Sampling Saproxylic Coleoptera: Scale Issues and the Importance of Behavior

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ABSTRACT Some currently used tree-scale sampling techniques targeting saproxylic insects capture individuals that are attracted to or landing on specific potential hosts. The success of such techniques is entirely dependent on strong primary attraction in targeted insects. However, up to this point, field experiments testing the primary attraction hypothesis have produced contradictory results. To test the efficiency of such techniques, and consequently, the strength of primary attraction for saproxylic Coleoptera, we sampled insects landing on contrasting snag types including new and old snags of five different tree species using sticky traps in a single mixed 135-yr-old boreal stand in Western Quebec, Canada. Ordination analyses showed homogenous assemblages among the different snag types and stovepipe controls, when considering either all species captured or only targeted functional groups, and very few species showed strong affinities to specific snag types. Species composition of assemblages was in several cases correlated with the species and status of trees neighboring the sampling units, which suggest that prelanding host selection mechanisms do not allow insects to single out a potential host while in flight. Our results suggest that primary attraction may play a role at larger spatial scales and help insects identify potential habitat patches, while selection of a single host at the local scale is done by trial-and-error through random landing. In such a context, future studies aiming at describing precise host-use patterns of saproxylic insects should rely on methods targeting larvae or emerging adults such as wood dissection and rearing.

KEY WORDS host-selection behavior, primary attraction, random attack, saproxylic Coleoptera, tree-scale sampling

MANY HOLOMETABOLOUS INSECTS CAN be characterized as living a double life, in that larvae and adults can belong to different trophic guilds and may use very different habitats. This is the case for most saproxylic beetles, especially in phloeophagous, xylophagous, and xylomycetophagous groups. While larvae are restricted to a single piece of decaying wood and can live as such for several years, adults are generally mobile, short-lived, and often feed only during a short maturation phase, when feeding at all (Haack and Slansky 1987, Hanks 1999). For these insects, larvae are definitely the dominant life stage, with adults being generally reduced to play a dispersal role besides reproduction. Thus, larval habitat requirements are generally much more definite and constraining and are likely to be more relevant to the persistence of the species at the local scale.

There is a growing interest in understanding the habitat requirements of saproxylic insects (Grove and Stork 1999, Grove 2002a), as they are sensitive to many forest management practices (Berg et al. 1994, Martikainen et al. 2000, Siitonen 2001, Grove 2002b, Maeto et al. 2002). Most of the work on saproxylic insects has focused thus far at describing and comparing assemblages at the stand scale, using different sampling techniques that target adults such as flight-intercept traps (Similä et al. 2003, Saint-Germain et al. 2004a), trunk-window traps (Martikainen et al. 1998, Rainius and Jansson 2000), Lindgren multiple funnels (Chénier and Philogène 1989a) and even mass rearing (Grohmann et al. 2004). Most of these approaches have limitations, because the adults caught are, for a high proportion of species, actively dispersing, and thus not necessarily closely tied to the habitat in which they were captured. The assumption that an adult caught flying will oviposit on some substrate present in the stand is not justified. However, one can try to sample adults as close as possible to oviposition, and thus be able to make inferences about actual host use.

Some studies have attempted to sample at the tree scale, using either trunk-window traps (Kaila et al. 1994, Økland 1996, Rainius and Jansson 2002, Hammond et al. 2003), sticky traps (Schroeder 1987, Shepherd and Goyer 2003), or logistically demanding rearing (Hammond et al. 2001, 2003, Hövemeyer and Schauermann 2003, Kappes and Topp 2004, Lindhe and Lindelöw 2004, Saint-Germain et al. 2004b), and

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bark dissection (Jonsell and Weslien 2003, Jonsell et al. 2004). Rearing and woody debris dissection give precise information about host use, but usually require a lot of space (i.e., for ex situ rearing) and/or a lot of time, and they usually do not produce many specimens. It would therefore be worthwhile to refine passive techniques to allow for reliable sampling at the tree scale.

Passive techniques used to sample at tree scale (trunk window and sticky traps) capture individuals that are attracted to or landing on specific potential hosts. The success of such techniques is entirely dependent on strong primary attraction in targeted insects, because it is assumed that they are able to discriminate between suitable and unsuitable hosts while in flight. The primary attraction hypothesis (Person 1931) states that selection is host-induced by chemical and/or visual cues while the beetle is still in flight. While several groups of insects have been shown to react physiologically to host and nonhost volatiles (Mustaparta et al. 1979, Tunset et al. 1993, Brattli et al. 1998, Huber et al. 2000, Belmain et al. 2002, Allison et al. 2004), other studies have shown random landing patterns in field experiments among hosts of contrasting quality (Goeden and Norris 1964, Berryman and Ashraf 1970, Moeck et al. 1981). Thus, actual support for a generalized and dominant primary attraction in the overall host-selection process of saproxylic insects is at best equivocal. There is evidence, at least for some groups, that insects may reject a high proportion of potential hosts after having landed (Berryman and Ashraf 1970). Therefore, we must question whether currently used passive tree-scale sampling techniques targeting adults before oviposition can provide precise information about actual host use.

In this study, we used sticky traps to sample saproxylic Coleoptera landing on different types of snags and on stovepipe controls in a boreal mixedwood forest of Western Quebec, Canada. Among sampling techniques, sticky traps capture insects closest to oviposition; captures obtained are thus more likely to reflect actual host use. Snags sampled included heavily decayed snags and new, mechanically killed snags of five different tree species (two deciduous and three coniferous). Coleoptera assemblages using such contrasting snag types were expected to be very different, as species are usually much more specialized at the beginning of the decay gradient than at the end, and the barrier between coniferous and deciduous hosts is very rarely crossed (Heliövaara and Väisänen 1984, Haack and Slansky 1987, Dajoz 2000). Our main objective was to compare saproxylic Coleoptera assemblages landing on these contrasting snag types and to use this data to determine if such passive preoviposition sampling techniques can be used to sample saproxylic Coleoptera at tree-scale.

Materials and Methods

Study Area. The study was conducted in Aiguebelle Provincial Park in western Quebec, Canada (48°32′ N, 78°39′ W). We chose a single ≈10-ha 135-yr-old mixed stand of which the living basal area consists of 30.8% black spruce *Picea mariana* (Miller), 28.0% balsam fir *Abies balsamea* L., 15.6% paper birch *Betula papyrifera* Marshall, 9.6% trembling aspen *Populus tremuloides* Michaux, 9.6% white spruce *Picea glauca* (Moench), 4.8% jack pine *Pinus banksiana* Lambert, and 1.5% eastern white-cedar *Thuya occidentalis* L. The density of snags over 10 cm in diameter at breast height (DBH) and over 1.5 m in height was estimated at 180.5/ha, and total snag basal area is distributed as follow: 39.1% jack pine, 28.3% paper birch, 18.8% balsam fir, 11.1% aspen, and 2.7% black spruce. Compositional data indicate that this stand is currently shifting from a jack pine/paper birch dominance to a black spruce/balsam fir dominance. Aiguebelle Park is 268.3 km^2 in area and is nested in a moderately fragmented aspen-dominated landscape.

Sampling Design. Saproxylic insects were sampled on snags of five tree species: two deciduous (trembling aspen and paper birch) and three coniferous (black spruce, jack pine, and balsam fir). Snags were selected along six parallel transects going through the stand, each 40 m apart. For each species except black spruce, of which old snags were almost absent, we selected four heavily decayed snags having a DBH over 16 cm. We also selected four healthy trees using the same DBH criterion, which were mechanically killed by girdling on the first day of sampling to create new snags. Old and new snags totalled 36 snags. In addition, we set up four 1.5-m-high stovepipes painted black to serve as inert controls (Chénier and Philogène 1989b). Unbaited stovepipes are thought to have a vertical shape reminiscent of snags (i.e., to beetles), without emitting any potentially attractant or repellent semiochemical. On each of these 40 sampling units, we pinned between 1.1 and 1.7 m, a 0.25-m^2 (≈60 by 40 cm) polyethylene sheet coated with Tree Tanglefoot Pest Barrier (The Tanglefoot Company, Grand Rapids, MI), centered on their southern aspect. Tree Tanglefoot is mainly composed of manila copal rosin, castor oil, and carnauba wax. Manila copal rosin is the nonvolatile fraction left after the distillation of turpentine from the resin of the tropical conifer genus *Agathis* Salisb., while carnauba wax comes from the tropical palm *Copernicia prunifera* (Mill.). Because none of its key components are volatile, Tree Tanglefoot does not interfere with primary attraction. Sticky traps were active for three 2-wk sessions during the summer. Session 1 spanned from 6 June to 20 June, session 2 from 28 June to 12 July and session 3 from 15 July to 30 July 2004. At the end of each session, the polyethylene sheets were covered with a plastic film, folded, and brought to the laboratory. All Coleoptera were removed from the resin and cleaned using the Histo-Clear histological clearing agent (National Diagnostics, Atlanta, GA). Polyethylene sheets were replaced by new ones at the beginning of each session. Coleoptera were identified to species or morphospecies for some families. Vouchers are deposited at the Lyman Entomological Museum (McGill University, Montreal, Canada).

Table 1. Beetle families representing at least 1% of total captures from all sticky traps

Family	Species	Individuals	Percent of total captures
Lathridiidae	11	4508	62.6
Melandryidae	6	440	6.1
Elateridae	19	378	5.3
Cantharidae	10	287	4.0
Staphylinidae	19	278	3.9
Mordellidae	7	133	1.9
Leiodidae	4	116	1.6
Alleculidae	1	107	1.5
Scolytidae	14	88	1.2
Curculionidae	15	88	1.2
Melyridae	4	73	1.0

A total of 7,194 individuals was captured.

Statistical Analyses. Mean number of captures and mean species richness were compared among the 10 snag types using one-way ANOVAs. Normality was confirmed using a Shapiro-Wilk test. Two-way ANOVAs could not be used because of the missing old black spruce snag type and to include the stovepipe controls. Individual-based rarefaction curves were used to compare species richness. Rarefaction curves provide more reliable estimates of species richness, because they remove the effect of differing sample sizes. Individual-based rarefaction is also useful to correct for sampling effort, in cases where frequent trap disturbance may have occurred (Buddle et al. 2005). Detrended correspondence analysis (DCA) was used to compare species composition among snag types. DCA is an eigenanalysis-based multivariate analysis that arranges sites along axes on the basis of data on species composition (ter Braak 1987). DCA ordination does not suffer from the major problems found in correspondence analysis, i.e., arch effects and compression of the ends of the gradients (Hill and Gauch 1980) and is widely used for analyzing ecological data sets. To study the specific response of targeted functional groups, species, and morphospecies were subdivided into wood-feeders, fungivores, and predators whenever published information about the taxon was available (wood-feeders: 37 species, 213 individuals; fungivores: 44 species, 5033 individuals; predators: 29 species, 458 individuals). These submatrices were analyzed with DCA ordinations to compare percentages of the explained species data variance and gradient lengths. Gradient length of the first DCA axis is a good estimator of species turnover between samples (Eilersten et al. 1990, Drapeau et al. 2000) and was used to quantify the homogeneity of assemblages between snag types for each functional group. To look at the influence of the immediate neighbors on sample composition, sample scores along axes one and two of all DCAs were correlated with the basal area (BA) of live and dead coniferous trees, BA of live and dead deciduous trees, and a total coniferous/deciduous BA ratio of trees found within a 3 m radius around the sample unit. Indicator species analyses (Dufrêne and Legendre 1997) were also used to identify species that were more or less restricted to

Table 2. Mean no. captures, mean species richness per snag ($n = 4$ per treatment) and individual-based rarefied richness for all taxa caught on each snag types ± 1 SD (N, new snag; O, old snag; Asp, aspen; PBi, paper birch; BSp, black spruce; JPi, jack pine; BFi, balsam fir; Stv, stovepipe

	NAsp	OAsp	NPbi	OPbi	NBsp	NJpi	OJpi	NBfi	OBfi	Stove
Abundance	194.0 ± 36.8	185.3 ± 73.8	167.0 ± 48.0	141.0 ± 32.1	276.7 ± 12.0	224.0 ± 22.7	166.5 ± 47.4	228.8 ± 102.6	161.8 ± 53.1	192.8 ± 36.7
Species richness	38.5 ± 13.4	36.5 ± 9.5	32.7 ± 6.0	32.8 ± 1.3	36.0 ± 3.6	42.8 ± 5.4	35.8 ± 8.9	44.5 ± 13.1	31.8 ± 6.7	49.0 ± 2.9
Rarefied species richness	72.0 ± 0.0	74.0 ± 7.0	61.6 ± 5.5	71.7 ± 4.3	56.9 ± 6.1	66.7 ± 6.3	71.0 ± 6.0	71.5 ± 7.5	59.5 ± 4.5	86.0 ± 7.0

No significant differences were detected.

Table 3. Results from detrended correspondence analyses performed on all species and on submatrices restricted to individual functional groups, and significant correlations of DCA sample scores with species composition and status of trees neighbouring the sampled snag (BA, basal area). Gradient lengths are used to estimate species turnovers among samples.

Trophic guild	Percent variance of species data explained	Length of gradient 1	Correlations of DCA axes with environmental factors
All	21.1	1.956	Axis 2—dead deciduous BA; $P = 0.007$
Wood feeders	26.5	6.740	None
Fungivores	29.3	0.891	None
Predators	31.2	2.632	Axis 1—dead deciduous BA; $P = 0.001$ Axis 2—dead coniferous BA; $P = 0.014$

specific types of snags, classified as coniferous versus deciduous, new versus old, by tree species, and by treatment (all species per snag stage plus stovepipes). ANOVAs and correlations were performed using SPSS 10.0.5 for Windows (SPSS, Chicago, IL). Rarefaction curves were calculated with the software Ecosim (Acquired Intelligence and Kesey-Bear. Burlington, VT). Detrended correspondence analyses were performed using CANOCO for Windows 4.0.2 (Microcomputer Power, Ithaca, NY) and indicator species analyses were done using PCOrd 4.17 (MJM Software Design, Gleneden Beach, OR).

Results

During the course of our experiment, a total of 7,194 beetles were captured, belonging to 207 species and morphospecies. Main families found in terms of abundance and species richness are summarized in Table 1. A single lathridiid morphospecies (*Corticaria* sp.) accounted for 51.8% of total abundance and was captured on all sampling units. No significant differences were found either in abundance ($F_{9,26} = 1.842$; $P = 0.108$) or species richness ($F_{9,26} = 2.108$; $P = 0.067$) between the snag types when analyzed with one-way ANOVAs (Table 2). Rarefied estimates of species richness, when standardized to 476 individuals (total captures for new aspen), was highest for the stovepipe controls and lowest in old balsam fir, new paper birch, and new black spruce (Table 2).

The DCA run for the full data matrix explained relatively little species data variance (Table 3). We were unable to discriminate clearly, using the graphical output of the DCA, between insect assemblages that landed on coniferous versus deciduous snags (Fig. 1a), on old versus new snags (Fig. 1b), on any of the sampled tree species (Fig. 1c), or either snag types (all combinations, data not shown), because the overlap between all groups is in most cases almost complete. The stovepipe controls had assemblages very similar to those of natural snags (Fig. 1). This total lack of specificity in captured assemblages was reflected in the indicator species analyses, as only one of the species captured >10 times obtained a significant indicator value >50 (*Pissodes* sp.; IndVal: 54.3 for coniferous snags; $P = 0.026$). Figure 2 shows species rank-abundance graphs based on species rank from all snag types combined (50 most abundant while captured on at least three snags) among contrasting treatment groups between which assemblages should differ the most according to our predictions. Again here the lack of specificity is explicit, as very few species among the 50 most abundant are totally absent from any of the treatment groups. The identity of these species and the number captured on each snag type is presented in Appendix 1.

The DCAs run on the matrices for different functional groups explained little more variance of the species data (Table 3). Gradient lengths of the first axes of each of these DCAs show that fungivore assemblages were much more homogenous than those of predators and wood-feeders (Table 3). Although species turnover was higher in assemblages of predators and wood-feeders, we were still unable to discriminate between assemblages having landed on any snag types (DCA graph for wood-feeders shown on Fig. 3).

Sample scores of some DCA ordinations were significantly correlated to species composition, basal area and physiological status of neighboring trees. Axis 2 of the DCA involving all species was positively correlated with dead deciduous trees basal area ($R^2 = 0.174$; $P = 0.007$). Axis 1 of the predators DCA was positively correlated with dead deciduous trees basal area within a 3-m radius ($R^2 = 0.279$; $P = 0.001$), whereas axis 2 was positively correlated with dead coniferous trees basal area ($R^2 = 0.154$; $P = 0.014$; Table 3).

Discussion

We found a high degree of similarity in Coleoptera assemblages of different snag types, despite of having sampled both extremes of the decay gradient and numerous tree species, including both deciduous and coniferous snags. Only one morphospecies (*Pissodes* sp.) showed some degree of specificity to a single snag type (coniferous). Based on the variety of snag types sampled in our study, we expected to obtain at least in some cases very different saproxylic beetle assemblages. Our expectations were well supported by current knowledge on saproxylic insect host use. Models of insect host use patterns along the decay gradient based on empirical data from other systems show a clear succession in assemblages, suggesting very different communities at both extremes of the gradient (Heliövaara and Väisänen 1984, Dajoz 2000). There is also a clear distinction between wood-feeding species using recently dead trees (stressed-host species) and others using the same host in the following years (dead-host species) (Wood 1982, Hanks 1999). Sa-

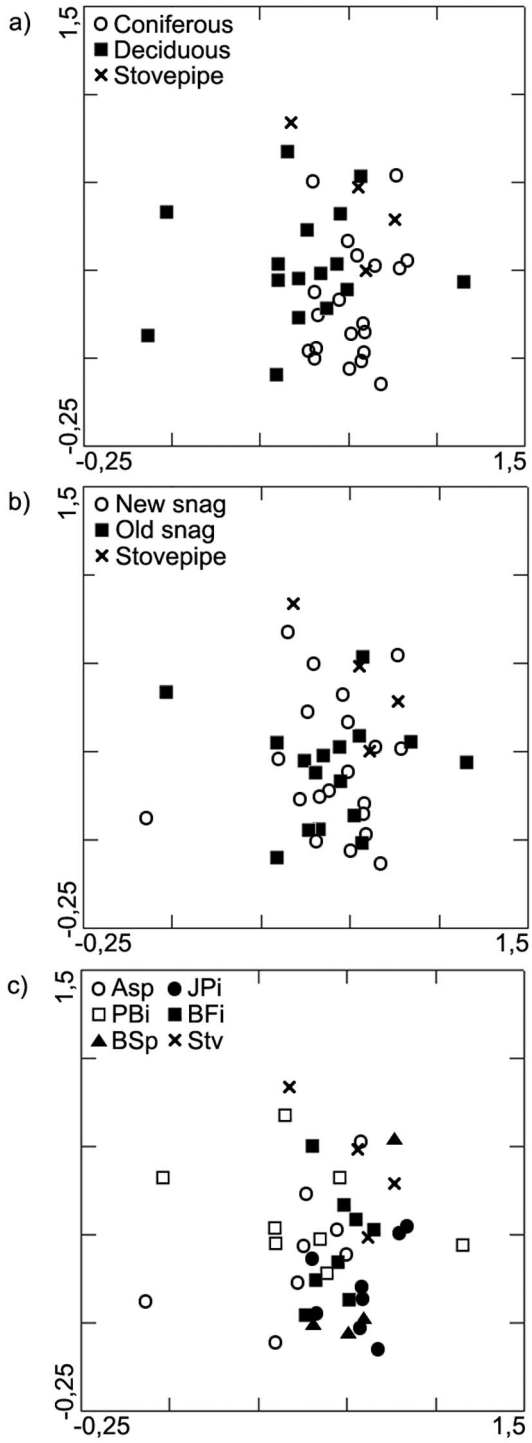

Fig. 1. DCA scatterplot for all taxa caught with (a) contrast between coniferous and deciduous species, (b) old and new snags, and (c) all tree species. All graphs also show stovepipe controls.

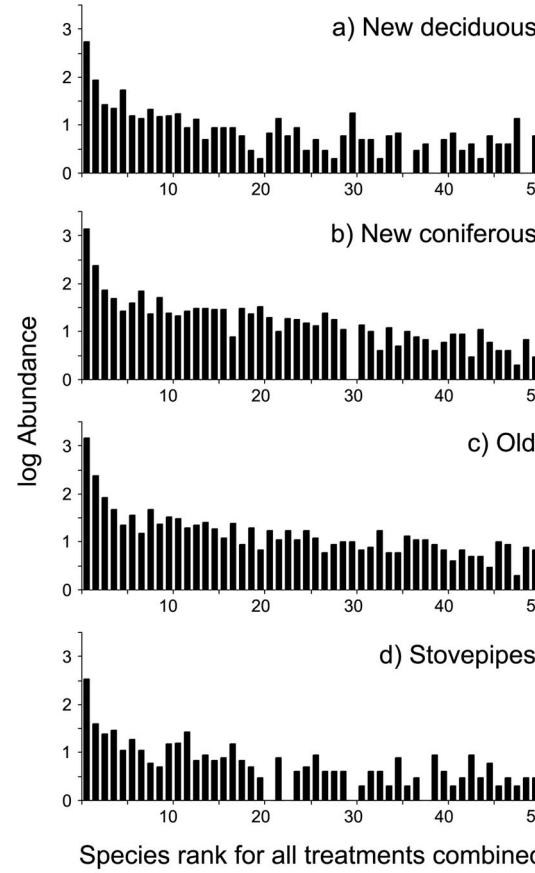

Fig. 2. Abundance of the 50 most common species in all treatments combined for (a) new deciduous snags, (b) new coniferous snags, (c) old snags all species combined, and (d) stovepipes, according to their overall ranks.

proxylic insects using less decayed wood are generally more specialized than species using older, more decayed hosts, but the barrier between deciduous and coniferous hosts is rarely crossed even in heavily decayed log stages (Haack and Slansky 1987). None of these well-known patterns was reflected in our results. In this context, it is clear that the assemblages obtained through our sampling did not closely reflect actual host use, either when using all species in the analyses or when targeting specific functional groups such as wood-feeders.

The potential success of a sampling approach targeting landing adults rests on strong and determinant prelanding host-selection behaviors. Two main hypotheses concerning prelanding host selection are still debated in the literature. The primary attraction hypothesis (Person 1931) states that selection is host-induced by chemical and/or visual cues while the beetle is still in flight. In contrast, the random attack hypothesis states that the insect lands randomly on a host and can evaluate its quality. These two hypotheses are not necessarily mutually exclusive, and either could be predominant in a particular species (Byers

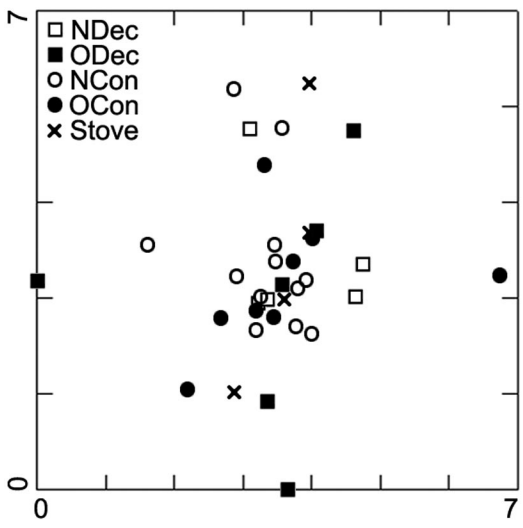

Fig. 3. DCA scatterplot for wood-feeding taxa, contrasting old coniferous (OCon), old deciduous (ODec), new coniferous (NCon), new deciduous (NDec) snags, and stovepipe controls (Stove).

1995). Several studies have showed that numerous species of several beetle families are attracted in some way to host volatiles (Curculionidae, Tunset et al. 1993, Brattli et al. 1998; Cerambycidae, Chénier and Philogène 1989a, Brattli et al. 1998, Allison et al. 2004, Pajares et al. 2004; Scolytidae, Borden et al. 1987, Chénier and Philogène 1989b, Tunset et al. 1993, Brattli et al. 1998, Macias-Samano et al. 1998, Fletchmann et al. 1999), apparently giving support to the primary attraction hypothesis. Some evidence also supports some sort of primary attraction for fungivores (Belmain et al. 2002) and some predators (Cleridae; Chénier and Philogène 1989b). However, there is a body of literature reporting equivalent landing rates on both high-quality and inappropriate hosts for several species of Scolytidae (Goeden and Norris 1964, Berryman and Ashraf 1970, Moeck et al. 1981), and thus supporting the random attack hypothesis.

Although at least some species of wood-feeders respond physiologically to host volatiles, it is not clear if this attraction helps the beetle to target a single host or rather to orient toward a habitat patch containing the potential host. Most studies focusing on primary attraction were not designed to make such a distinction. It would be expected that neighboring trees all contribute to a common pool of volatiles. It is far from clear if the olfactive signal emitted by a single tree is clear enough in this mixture of contradictory chemical cues to allow the insect to target a single host while still in flight. Such a conception of the host-selection process is to some degree invalidated in our study by the fact that the species composition and status of neighboring trees had a significant influence on the insect assemblages caught on specific snags, an influence that seems to be greater than the identity of the sampled snag itself. The importance of neighboring trees, the lack of specificity showed in the ordination analyses and the ability of stovepipe controls to collect assemblages very similar to the ones caught on natural snags without emitting any potentially attractant semiochemicals all support that beetles in flight might orient themselves toward a promising habitat patch using host volatiles, but, at smaller scale, land randomly on trees to perform postlanding host-selection steps in a trial-and-error fashion. Primary attraction would thus play a role in orienting long-range dispersal, while host selection at short range would be the result of random landing. The fact that only one species showed specificity to some snag type in our results suggest that primary attraction plays a role at short range for a very limited number of species.

Although some studies show that predators and fungivores can be attracted by host volatiles (Chénier and Philogène 1989b, Belmain et al. 2002), most of the evidence for such a behavior concerns wood-feeders. Hence, we analyzed wood-feeder data separately but did not observe any more patterns in results from this functional group (Fig. 3). Because the number of captures for this functional group was relatively low (37 species with 213 individuals), it may be necessary to sample this group with an active area larger than 0.25 m^2 to catch sufficient specimens. However, even with a small sample size, the almost total absence of patterns in wood-feeder distribution still goes against our initial predictions. We can also point out that the stand in which the experiment was performed is exceptionally mixed; a higher proportion of nonhost volatiles in the environment can possibly obscure chemical signals, and thus result in such random landing patterns. Several behavioral experiments have shown that some green-leaf volatiles (C-6 alcohols) produced by angiosperm trees disrupt the attraction of some coniferophagous bark beetles and cerambycids to host volatiles and pheromones (Huber et al. 2000, Huber and Borden 2001, Morewood et al. 2003, Zhang and Schlyter 2004). In such a mixed forest, several nonhost volatiles were most probably present in the environment for both coniferous- and deciduous-using saproxylic beetles and they may have in some way influenced the behavior of these insects. Wood-feeder assemblages sampled with sticky traps could possibly have been more structured in purely coniferous or deciduous stands, without the interference of an array of nonhost volatiles.

These results force us to reconsider how we should sample saproxylic insects depending on the scale of interest (Fig. 4). Flight-intercept and multiple-funnel traps are convenient ways to sample at a stand scale, even if they are likely to catch, at least for some insect groups dispersing over long distances, some proportion of transient individuals having no real affinity with the immediate environment in which they are caught. They paint in some cases a somewhat blurred portrait of the local communities but can give valuable information on regional diversity. Trunk-window traps and sticky traps suffer to a larger degree from the same problem, because the composition of their catches is tainted by both stand- and tree-scale influences. Our

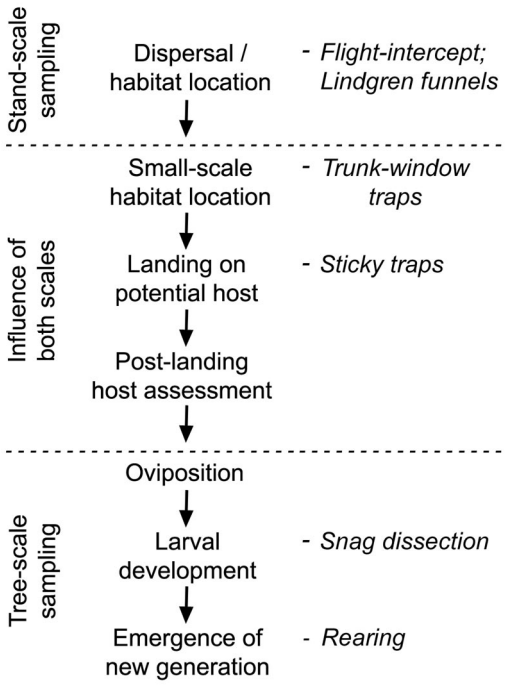

Fig. 4. Conceptual model of the behavioral sequence of host selection for saproxylics. Common sampling methods are associated with the step at which they capture insects and the scale at which we think they are effective.

study even shows that, at least in some cases when using such techniques, the tree-scale influence can be minimal. In a recent study characterizing saproxylic beetles using aspen in old-growth boreal forests and clear-cuts using trunk-window traps (Martikainen 2001), >40% of individuals and 65% of species caught were confirmed transient, because they were either not saproxylic, or were dependent on coniferous tree species. Caution must be taken when interpreting results gathered using either of these techniques, because they are bound to produce, at best, weak patterns. Rearing and dissection are still the most appropriate ways to sample at tree scale, because they cannot produce, when properly used, significant numbers of transient individuals.

Insect assemblages landing on a specific snag could not be used in our study to obtain precise information on actual host use patterns. Our results also suggest that the relative importance of prelanding host-selection steps is low. Extreme caution must be taken when interpreting results gathered using methods targeting adults at the tree-scale. More time-costly and possibly destructive methods such as in situ or ex situ rearing and wood dissections will have to be used in future research aiming at explaining host-use patterns of saproxylic insects at tree scale. This study also shows that postlanding host-selection steps are crucial in the overall host-selection behavior and should be a focus of future behavioral research.

Acknowledgments

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Appendix 1. Mean abundance ± SD for each snag type of the 50 most abundant species (all snag types combined)

Rank	Species	NAsp	OAsp	NPbi	OPbi	NBsp	NJpi	OJpi	NBfi	OBfi	Stove
1	*Corticaria* sp.(Lathridiidae)	65.5 ± 51.1	106.0 ± 56.2	72.8 ± 38.9	77.3 ± 23.8	123.8 ± 68.8	113.3 ± 29.3	84.3 ± 32.4	89.5 ± 50.0	89.5 ± 31.4	85.0 ± 21.0
2	*Melanophthal*ma sp.(Lathridiidae)	9.8 ± 6.1	15.0 ± 4.1	12.3 ± 7.6	9.8 ± 6.1	22.8 ± 14.8	22.5 ± 9.3	18.0 ± 9.2	15.0 ± 7.2	17.8 ± 2.5	9.5 ± 7.2
3	*Scraptia sericea* Melsheimer (Melandryidae)	2.0 ± 1.6	4.0 ± 1.6	4.5 ± 3.4	2.0 ± 1.6	6.5 ± 4.7	6.8 ± 1.7	9.0 ± 2.4	4.5 ± 2.4	6.0 ± 3.2	6.0 ± 3.5
4	*Ctenicera triundulata* (Randall) (Elateridae)	1.3 ± 1.0	3.8 ± 3.3	4.0 ± 3.3	3.8 ± 3.1	4.3 ± 3.9	4.8 ± 2.6	1.0 ± 1.4	3.0 ± 2.2	3.3 ± 2.9	7.0 ± 5.8
5	Nitidulidae sp.#1 (Nitidulidae)	1.3 ± 1.9	1.8 ± 3.5	12.3 ± 15.3	0.8 ± 1.0	1.0 ± 2.0	0.8 ± 1.0	1.3 ± 1.3	4.8 ± 4.3	1.5 ± 1.7	2.5 ± 3.7
6	*Isomira quadristriata* Couper (Alleculidae)	0.5 ± 1.0	2.5 ± 2.4	3.3 ± 2.5	0.8 ± 1.0	5.0 ± 1.6	1.3 ± 1.3	2.5 ± 2.1	3.3 ± 2.6	3.3 ± 3.3	4.5 ± 3.7
7	*Serropalpus coxalis* Mank (Melandryidae)	0	0.3 ± 0.5	3.3 ± 5.9	1.0 ± 2.0	4.3 ± 3.3	3.8 ± 1.3	0.3 ± 0.5	9.0 ± 7.3	2.0 ± 2.8	2.5 ± 3.7
8	*Podabrus* sp.#1 (Cantharidae)	1.8 ± 2.1	1.5 ± 0.6	3.3 ± 2.2	4.5 ± 3.9	2.5 ± 2.1	1.3 ± 1.3	2.5 ± 2.9	1.8 ± 2.4	3.0 ± 1.2	1.3 ± 1.3
9	*Mordellistena* sp. (Mordellidae)	0.8 ± 1.0	0.5 ± 1.0	2.8 ± 2.4	1.8 ± 0.5	2.3 ± 0.5	6.8 ± 8.3	2.3 ± 1.0	3.5 ± 2.4	1.0 ± 0.8	1.0 ± 1.4
10	*Melandrya connectens* (Newman) (Melandryidae)	1.0 ± 1.2	2.3 ± 2.5	2.8 ± 0.5	2.5 ± 1.7	0.8 ± 1.0	0.5 ± 0.6	1.3 ± 1.0	4.8 ± 5.7	2.0 ± 1.4	3.5 ± 3.4
11	Leiodidae sp.#1 (Leiodidae)	1.3 ± 1.5	3.0 ± 1.4	2.8 ± 2.6	1.0 ± 0.8	0.8 ± 1.0	1.8 ± 1.0	2.3 ± 1.9	2.5 ± 3.3	1.3 ± 1.5	3.8 ± 3.3
12	*Lathridius* sp. (Lathridiidae)	0.5 ± 0.6	1.5 ± 2.4	1.5 ± 1.3	1.0 ± 0.0	2.8 ± 3.6	1.8 ± 0.5	1.3 ± 1.0	2.0 ± 2.2	1.0 ± 0.8	6.5 ± 6.9
13	*Podabrus* sp.#2 (Cantharidae)	0.8 ± 1.5	1.8 ± 1.5	2.3 ± 1.3	1.5 ± 0.6	4.0 ± 4.1	0.8 ± 1.0	1.3 ± 1.0	2.8 ± 2.1	0.8 ± 1.0	1.5 ± 1.3
14	Staphylinidae sp.#1 (Staphylinidae)	0.8 ± 1.0	1.5 ± 1.3	0.3 ± 0.5	1.5 ± 0.6	2.5 ± 2.6	1.5 ± 1.7	2.3 ± 3.2	3.3 ± 1.7	1.0 ± 0.8	2.0 ± 1.2
15	Staphylinidae sp.#2 (Staphylinidae)	0.8 ± 1.0	1.8 ± 2.9	1.3 ± 1.0	1.5 ± 1.3	1.5 ± 1.3	3.5 ± 2.5	0.3 ± 0.5	2.0 ± 2.2	1.0 ± 2.0	1.5 ± 1.3
16	Staphylinidae sp.#3 (Staphylinidae)	0.5 ± 0.6	1.5 ± 1.3	1.5 ± 1.7	1.0 ± 1.2	0.8 ± 1.5	5.0 ± 3.6	0.3 ± 0.5	1.3 ± 1.9	0	1.8 ± 1.0
17	Lathridiidae sp.#1 (Lathridiidae)	1.0 ± 1.2	0.5 ± 0.6	1.0 ± 1.4	2.5 ± 1.0	0	0.3 ± 0.5	1.5 ± 1.9	1.5 ± 1.3	1.5 ± 1.0	3.5 ± 3.3
18	*Polygraphus rufipennis* (Kirby) (Scolytidae)	1.0 ± 1.4	0.8 ± 1.0	0.3 ± 0.5	0.3 ± 0.5	2.5 ± 2.1	2.8 ± 2.4	0.3 ± 0.5	2.3 ± 2.6	0.8 ± 0.5	1.5 ± 1.3
19	Ciidae sp.#1 (Ciidae)	0	0.5 ± 0.6	0.5 ± 1.0	1.0 ± 1.2	3.8 ± 5.2	1.8 ± 1.3	0.8 ± 1.5	0	2.5 ± 5.0	1.0 ± 1.4
20	*Pissodes* sp. (Curculionidae)	0.3 ± 0.5	0.3 ± 0.5	0	0.3 ± 0.5	4.0 ± 3.9	2.0 ± 1.2	0.5 ± 0.6	2.0 ± 1.4	0.5 ± 0.6	0.5 ± 0.6
21	*Mulsantina hudsonica* (Casey) (Coccinellidae)	0.5 ± 0.6	0.5 ± 1.0	1.0 ± 0.8	0.3 ± 0.5	2.3 ± 2.2	1.8 ± 1.7	2.3 ± 1.7	0.8 ± 1.0	1.0 ± 1.2	0
22	*Limonius aeger* LeConte (Elateridae)	0.5 ± 1.0	1.3 ± 1.0	2.8 ± 1.3	0	0	1.8 ± 2.4	1.0 ± 1.2	0.5 ± 0.6	0.3 ± 0.5	1.8 ± 1.5
23	*Attalus nigrellus* LeConte (Melyridae)	0.5 ± 1.0	1.3 ± 1.9	0.8 ± 1.0	0	1.8 ± 2.2	0.8 ± 1.0	1.5 ± 1.7	2.0 ± 0.8	1.3 ± 1.9	0
24	*Dalopius sp.* (Elateridae)	0	0.3 ± 0.5	2.0 ± 4.0	1.3 ± 1.9	1.0 ± 1.4	1.3 ± 1.5	1.0 ± 1.2	2.0 ± 4.0	0	0.8 ± 1.0
25	*Podabrus* sp.#3 (Cantharidae)	0.3 ± 0.5	0	0.3 ± 0.5	0.5 ± 0.6	2.5 ± 5.0	1.0 ± 1.4	2.8 ± 2.2	0	0.8 ± 1.0	1.0 ± 1.4
26	Elateridae sp.#1 (Elateridae)	0.3 ± 0.5	0.3 ± 0.5	0.8 ± 0.5	0.5 ± 0.6	0.5 ± 0.6	1.3 ± 1.9	1.0 ± 1.4	1.3 ± 1.0	1.0 ± 0.8	2.0 ± 1.6
27	Staphylinidae sp.#4 (Staphylinidae)	0	0.3 ± 0.5	0.5 ± 0.6	0.3 ± 0.5	0.8 ± 1.5	4.5 ± 4.2	0.5 ± 1.0	0.5 ± 0.6	0.3 ± 0.5	0.8 ± 1.0
28	Melyridae sp.#1 (Melyridae)	0	0.3 ± 0.5	0.3 ± 0.5	0	0.8 ± 0.5	1.0 ± 0.8	0.5 ± 1.0	2.5 ± 3.7	1.3 ± 2.5	0.8 ± 1.0
29	Mordellidae sp.#1 (Mordellidae)	1.0 ± 1.4	0.8 ± 1.5	0.3 ± 0.5	0.8 ± 0.5	1.0 ± 1.4	0.8 ± 1.0	0.8 ± 0.5	0.8 ± 1.0	0	0.8 ± 1.0
30	Tenebrionidae sp.#1 (Tenebrionidae)	4.0 ± 8.0	0.3 ± 0.5	0.3 ± 0.5	2.0 ± 4.0	0	0	0	0	0	0
31	*Limonius* sp. (Elateridae)	0	0.3 ± 0.5	1.0 ± 1.4	0.3 ± 0.5	1.0 ± 1.4	2.3 ± 1.7	0.3 ± 0.5	0	0.8 ± 1.0	0.3 ± 0.5
32	*Orchesia ovata* Lalibert (Melandryidae)	0.5 ± 1.0	0.3 ± 0.5	0.5 ± 0.6	0.5 ± 1.0	0.5 ± 1.0	0.8 ± 1.0	1.0 ± 0.0	1.0 ± 0.8	0	0.8 ± 0.5
33	*Eucinetus morio* LeConte (Eucinetidae)	0	2.5 ± 2.9	0.3 ± 0.5	0.8 ± 1.0	0.3 ± 0.5	0	0.3 ± 0.5	0.5 ± 0.6	0.5 ± 0.6	0.8 ± 1.0
34	*Celetes basalis* LeConte (Lycidae)	0.5 ± 1.0	0	0.8 ± 1.0	0.3 ± 0.5	1.3 ± 1.5	0	0.3 ± 0.5	1.5 ± 1.3	0.8 ± 0.5	0.3 ± 0.5
35	Leiodidae sp.#2 (Leiodidae)	1.5 ± 1.3	0.8 ± 1.5	0	0	0	0	0	1.0 ± 2.0	0.5 ± 0.6	1.8 ± 1.7
36	*Ampedus pedalis* Germar (Elateridae)	0	0.8 ± 1.5	0	2.0 ± 4.0	0	0	0.3 ± 0.5	2.3 ± 4.5	0	0.3 ± 0.5
37	*Phymaphora pulchella* Newman (Endomychidae)	0.3 ± 0.5	1.3 ± 1.3	0.3 ± 0.5	0.8 ± 1.0	0.3 ± 0.5	0	0.3 ± 0.5	1.5 ± 1.3	0.3 ± 0.5	0.5 ± 0.6
38	*Podabrus* sp.#4 (Cantharidae)	0.5 ± 1.0	0.8 ± 1.0	0.3 ± 0.5	0	0.3 ± 0.5	0.8 ± 0.5	0.8 ± 1.0	0.5 ± 1.0	1.0 ± 1.2	0
39	Tenebrionidae sp.#2 (Tenebrionidae)	0	0.3 ± 0.5	0	0	0.3 ± 0.5	0	1.0 ± 1.4	0.5 ± 1.0	0.8 ± 0.5	2.0 ± 2.3
40	*Dictyopterus aurora* Herbst (Lycidae)	0.3 ± 0.5	0	0.8 ± 1.0	0	0.3 ± 0.5	0.5 ± 0.6	0.5 ± 0.6	0.5 ± 0.6	1.0 ± 0.8	0.8 ± 0.5
41	*Ellychnia corrusca* LeConte (Lampyridae)	0	0.5 ± 0.6	1.5 ± 1.7	0	0	0	0.3 ± 0.5	2.0 ± 1.2	0	0.3 ± 0.5
42	Anobiidae sp.#1 (Anobiidae)	0.3 ± 0.5	0	0.3 ± 0.5	0.8 ± 1.0	0.5 ± 0.6	0.8 ± 1.0	0.3 ± 0.5	0.8 ± 1.0	0.5 ± 0.6	0.5 ± 1.0
43	*Denticollis denticornis* (Kirby) (Elateridae)	0.3 ± 0.5	0.5 ± 0.6	0.5 ± 1.0	0.5 ± 1.0	0	0	0	0.5 ± 1.0	0	2.0 ± 4.0
44	*Epuraea sp.* (Nitidulidae)	0.3 ± 0.5	0.3 ± 0.5	0	0.3 ± 0.5	0.5 ± 1.0	2.0 ± 1.6	0.3 ± 0.5	0	0.3 ± 0.5	0.5 ± 0.6
45	Staphylinidae sp.#5 (Staphylinidae)	1.3 ± 1.9	0	0	0	0.3 ± 0.5	0.5 ± 1.0	0	0.5 ± 1.0	0.5 ± 0.6	1.3 ± 1.0
46	*Atomaria pumilio* Casey (Cryptophagidae)	0.3 ± 0.5	0.8 ± 1.0	0.5 ± 0.6	0	0.3 ± 0.5	0	0.5 ± 0.6	0.5 ± 0.6	1.0 ± 0.0	0.3 ± 0.5
47	Cryptophagidae sp.#1 (Cryptophagidae)	0.8 ± 1.5	1.0 ± 0.5	0	0.8 ± 0.5	0	0	0.3 ± 0.5	0.8 ± 0.5	0	0.5 ± 0.6
48	Helodidae sp.#1 (Helodidae)	2.3 ± 4.5	0	1.0 ± 1.2	0	0	0	0	0.3 ± 0.5	0.3 ± 0.5	0.3 ± 0.5
49	*Ips latidens* (LeConte) (Scolytidae)	0	0.3 ± 0.5	0	0	0	0.8 ± 1.5	1.5 ± 2.4	0.8 ± 1.5	0	0.5 ± 1.0
50	*Endomychus biguttatus* Say (Endomychidae)	0.5 ± 1.0	0.3 ± 0.5	0.8 ± 0.5	0.3 ± 0.5	0.3 ± 0.5	0	0.8 ± 1.0	0.3 ± 0.5	0.3 ± 0.5	0.5 ± 0.6