synthetic conifer host kairomone blend of  $\alpha$ -pinene and ethanol), and “Ipslure + Host” (host kairomone blend plus the commercial *Ips typographus* lure containing methylbutenol, cis-verbenol, and ipsdienol)

#### Dendroctonus rufipennis lure response experiment (Ås, Norway)

From Norwegian collections, we quantified four predatory clerids and staphylinids and eleven bark and ambrosia beetles. Community composition differed among semiochemical treatments (PERMANOVA, Pseudo- $F_{(3, 36)} = 36.8$ ,  $P < 0.001$ ). Seven of 16 taxa showed differences in abundance among treatments (taxon-specific ANOVAs; Table 3).

No predatory beetle responded positively to the combination of host kairomone and *D. rufipennis* pheromone blend relative to the host kairomone alone (*Thanasimus formicarius* L. showed *reduced* attraction to the DRLure+Host treatment). Two taxa, *T. formicarius* and *Placusa depressa* Mäklin responded significantly to the combined Ipslure® and host kairomone treatment over all other treatments (Fig. 2).

Only one bark beetle (*Crypturgus subcubrosus* Eggers) responded positively to DRLure+Host treatment relative to the host kairomone alone. Several taxa (*Crypturgus cinereus* Herbst, *Ips duplicatus* Sahlberg, *I. typographus*, and *Pityogenes chalcographus* L.) showed a significant response to the

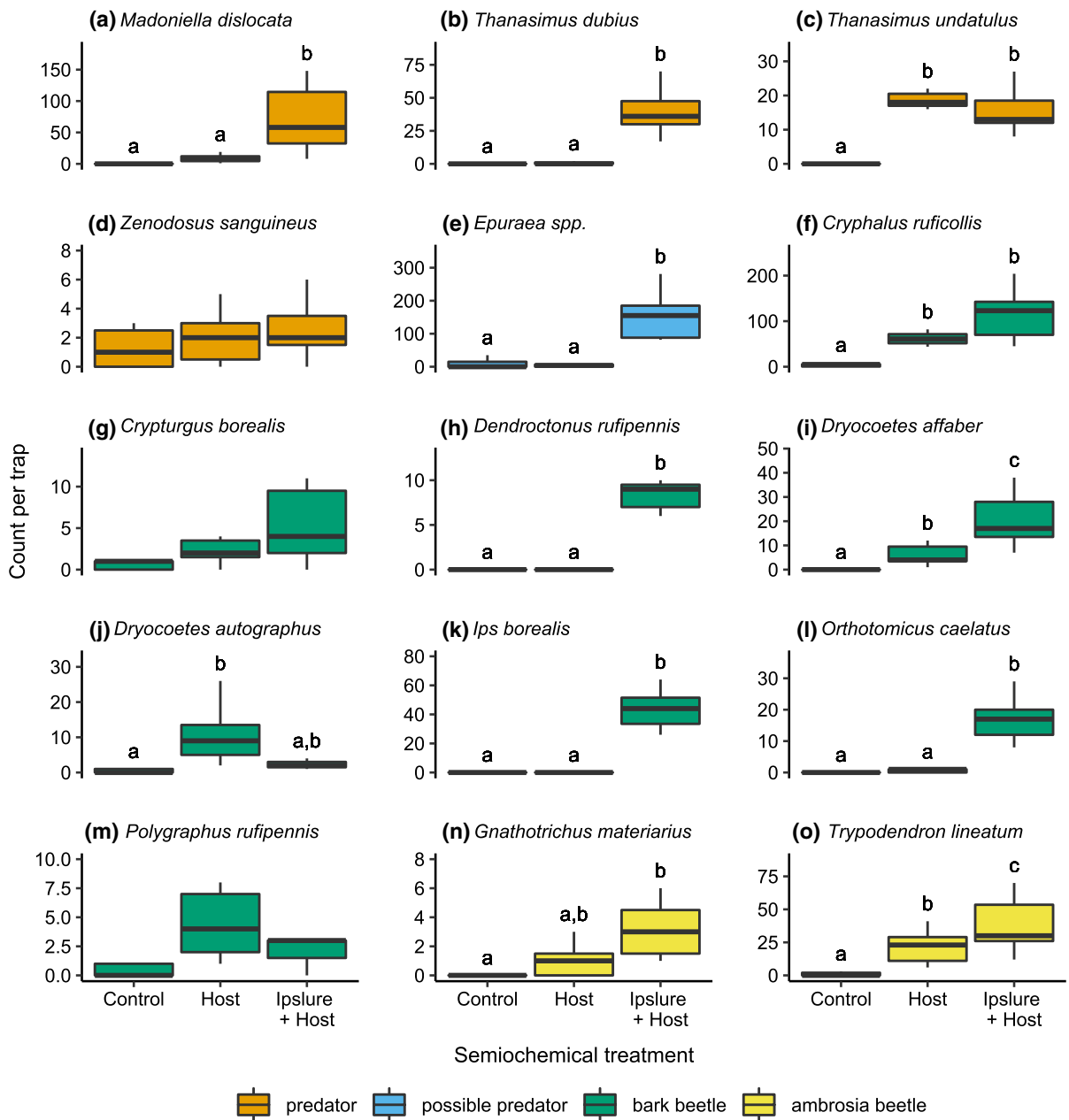
Ipslure + Host treatment when compared to the host kairomone treatment (Fig. 2).

#### Discussion

Our study allows us to make predictions about the relative magnitude of positive and negative heterospecific interactions (Table 4) that may affect the early establishment success of non-native spruce bark beetles in Europe and North America. These interactions can be broken down into two categories: biotic resistance (e.g., predation and competition) from the recipient community that inhibits successful establishment, and facilitative interactions that promote establishment.

##### Biotic resistance

There were clear differences in the responses of the recipient biology communities in Canada and Norway to the pheromone blends of non-native *I. typographus* and *D. rufipennis*, respectively. *Ips typographus* is likely to be more semiochemically conspicuous



**Fig. 1** Counts of bark beetles and associated predators captured in multiple-funnel traps deployed in New Brunswick, Canada (n=7 for each treatment). “Control” treatments did not receive a semiochemical amendment. “Host” treatments received a synthetic conifer host kairomone blend (α-pinene and ethanol). “Ipslure+Host” treatments received the host kai-

romone blend further amended by the commercial *Ips typographus* lure (Ipslure®). Boxplot whiskers extend from the first and third quartiles to the most extreme sample values within 1.5 × interquartile range. Different letter designations above the boxplots indicate statistically significant differences (α=0.05) according to Tukey’s HSD tests following ANOVA

**Table 3** Results of taxon-specific ANOVAs testing for an effect of four semiochemical treatments on the counts of spruce-associated bark and ambrosia beetles (Curculionidae) and bark beetle predators (Staphylinidae, Cleridae) captured in multiple-funnel traps in Norway (n = 10 for each treatment)

Family	Species	Ecological role	$F_{(3,27)}$	$P$
Staphylinidae	<i>Nudobius lentus</i>	Predator (Weslien 1992)	0.21	~ 1
	<i>Placusa depressa</i>		197	<0.001
	<i>Quedius</i> spp.		2.6	0.53
Monotomidae	<i>Rhizophagus ferrugineus</i>	Predator (Weslien 1992)	5.21	0.052
Cleridae	<i>Thanasimus formicarius</i>	Predator (Bakke and Kvamme 1993)	38.4	<0.001
Curculionidae	<i>Crypturgus cinereus</i>	Bark beetle (Bakke and Kvamme 1993; Haack 2001; Jordal and Knížek 2007)	22	<0.001
	<i>Crypturgus hispidulus</i>		0.15	~ 1
	<i>Crypturgus pusillus</i>		0.22	~ 1
	<i>Crypturgus subcribrosus</i>		10.6	<0.001
	<i>Dryocoetes autographus</i>		0.84	~ 1
	<i>Hylastes</i> spp.		2.97	0.40
	<i>Ips duplicatus</i>		259	<0.001
	<i>Ips typographus</i>		267	<0.001
	<i>Orthotomicus</i> spp.		0.33	~ 1
	<i>Pityogenes chalcographus</i>		44.4	<0.001
	Curculionidae	<i>Trypodendron lineatum</i>	Ambrosia beetle (Bright 1976)	0.89

The semiochemical treatments consisted of: “Control” (no semiochemical amendment), “Host” (synthetic conifer host kairomone blend of  $\alpha$ -pinene and ethanol), “Ipslure + Host” (host kairomone blend plus the commercial *Ips typographus* lure containing methylbutenol, cis-verbenol, and ipsdienol) and “DRlure + Host” (host kairomone blend plus a commercial *Dendroctonus rufipennis* lure containing frontalinal, seudenol, and MCOL)

in North America than *D. rufipennis* would be in Europe.

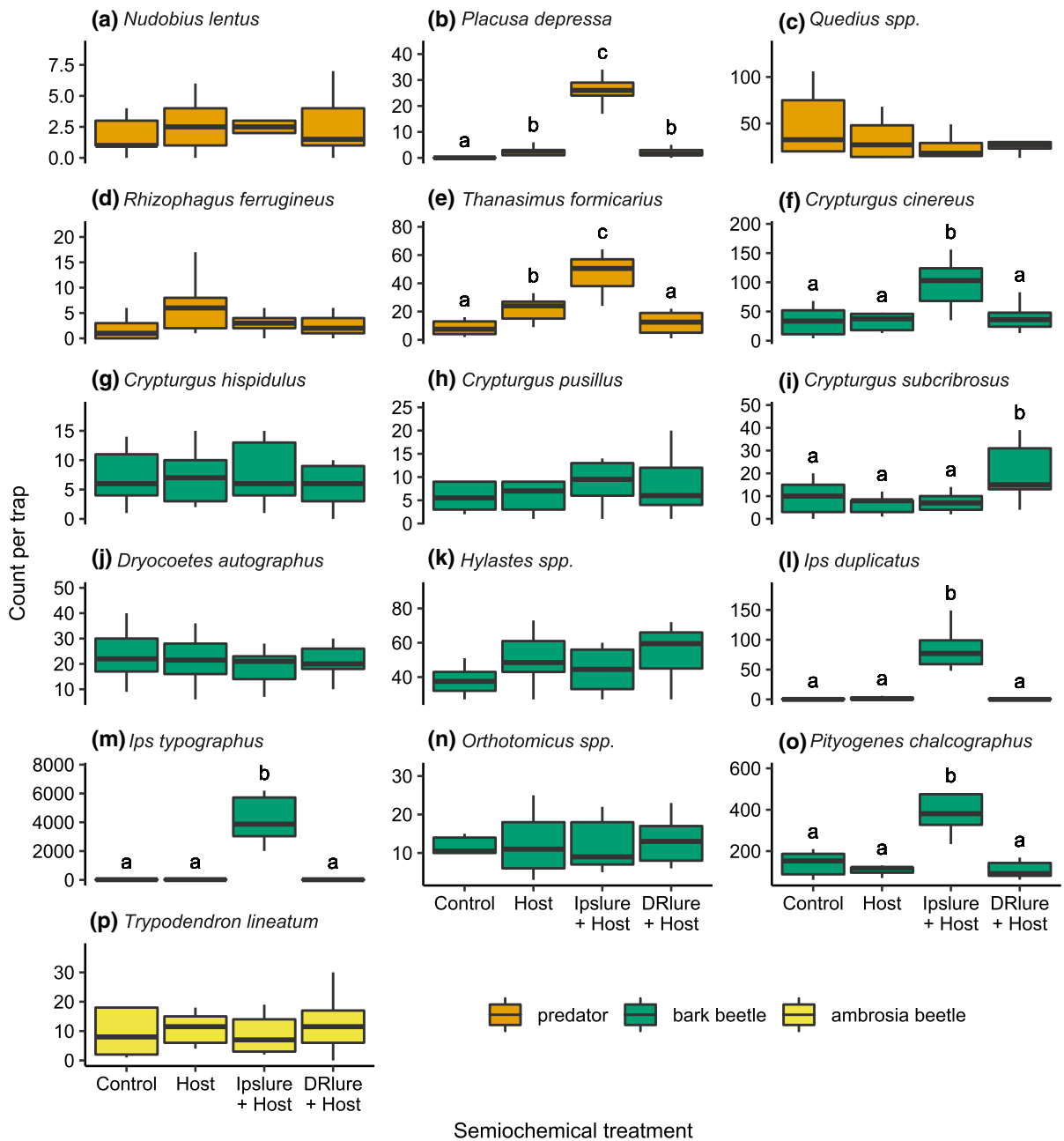
In New Brunswick, Canada, the staphylinid predators *M. dislocata* and *T. dubius* were attracted to Ipslure®, while *T. undatulus* responded predominantly to host kairomone. North American *Eपुरaea* species were also strongly attracted to Ipslure®. Although the ecology of these species is unknown, larvae of European congeners are predators of bark beetles (Kenis et al. 2004). Because there are several native North American *Ips* species, we expect North American predators to be preadapted to finding and handling *I. typographus* prey. Consequently, *I. typographus* may experience similar predation pressures to native *Ips* in North America.

Several spruce-inhabiting bark and ambrosia beetles in North America responded to Ipslure®. *Ips borealis* and *Orthotomicus caelatus* probably responded to the ipsdienol component, which is also produced by North American *Ips* species (Symonds and Elgar 2004) and (likely) *O. caelatus* (Phillips et al. 1989). *Dryocoetes affaber* and *D. rufipennis* were also attracted to Ipslure®, and *Cryphalus*

*ruficollis* and *Crypturgus borealis* showed similar (but non-significant) responses. Trees under attack by *I. typographus* in North America would thus likely be colonized by numerous native species, resulting in both negative (competitive) and positive (facilitative) interactions.

In contrast, our results suggest that if *D. rufipennis* were introduced into Europe, very few hetero-specifics would be attracted to its pheromone blend. The only native *Dendroctonus* species in Europe is *D. micans* (Grégoire 1988). Its gregarious larvae produce a short-range aggregation pheromone consisting of *trans*-verbenol, *cis*-verbenol, verbenone, and myrtenol, whereas adults do not mass-attack hosts and are not known to produce pheromone (Grégoire et al. 1981). Verbenene, a component of *D. rufipennis* pheromone, resembles these molecules structurally, but the *D. rufipennis* pheromone blend would be otherwise novel in Europe. The lack of response by European beetles to *D. rufipennis* pheromone may therefore be due to limited co-evolution with species producing similar pheromone blends. Some predation may still occur from species





**Fig. 2** Counts of bark beetles and associated predators captured in multiple-funnel traps deployed in a clear-cut near Ås, Norway (n=10 for each treatment). “Control” treatments did not receive a semiochemical amendment. “Host” treatments received a synthetic conifer host kairomone blend ( $\alpha$ -pinene and ethanol). “Ipslure + Host” treatments received the host kairomone blend further amended by the commercial *Ips typogra-*

*phus* lure (Ipslure®). “DRIlure + Host” treatments received the host kairomone blend further amended by a commercial *Dendroctonus rufipennis* lure. Boxplot whiskers extend from the first and third quartiles to the most extreme sample values within 1.5  $\times$  interquartile range. Different letter designations above the boxplots indicate statistically significant differences ( $\alpha=0.05$ ) according to Tukey’s HSD tests following ANOVA

**Table 4** Summary of factors that may increase (↑) or decrease (↓) the likelihood of establishment of invasive populations of *Ips typographus* and *Dendroctonus rufipennis* into North America or Europe, respectively

	<i>Ips typographus</i> into North America	<i>Dendroctonus rufipennis</i> into Europe
Climate suitability	↑ Yes (Bentz et al. 2019)	↑ Yes (Godefroid et al. 2016)
Host availability	↑ Yes (Økland et al. 2011; Flø et al. 2018)	· Likely, possibly suboptimal (Isitt et al. unpublished data)
Biotic resistance	↓ Likely on par with native <i>Ips</i> spp.	↑ Likely less than native species
Facilitation of mass attack by native species	↑ Likely	↑ Likely

such as *Nudobius lentus*, *Quedius* spp., *Rhizophagus ferrugineus*, and *Thanasimus formicarius*, which all showed some response to the control traps (the shape of the trap is intended to resemble a tree) and might arrive at trees under attack by *D. rufipennis*. *Rhizophagus grandis* is a known predator of *D. micans* in Europe and has been found to respond to novel *Dendroctonus* prey (Grégoire et al. 1991). However, we did not capture any individuals of this species.

Only two heterospecifics in Norway responded significantly to *D. rufipennis* pheromone. The clerid predator *T. formicarius* was either repelled by the *D. rufipennis* pheromone lure, or its attraction to the host kairomone was nullified by the addition of the lure. The bark beetle *Crypturgus subcribrosus* was attracted to the *D. rufipennis* lure but does not compete with *I. typographus* (Weslien 1992) and thus is unlikely to compete with *D. rufipennis*. *Crypturgus subcribrosus* is closely related to Nearctic *Crypturgus* species (Jordal and Knížek 2007), and its response to the *D. rufipennis* pheromone blend may be a remnant of ancestral co-evolution in North America.

Because North American predators and competitors are attracted to its aggregation pheromone, we predict that *I. typographus* would face greater biotic resistance in North America than *D. rufipennis* would experience in Europe. This may make *I. typographus* less likely to establish in North America by pushing founding populations below their Allee threshold. The main competitor of *I. typographus* in North America may be *D. rufipennis*, which has similar habits and hosts. However, *I. typographus* may be able to reduce this competition by infesting spruce hosts that are suboptimal for *D. rufipennis*. One such option is black spruce, which appears to be a suitable host for *I. typographus* (Økland et al. 2011; Flø et al. 2018), is

widely distributed across North America, and is seldom attacked by *D. rufipennis*.

#### Facilitation between heterospecifics

Biotic interactions can also be facilitative, potentially favouring invasion by raising populations above their Allee threshold. For some bark beetles, facilitation may result from a need for rapid, cooperative colonization (mass attacks) of live host trees. Tree-killing bark beetles such as *I. typographus* and *D. rufipennis* may either colonize a stressed, dead, or dying tree, or attack a healthy tree in sufficient numbers to exhaust the tree's defenses (Krokene 2015). Failure to meet the attack threshold in healthy trees leads to high brood mortality, but success opens up an abundant, high-quality resource that can reduce interspecific competition (Raffa et al. 2008).

In simulations, Økland et al. (2009) showed highly facilitative interactions among bark beetle species, particularly between tree-killing species that need to overcome attack thresholds for colonizing living trees. Species with lower population density, such as recently introduced species, would especially benefit from this facilitation, piggybacking on native species in heterospecific mass attacks to exploit abundant but less susceptible hosts. Our results, which show attraction of *D. rufipennis* to the aggregation pheromone of *I. typographus*, suggest the possibility of strong interactions between them. Both species disperse from overwintering sites in the spring, with similar flight temperatures (14.5 °C for *D. rufipennis*, Holsten and Werner 1987; 16.5 °C for *I. typographus*, Mezei et al. 2017). If either species is introduced into the range of the other, facilitation may promote the establishment of the newcomer; but this effect might be stronger for *D. rufipennis* invading Europe (where it would

encounter abundant *I. typographus*). If either species should establish in the other's range, this facilitation could also lead to simultaneous outbreaks of the two species.

While the number of *D. rufipennis* captured in Ipslure®-baited traps was only moderate, we interpret this as a strong response. An unrelated experiment conducted in the same study area in New Brunswick simultaneously failed to attract spruce beetles to felled white spruce (Isitt et al. unpublished data), consistent with a low local population density of *D. rufipennis*. Additionally, *D. rufipennis* is likely to respond more strongly to the natural pheromone blend of *I. typographus* than to a synthetic lure. Ipslure® contains racemic ipsdienol, which inhibits attraction of *D. rufipennis*, whereas *I. typographus* produce pure (–)-ipsdienol which does not inhibit attraction (Kohnle et al. 1991; Poland and Borden 1998).

Facilitation between exotic and native bark beetles may have already been observed in nature. In China, the invasive *Dendroctonus valens* is attracted to the pheromone of the native *Hylastes parallelus* Chapuis, and the two species have become common associates within their shared host, *Pinus tabulaeformis* Carrière. Lu et al. (2007) propose that these species jointly attack their host trees, and that this may have promoted the *D. valens* invasion by facilitating their aggregation. With both theoretical and observational support for the possibility of facilitation between bark beetles, the attraction of *D. rufipennis* to *I. typographus* lures is concerning as it may increase invasion and outbreak risks for both species.

## Conclusion

We have shown how *in-situ* semiochemical-based assays can be used to identify behavioral responses to potential invaders by native species. These responses may shape the tri-trophic niches of potentially invasive phytophagous insects, and thus their likelihood of successful invasion. Our approach allows responses to be assessed across numerous species in broad taxonomic groups depending on trap design, with no risk of introducing potentially invasive insects.

The evolutionary histories of the potential invader and recipient community may result in very different outcomes for different invading species and recipient communities. Our study provides a compelling

example of this: *Ips typographus* pheromone elicited a strong response from heterospecifics in eastern Canada, but *Dendroctonus rufipennis* pheromone deployed in Norway did not (Table 4). Coevolution with other *Ips* species in North America has likely pre-adapted North American predators and other heterospecifics to responding to Ipslure®, while the absence of pheromone-producing *Dendroctonus* in Norway made reciprocal pre-adaptation unlikely. Although the beetle communities in our sites are unlikely to be representative of all of North America or Europe, the clear patterns that we see across numerous broadly distributed species suggests that we should expect similar results in other locations.

Our approach can be extended beyond the study of phytophagous insects. For example, plants produce scents which attract insect herbivores, predators, and pollinators (e.g., Metcalf and Kogan 1987; Druker et al. 2000). Chemical extracts from potentially invasive plant species could be deployed in the field to assess responses by native insects, informing us about ecological interactions that could influence the plant's establishment. Semiochemical communication is also prevalent among fish (Sorensen and Johnson 2016) and their parasites (Mordue and Birkett 2009), which may enable similar studies for potentially invasive fish.

Of course, there are other major factors influencing establishment success that a study like ours cannot assess. Frequency and magnitude of introduction, habitat suitability, and intrinsic biological traits may all strongly influence establishment (Carlton and Ruiz 2005; Hayes and Barry 2008). Thus, field experiments like ours may be especially useful in combination with other studies, such as climate suitability simulations, host-use experiments, and vector analyses. A major advantage of semiochemical-based trapping experiments, though, is that they can provide data on interactions across many taxa simultaneously, without requiring that those be identified or selected in advance. Studies like ours will improve invasive species risk assessments, advance our understanding of the evolution of pheromone systems, and help identify promising biocontrol agents for use against already-invasive species.

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**Data availability** The datasets generated during and/or analysed during the current study are available in the Dryad repository, <https://doi.org/10.5061/dryad.tb2rbp01f>.

**Code availability** Not applicable.

#### Declarations

**Conflict of interest** The authors declare no conflicts of interest.

**Ethics approval** Not applicable.

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