REVIEW



Factors affecting catches of bark beetles and woodboring beetles in traps

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Abstract

The use of semiochemical-baited traps for detection, monitoring, and sampling bark beetles and woodboring beetles (BBWB) has rapidly increased since the early 2000s. Semiochemical-baited survey traps are used in generic (broad community level) and specific (targeted toward a species or group) surveys to detect nonnative and potentially invasive BBWB, monitor established populations of invasive or damaging native species, and as a tool to survey natural communities for various purposes. Along with expansion in use, much research on ways to improve the efficacy of trapping surveys for the detection of specific pests as well as BBWB in general has been conducted. In this review, we provide information on intrinsic and extrinsic factors and how they influence the efficacy of detecting BBWB in traps. Intrinsic factors, such as trap type and color, and other factors are described, as well as important extrinsic factors such as habitat selection, horizontal and vertical placement, and disturbance. When developing surveys, consideration of these factors should increase the species richness and/or abundance of BBWB captured in traps and increase the probability of detecting nonnative species that may be present. During generic surveys, deploying more than one trap type or color, using an array of lures, and trapping at different vertical and horizontal positions is beneficial and can increase the number of species captured. Specific surveys generally rely on predetermined protocols that provide recommendations on trap type, color, lure, and trap placement.

Keywords Trapping · Scolytinae · Cerambycidae · Buprestidae · Ports · Nonnative species · Detection

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Key Message

- Semiochemical-baited traps are important tools for detecting native and nonnative species.
- Generic and specific surveys benefit from incorporating research findings on trapping efficacy.
- Trap design, color, and killing agent are important intrinsic factors.
- Site selection, habitat, disturbance, and spatial placement are important extrinsic factors.
- Recommendations for optimally deploying traps will improve survey results.

Introduction

Bark beetles and woodboring beetles (BBWB) are important insects in forested ecosystems. They are key contributors to ecosystem processes (Müller et al. 2002; Ulyshen 2016), influence structure of stands (Feller and McKee 1999; Dodds et al. 2010a) and landscapes (Rodman et al. 2021), provide important food sources for invertebrate and vertebrate predators (Linsley 1959; Fayt et al. 2005), and can affect a wide array of ecosystem services (Embrey et al. 2012). Interest in BBWB has further increased because several species have been transported around the globe and introduced into new environments (Haack 2001; Barnouin et al. 2020; Marchioro et al. 2022b; Ruzzier et al. 2023), where some have become invasive pests, causing severe ecological and economic impacts threatening natural and managed forests (Seidl et al. 2018). Ecological impacts vary from changes to forest structure (Dodds and Orwig 2011; Haavik et al. 2018) to near or wholesale elimination of certain tree species in some forests (Klooster et al. 2014). Economic impacts can also be severe and wide ranging (Kovacs et al. 2010; Aukema et al. 2011; Kondo et al. 2017), especially considering the key value of urban and forest trees (Pearce 2001; McPherson et al. 2017). Thus, various techniques have been initiated to limit the movement of BBWB species into new environments, including treatment of goods and packing material with heat or pesticides prior to movement, product quarantines, and port inspections (Magarey et al. 2009; Nahrung et al. 2023). Even with these measures, BBWB continue to be intercepted in wood packaging used in global transport of container-ized goods (Haack et al. 2022) resulting in a clear need to optimize the use of traps and lures for surveillance and early detection of nonnative BBWB.

Semiochemical-based forest insect surveys for BBWB have become commonplace across the globe (Suckling 2015) and represent an important second line of defense at ports of entry and surrounding high-risk areas (Fig. 1A) where nonnative species may gain footholds in new areas

Cemetery Forested area Semi-forested park Within-port survey area International Port

Fig. 1 International port and surrounding area where traps can be deployed to survey for arriving or established nonnative bark beetles and woodborers (**A**), map depicting the initial (blue circles) and expanded (orange circles) trapping response in New York to delimit *Sirex noctilio* populations in the region (**B**), and multiple-funnel trap used to sample insect communities after a windstorm and salvage logging disturbance (**C**), photo credit—Shawn Fraver (Brockerhoff et al. 2006; Rassati et al. 2014; Rabaglia et al. 2019; Hoch et al. 2020; Mas et al. 2023; Melin et al. 2023). In addition, they are important tools for delineating the spatial extent of damaging BBWB species and monitoring population levels once a species becomes established in an area (Haack and Poland 2001; Dodds and de Groot 2012) (Fig. 1B). Outside of purely programmatic detection surveys, semiochemical-baited traps are also important tools to sample insect communities of both native and nonnative species for various ecological and/or conservation objectives (Sullivan et al. 2003; Gandhi et al. 2009; Larsson 2016; Dodds et al. 2019) (Fig. 1C). In fact, semiochemical-baited traps provide a cost-effective alternative to visual surveys because they can detect species that were previously unknown in an area (e.g., Webster et al. 2012b; Santos-Silva et al. 2020) or which are cryptic and not easily detectable by visual means. Traps do have limits, however, as it is generally unknown how well trap catches represent actual BBWB communities present in an area, and how well relative abundance relates to true abundance or rarity.

Using traps to survey for nonnative BBWB generally falls into two broad categories, generic or specific surveys (Poland and Rassati 2019). Generic surveillance implements lures and traps to survey sites deemed high risk to detect invasive species early in the invasion. These surveys are becoming more common with examples from Australia, Canada, Czech Republic, Great Britain, Italy, New Zealand, Spain, and the USA (Brockerhoff et al. 2006; Bashford 2012; Rassati et al. 2014, 2015b; CFIA 2017; Inward 2019; Rabaglia et al. 2019; Fiala and Holuša 2023; Mas et al. 2023). Broad spectrum lures, such as ethanol, or multi-lure blends including several semiochemicals on a trap are usually employed (e.g., Fan et al. 2019; Roques et al. 2023) with the hope of maximizing species richness over abundance in collections. This same approach is often used for biodiversity and ecological studies focused on sampling at the community level (Sullivan et al. 2003; Gandhi et al. 2009; Dodds et al. 2019, 2023). Targeted surveys (i.e., specific surveys) that focus on only one species, a few species, or members of the same genera at the same time are the second type of BBWB surveys. Specific semiochemical lures and/ or specific trapping protocols are used during these surveys often to track damaging insect populations (Billings and Upton 2010), but also when targeting rare or protected native species for conservation purposes (Žunič Kosi et al. 2017). The same approach is used when delimiting a population after detection, gaining a relative measure of abundance, and attempts to influence populations with mass trapping. In these surveys, abundance, while often difficult to interpret in relation to tree damage, is generally helpful. These specific surveys may also provide an opportunity to screen bycatch for other species of interest (Peck et al. 1997; Dodds and Ross 2002b; Skvarla and Holland 2011; DiGirolomo and Dodds 2014; Thurston et al. 2022).

Given the multiple potential uses of semiochemical-baited traps, an extensive testing of factors that may influence the efficacy of detecting BBWB in traps has been undertaken over the last 2 decades. Much of this information has not been consolidated. Our objective was to review and summarize the relevant literature on factors affecting BBWB trapping efficacy and provide natural resource professionals with guidance on ways to improve generic and specific surveys. With only one exception, Sirex noctilio F. (Hymenoptera: Siricidae), the focus will remain on bark and ambrosia beetles (Scolytinae), longhorned beetles (Cerambycidae), and jewel beetles (Buprestidae). These taxa were chosen due to their economic importance worldwide and the prevalence of important invasive species within these families. Early research that led to the development of semiochemicalbaited trapping, mechanisms underlying trap efficacy, and factors related to successful trapping of these families will be covered. General guidelines for developing general and pest-specific surveys are also provided. We broadly reviewed the scientific literature and technical reports focused on semiochemical-baited traps and their applications, but without using specific criteria to select articles to include in this review.

Steps toward semiochemical-based trapping for BBWB

Early BBWB research observed patterns of saproxylic insect succession on host trees or logs, as well as specificity to plant tissues (Graham 1925; Savely 1939; Wallace 1953). Mechanisms for these patterns were generally focused on host condition including moisture and temperature, as well as size and decay class of host material. Specific chemical cues driving these patterns were largely unknown at the time, but the possibility of chemical host location cues were considered (Person 1931). Later, ethanol, a host volatile produced by injured and stressed trees (Kelsey and Joseph 2003) was observed and identified as a field attractant for many BBWB (Moeck 1970, 1971; Schroeder 1988). Consequently, ethanol-baited traps were some of the earliest semiochemical reliant surveys for BBWB (Roling and Kearby 1975; Montgomery and Wargo 1983). Ethanol is still the key lure for ambrosia beetles (Reding et al. 2011; Galko et al. 2014; Fiala and Holuša 2023) and an important synergist to other lures when targeting broader BBWB communities (Hanks and Millar 2013; Miller et al. 2015). Terpenes were also recognized as important attractants in the field (Jantz and Rudinsky 1966; Knopf and Pitman 1972; Bauer and Vité 1975; Chenier and Philogene 1989). In particular, Bauer and Vité (1975) recognized a synergistic effect of ethanol and alpha-pinene on trap catches of *Trypodendron lineatum* (Olivier). Alpha-pinene and ethanol have since been used extensively to sample BBWB communities (Schroeder 1988; Schroeder and Lindelöw 1989; Miller and Rabaglia 2009).

Host volatiles became useful for broad surveys of BBWB, however, pheromones outperform host volatiles when the survey objectives are to detect or monitor the spread of a specific target species. The first bark beetle pheromones were identified from Ips confusus (LeConte) in 1966 (Silverstein et al. 1966). After that discovery, pheromone identification occurred across several genera of bark beetles. Identification of long-range pheromones in Cerambycidae began a few decades after bark beetles (e.g., Sakai et al. 1984; Noldt et al. 1995) and rapidly expanded in the early 2000s with identification of pheromones of native and nonnative species in North America (Lacey et al. 2004; Silk et al. 2007; Millar and Hanks 2017). The cross attractiveness of some identified cerambycid pheromones, especially within the same subfamily, made them especially useful for broader surveys (Hanks and Millar 2013), while specific pheromones could target individual (or a small number of) species of high value or concern (Silk et al. 2007; Rassati et al. 2021). Unlike sex pheromones of Lepidoptera (which are emitted by females, attract males only, and are highly species-specific) most pheromones identified in longhorn beetles are emitted by males, attract both sexes, and often several species. For example, 3-hydroxyhexan-2-one, 2,3-hexanediols, fuscumol, and fuscumol acetate are shared by species in different genera and subfamilies (Hanks and Millar 2016), making them especially useful for generic surveys. Identifying pheromones from Buprestidae has been even more challenging than for Cerambycidae. A pheromone identified from Agrilus planipennis Fairmaire represented the first time one was described in the family (Bartelt et al. 2007; Silk et al. 2011), but since then no important progress has been made on buprestid chemical ecology. Similarly, S. noctilio is the only economically important siricid for which lures have been specifically developed. However, none of the host volatiles and pheromones (Böröczky et al. 2009; Cooperband et al. 2012; Crook et al. 2012) identified for S. noctilio was effective as trap lures when tested in South Africa (Hurley et al. 2015).

In more recent years, it has become more common to combine host volatiles and pheromones on the same trap. For example, the combination of *Ips* bark beetle pheromones, including ipsenol and ipsdienol, and host volatiles, including ethanol and alpha-pinene, are effective for sampling large communities of BBWB in forests (Miller et al. 2011; Allison et al. 2013), urban and peri-urban areas (e.g., ports) (Rassati et al. 2015a, 2015b; Rabaglia et al. 2019). Similarly, traps baited with cerambycid pheromone blends have shown promise for capturing a larger array of cerambycid species across the Americas, Europe, and Asia (Hanks

et al. 2012; Sweeney et al. 2014; Wickham et al. 2014; Fan et al. 2019; Santos-Silva et al. 2020; Roques et al. 2023), as well as other BBWB when combined with host volatiles (Sweeney et al. 2016; Rassati et al. 2019).

Mechanisms underlying trap efficacy

To develop an effective trap design, lure, and deployment strategy for detecting BBWB, it pays to "think like a beetle," i.e., to understand their behavior (i.e., foraging, dispersal, mating, oviposition, etc.) and the factors affecting them, and to exploit them to our advantage. To survive and reproduce, most BBWB must find food, mates, and suitable brood hosts in a heterogeneous environment within a relatively short adult lifespan of a few days or weeks, and they do so with the aid of sophisticated sensory systems that detect and integrate olfactory and visual stimuli in their environment (Allison et al. 2004; Campbell and Borden 2009; Carrasco et al. 2015; Dodds et al. 2023). Other stimuli such as auditory (Rudinsky et al. 1973), gustatory/tactile cues (Ginzel and Hanks 2003), and even infrared (Evans 1964) can play a role in host/mate location and acceptance by BBWB, but it is chiefly olfactory and visual cues that have been exploited in the development of attractants and traps for BBWB surveys.

Olfaction

As discussed above, olfactory cues used by BBWB include volatiles emitted from host- and non-host trees (Metcalf and Kogan 1987; Bruce and Pickett 2011; Xu and Turlings 2018) and sex- or aggregation pheromones of both conspecifics and heterospecifics (Lu et al. 2007; Hanks and Millar 2016), the latter of which may serve as kairomones (e.g., Allison and Borden 2001). Plant volatiles play an important role in insect host location and are important for some BBWB (Moeck 1970; Brattli et al. 1998; Pureswaran and Borden 2005; McCullough et al. 2009; Tluczek et al. 2011; Flaherty et al. 2013; Silk et al. 2020). Plants share many of the same volatile compounds such as terpenes and sesquiterpenes and the relative amounts of these compounds may vary among species (Pureswaran et al. 2004), plant tissues (e.g., Zeneli et al. 2001), seasons (e.g., Zhang et al. 1999), time of day (e.g., Martin et al. 2003), stages of growth (e.g., Johnson et al. 2004), levels of moisture stress, and levels of herbivory (Dicke and van Loon 2000). It is the particular ratio of these common volatiles, rather than unique species-specific volatiles, that allows most insects to discriminate between host and non-host plants, or stressed versus healthy trees, by integrating signals from antennal olfactory receptors in the central nervous system (Bruce et al. 2005). Recognition and avoidance of non-host volatiles may be as important as positive response to host odors to a beetle seeking a suitable host in a forest composed of many different tree and plant species (Zhang and Schlyter 2003, 2004; Byers et al. 2004; Campbell and Borden 2009). For example, odors from nonhost trees inhibit response of some bark and ambrosia beetles to their hosts (Schroeder and Lindelöw 1989; Schroeder 1992).

Experiments in wind tunnels have shown that beetles orient to pheromone sources using positive optomotor anemotaxis (Fadamiro et al. 1998) as previously shown for moths (Kennedy et al. 1980; Kuenen and Baker 1982; Baker et al. 1984; Cardé 1984; Cardé and Willis 2008). When insects detect their sex or aggregation pheromone they initiate upwind flight and maintain a constant velocity of image motion across the eyes (optomotor anemotaxis) which results in a constant ground velocity independent of wind speed (Murlis et al. 1992). Variation in pheromone concentration in the plume (i.e., pockets of air with and without pheromone) caused by turbulence downwind of the source is necessary for upwind flight and also induces the zig-zag pattern (casting) (Elkinton and Cardé 1984; Murlis et al. 1992). The attractive radius or active space [defined as the distance from the pheromone source at which the odor concentration is sufficient to produce a response in the receiving organism (Elkinton and Cardé 1984)] of a pheromone-baited trap is affected by a number of factors such as pheromone release rate, wind speed, and turbulence, which affect dispersion of the odor plume and concentration of attractant in the odor filaments downwind (Schlyter 1992; Thistle et al. 2011; Bouwer et al. 2020). Turbulence produced by the trap itself can affect pheromone dispersion and trap performance (Wyatt et al. 1993; Cooperband and Cardé 2006). Estimates of the attractive radius of BBWB pheromone-baited traps, from mark-release-recapture or trap spacing-interference experiments, have ranged from 10 to 500 m (Schlyter 1992; Dodds and Ross 2002a; Maki et al. 2011; Torres-Vila et al. 2013; Jactel et al. 2019; Parker et al. 2020; Wittman et al. 2021).

Semiochemical release rate is an important factor that can affect BBWB trap catches (e.g., de Groot and Zylstra 1995; Ross and Daterman 1998; Borden and Miller 2000; Erbilgin et al. 2003; Grommes et al. 2023), yet optimal release rates are unknown for most species. Higher release rates, especially for host volatiles, are believed to generally increase insect capture by dispersing higher attractant concentrations around and downwind from a trap. High release host volatile lures are often components of generic trapping surveys for this reason. Nonetheless, the relationship between trap catch and release rate is not always positively linear, as high release rates can have a repellant effect on some species. For example, in Lepidoptera (e.g., Baker et al. 1981; Baker and Roelofs 1981) there is usually an optimal release rate of pheromone or host volatiles above or below which attraction and trap catches decline. Some BBWB have also demonstrated this behavior (e.g., Klimetzek et al. 1986; Ross and Daterman 1998; Erbilgin et al. 2003; Grommes et al. 2023), while others show limited differences among release rates (Sun et al. 2004) or a positive response to tested release rates but no upper limit detected (Fatzinger 1985; Franklin and Grégoire 2001; Gallego et al. 2008). As shown for ambrosia beetles, such preferences may correspond to the optimal concentration of the targeted host volatile which maximize colonization success in attacked trees (Cavaletto et al. 2023).

Vision

Size, shape and color are the key components used by insects to visually discriminate between host and non-host plants (Prokopy and Owens 1978) and these are important for some insects orienting to traps. The spatial distribution of photon flux provides information on shape, size, distance, and motion. Many species of BBWB orient toward objects that stand out against or contrast with their background, such as a tall tree or a dark silhouette. For example, mountain pine beetles, Dendroctonus ponderosae Hopkins, were attracted to dark cards placed against a white background; the larger the card, the greater the attraction (Shepherd 1966). Black multiple-funnel traps and intercept panel traps, designed to resemble dark tree trunks, often catch more BBWB than transparent or white traps (de Groot and Nott 2001; Kerr et al. 2017). However, response to visual stimuli often occurs only when combined with suitable olfactory stimuli, such as host volatiles and pheromones. For example, catches of the southern pine beetle, Dendroctonus frontalis Zimmermann (Strom et al. 1999), and black turpentine beetle, Dendroctonus terebrans (Olivier) (Fatzinger 1985), on pheromonebaited or turpentine-baited traps, respectively, were significantly reduced on white traps compared to black traps. In Buprestidae, there is evidence that visual stimuli drive host selection, although the roles of olfactory cues and their interactions are not as well understood (Imrei et al. 2020a; Santoiemma et al. 2024). Prokopy and Owens (1978) suggested that monophagous and oligophagous insects were more likely to use specific visual stimuli, in concert with olfactory and/or contact chemical stimuli, when foraging for food, mates or oviposition sites than are polyphagous species. Trichromatic color vision is common in insects (Prokopy and Owens 1978; Briscoe and Chittka 2001; van der Kooi et al. 2021) and preferences for different colors have been demonstrated for several BBWB (Campbell and Borden 2006; Crook et al. 2009; Francese et al. 2010a; Kerr et al. 2017; Skvarla and Dowling 2017; Rassati et al. 2019; Cavaletto et al. 2020, 2021; Perkovich et al. 2022; Sukovata et al. 2022) likely because they reflect similar hues as food or brood hosts.

Considering the above-described mechanisms, it is evident that a number of factors can potentially affect trap efficacy. These factors can be both directly linked to the trap (e.g., trap design, trap color, lure placement) but also to the position of the trap in the environment (e.g., trap height) and the characteristics of the environment in which the trap is located (e.g., forest type, disturbance history).

Intrinsic factors

Trap design

Several trap types for BBWB surveys have been developed over the years, but multiple-funnel and intercept panel traps are the most ubiquitous in trapping studies. Multiple-funnel traps, also known as multi-funnel or Lindgren funnel traps, were first developed by Lindgren (1983) for trapping bark and ambrosia beetles. Subsequent studies have demonstrated their efficacy for woodboring beetles as well (de Groot and Nott 2001; McIntosh et al. 2001; Morewood et al. 2002; Dodds et al. 2010b; Miller and Crowe 2011; Rassati et al. 2012). This trap type consists of a series of black vertically aligned funnels (typically twelve total) meant to mimic a tree bole, fitted with a collection cup on the bottom, and topped by a rain cover (Fig. 2A). BBWB are attracted by the shape of the trap and/or the odor plume released from the lures, arrive at the trap, hit the funnels, and then fall into the collecting cup because they cannot regain grip on the slanted slippery surface of the funnels (Lindgren 1983).

Similar to multiple-funnel traps, intercept panel traps were also initially commercially developed for bark beetles (Czokajlo et al. 2001) but then also found to be efficient for woodboring beetles (McIntosh et al. 2001; Miller and Crowe 2011). This trap type consists of two corrugated black plastic panels or reinforced PVC sheets placed perpendicularly to one another, a rain cover on top, and a funnel connected to a collection cup at the bottom (Fig. 2B). Additionally, a hole is cut in the middle of the PVC sheets to allow for lure placement. BBWB attracted by the shape of the trap and/or the odor plume released from the dispenser used to bait it, hit the panels, and fall into the funnel connected to the collection cup. A benefit of intercept panel traps over multiple-funnel traps is they break down into flattened pieces that can be more easily stored when not deployed.

Several modified versions of both multiple-funnel and intercept panel traps have been developed over the years. Examples of variations include number of funnels, ranging from 4 to 16 (e.g., Brar et al. 2012; Francese et al. 2013; Miller et al. 2018; Miller and Crowe 2022), modifications to increase the lower diameter of each funnel (Miller et al. 2013), funnels and panels of colors different than black (Fig. 2C), including transparent ones (Fig. 2D) (de Groot and Nott 2001; Rassati et al. 2012; Kerr et al. 2017; Cavaletto et al. 2021), the addition of glue (Francese et al. 2011) or pure and diluted lubricants on trap surface (Fig. 2E) (Graham et al. 2010; Allison et al. 2011, 2016; Graham and Poland 2012), the addition of liquid to the collection cup (Sweeney et al. 2006; Miller and Duerr 2008; Graham and Poland 2012; Allison et al. 2014), bottom funnel modifications to reduce catches of beneficial insects or non-targets (Ross and Daterman 1998; Martín et al. 2013; Bracalini et al. 2021) and enlargement of funnels connected to the collection cup (Morewood et al. 2002; Allison et al. 2014) (Fig. 2F). Both multiple-funnel and intercept panel traps are durable and can provide five or more years of service, while being moderately priced.

Most of the comparisons between standard or modified versions of multiple-funnel vs. intercept panel traps led to heterogeneous results depending on the target families or species. For example, some studies found that intercept panel traps are more effective than multiple-funnel traps in capturing longhorn beetles (de Groot and Nott 2001, 2003; McIntosh et al. 2001; Morewood et al. 2002; Miller and Crowe 2011; Marchioro et al. 2022a) while others found the opposite trend for species in the same (Rassati et al. 2012; Allison et al. 2014) or other (Dodds et al. 2010b) families. Others found no differences between the two trap types (Haavik et al. 2014). Nonetheless general patterns have been identified. A recent meta-analysis highlighted that (i) intercept panel traps are generally superior to multiple-funnel traps (except for buprestid beetles), (ii) traps treated with a surface treatment to make them slippery perform better than untreated traps and (iii) traps equipped with wet collection cups perform better than traps equipped with dry collection cups (Allison and Redak 2017). Further general patterns also arise when considering morphological traits associated with flight efficiency, maneuverability and eye size, potentially leading to improved predictability of optimal trap design according to species (Staton et al. 2023). A mechanistic understanding of trap functioning will provide insight into why one trap model performs better than another, or why the same trap design differs in its performance among taxa and habitats (Bouwer et al. 2020; Burner et al. 2020), and may lead to improvements in trapping efficacy.

Besides multiple-funnel and intercept panel traps, several other trap types for BBWB are currently in use. SLAM (Sea, Land and Air Malaise) traps represent another albeit less adopted option. Malaise traps are traditionally used to collect flying arthropods, especially Hymenoptera and Diptera (Skvarla et al. 2021), but with a few modifications they can be employed to sample BBWB (Vance et al. 2003; Skvarla and Dowling 2017; Varandi et al. 2018). SLAM retain the structure of a terrestrial Malaise trap, but they are usually equipped with top and bottom collecting cups and are often hung between trees (Fig. 2G). While canopy Malaise traps sometimes catch fewer total specimens of BBWB than do multiple-funnel or intercept panel traps, they often capture a greater number of species, including unique and rare species



Fig. 2 Trap types used to survey bark beetles and woodboring beetles for various purposes. Traps include multiple-funnel (\mathbf{A}), intercept panel (\mathbf{B}), purple multiple-funnel (\mathbf{C}), transparent intercept panel (\mathbf{D}), fluon coated intercept panel (\mathbf{E}), green multiple-funnel with enlarged funnels and collecting cup (\mathbf{F}), SLAM aerial malaise (\mathbf{G}), bottle (\mathbf{H}),

glue-coated sticky prism (**I**), double decker sticky prism (**J**), fan (**K**), and Multitrap system (**L**) traps. Photo credits: KJD—A, B, F, G, H; JAF—C, I; DR—D; Joshua Bruckner—E; Nathan Siegert—J; Emilio Caiti—K; Synergy Semiochemicals—L

(Dodds et al. 2010b, 2015). Unfortunately, these traps are much more expensive and less durable than the other traps. Simple traps (e.g., bottle traps) (Fig. 2H) baited with fermenting baits or host volatiles have also been demonstrated to be an efficient tool for monitoring longhorn beetles (Miller et al. 2018; Ruchin et al. 2021) and ambrosia beetle communities (Steininger et al. 2015; Tarno et al. 2021), as well as for citizen science projects to broaden the area surveyed for nonnative ambrosia beetles (Steininger et al. 2015; Ruzzier et al. 2021; Colombari and Battisti 2023). These traps cost very little to make and can be created from recyclables (Frost and Dietrich 1929; Reding et al. 2010), however, they are generally only used for a single season. Theysohn bark beetle traps, commonly employed for monitoring *Ips typographus* L. population density in Europe (Bakke 1985; Weslien et al. 1989; Galko et al. 2016), consist of a series of horizontal slots across a flat plastic surface. These traps are similar in price to intercept panel traps or multiple-funnel traps and can also provide years of service but are generally recommended only for certain bark beetles. While not broadly implemented, UV light traps capture large communities of insects, including BBWB, and provide a strong tool to broadly survey insects (Wardhaugh and Pawson 2023) or for specific target species (Pawson et al. 2009).

Various traps have been developed over the years driven by survey needs to detect or delimit invasive species. Gluecoated sticky prism traps, for example, (Fig. 2I) have been extensively used for monitoring the invasive buprestid beetle A. planipennis in the USA and Canada (Petrice et al. 2013; Poland et al. 2019). This trap type consists of a three-sided prism made of corrugated plastic, usually green or purple (Crook et al. 2009), covered with insect glue, where each side is 36 cm wide by 60 cm tall (Francese et al. 2008, 2010b) and can be used either baited or unbaited. A more complex but more efficient version of the sticky prism traps developed for monitoring A. planipennis in the USA is represented by the double-decker trap (Poland et al. 2011, 2019; McCullough and Poland 2017). This trap type consists of a 3 m tall PVC pole used as a support of two glue-coated green or purple prism traps built from corrugated plastic which are attached at different heights on the pole (Fig. 2J). The configuration, while equally efficient to a green prism canopy trap, is more effective than a single purple prism trap (Tobin et al. 2021). Canopy-placed sticky panel traps are still used for A. planipennis survey in Canada, but in the USA have now mostly been replaced by multiple-funnel traps. Branch-traps, i.e., green sticky plastic cards fastened to sunlit branches and baited or not with a 3D-printed decoy, have also been employed for monitoring Agrilus spp. (Domingue et al. 2013, 2015), as well as a lighter weight light-green non-sticky multiple-funnel trap developed for jewel beetles (Imrei et al. 2020b) in Europe.

For ambrosia beetles, a recent study showed that a single white panel trap that is sticky on both sides is generally superior to 8-unit multiple-funnel and intercept panel traps (Kendra et al. 2020). Commercially available Japanese beetle traps have also been used successfully to trap ambrosia beetles (Burbano et al. 2012), as have artificially stressed trees (e.g., Ranger et al. 2010) and trap logs (e.g., Reding and Ranger 2020). Trees or logs may also have the benefit of providing substrate for ambrosia beetle fungal mutualists, potentially enhancing attraction to the traps through the addition of fungal volatiles caused by inoculated fungi (Hulcr et al. 2011; Kuhns et al. 2014; Gugliuzzo et al. 2023; but see Tobin et al. 2024).

There are also several new traps available that have mostly been untested against existing trap types. Foldable fan traps (Grégoire et al. 2022) (Fig. 2K) are laser cut from a sheet of polypropylene that can be rapidly produced in large numbers in a lab or by a commercial company and easily transported and deployed in the field with very little effort. They offer a cheaper alternative to more expensive traps, with the potential for multi-year use. The Multitrap system (Synergy Semiochemicals, Canada), consisting of a set of modular parts from which a variety of trap configurations can be constructed, including standard multi-funnel traps, intercept traps, but also a combination of the two (Fig. 2L) is also a new trap design that awaits further testing. Cameraintegrated traps have also been developed for BBWB surveillance (Rassati et al. 2016). These traps allow the user to focus the on-site checking only on those traps showing the presence of target insects, avoiding checking of empty traps and reducing the time and costs of the surveillance. To date, camera-integrated traps are commercially available and used operationally for monitoring specific insect pests in traps baited with species-specific sex pheromone, e.g., codling moth in apple orchards, but with improvements in machine learning and image recognition technology (Preti et al. 2021), may eventually be useful for generic BBWB surveys as well.

Lure placement on trap

The placement of lures on traps can influence trapping results. For example, early wind tunnel tests of multiplefunnel traps suggested that two lures, one each placed inside a trap at the center of the middle and bottom funnels would optimize pheromone plumes, thereby increasing catch (Lindgren 1983). Similar results were found using other trap types (Lindgren 1983). When lures were placed inside of modified multiple-funnel traps where lower funnel holes had been enlarged, several BBWB responded positively to modified traps over standard multiple funnel traps with lures outside of traps, while none responded negatively (Miller et al. 2013). It was suggested that this pattern was due to either the ability of the lures to create a large plume emitting from the middle of the trap and expanding outward or to the larger funnel holes that may have facilitated higher capture rates. There are many unknowns about how pheromones on traps interact (i.e., separate point source or single point source) and how this may influence BBWB orientation to traps. Antagonistic effects of multiple-component, generic lures for cerambycids can reduce catches of some beetles (e.g., Miller et al. 2017) but generally do not interfere with the majority of species (Hanks et al. 2012). However, new questions may arise about separating the release devices

on different funnels to avoid interference among plumes. Resulting plume structure generated by lure placement is one way trap catches may be influenced. The other way is by blocking of incoming insects, although there is no evidence that even large lures on side of traps reduce BBWB catches (Dodds et al. 2010b). Similar difficulties may be found with intercept panel traps, when multiple lures are placed tightly together at the same hole, and these questions may warrant future research.

Lubricant treatments on trap surface

Initially, multiple-funnel and intercept panel traps were designed for bark beetles, but as their use expanded to include larger taxa (cerambycids, buprestids), it was observed that some of these insects could land on and escape from trap surfaces (McIntosh et al. 2001; de Groot and Nott 2003). These initial observations led to treatments of traps with substances that make the surface more slippery, thereby increasing the chances of capturing BBWB that land on the trap and reducing chances of their escape. When multiple-funnel traps were treated with the lubricant Rain-X (active ingredient polydimethylsiloxane), they generally caught more cerambycids as well as three large buprestid species [(Chalcophora virginiensis (Drury), Buprestis maculativentris (Say), Dicerca tenebrosa (Kirby)] than did untreated traps (de Groot and Nott 2003). The active ingredient, usually used as a lubricant for car windshields temporarily smooths trap surfaces, making them more slippery and preventing beetles from being able to stand or perch on it. Rain-X soon became a standard treatment for multiplefunnel and intercept panel traps (Sweeney et al. 2004; Hanks et al. 2007; Allison et al. 2011; Francese et al. 2011).

With insight gained from Rain-X treatments, other lubricants were tested. Graham et al. (2010) found that intercept panel traps treated with the fluoropolymer, fluon (active ingredient polytetrafluoroethylene), originally used to keep insects from escaping containers during laboratory behavioral assays, caught ~14 times more cerambycids than Rain-X or untreated traps. Additionally, fluon-treated multiplefunnel traps caught more longhorned beetles than untreated traps, and treatments lasted for at least two seasons (Graham and Poland 2012). However, a significant drop-off in catch happens 3 years post-application (Dong et al. 2023). Further testing of fluon treatments supported its importance for increasing trap catches while also not interfering with visual cues, such as trap color, on target insects (Lyons et al. 2012; Francese et al. 2013). In addition, fluon can be potentially diluted in water, decreasing the total amount needed and the overall costs. For some cerambycid species, traps coated with fluon concentrations of 100%, 50%, and 10% captured similar numbers of insects (Allison et al. 2016). However, A. planipennis traps treated with a 10% fluon concentration captured fewer insects than 50% fluon concentration (Francese et al. 2013).

The cost of fluon, difficulties applying it uniformly to trap surfaces, and safety concerns for those treating traps (i.e., the need for personal protective equipment) has led to other alternatives being tested. Aerosol Teflon- (also polytetrafluoroethylene) and silicone-based treatments of traps have resulted in increased catches of some BBWB over untreated traps (Allison et al. 2011), however silicone treatments did eventually form a "tacky" film on the trap as the season progressed. When compared with fluon-treated versions, aerosol Teflon-treated multiple-funnel and intercept panel traps were equally successful in capturing some BBWB (Allison et al. 2014), suggesting an effective alternative to fluon.

Trap cleaning

Trap surfaces can become coated in dust and pollen while other debris such as spider webs and plant material can clog or reduce trap openings to collection cups potentially reducing BBWB catches (Wilkening et al. 1981; Lindgren 1983). When tested, cleaning traps in the field or replacing field deployed traps with clean traps every maintenance period provided mixed results (Dodds and DiGirolomo 2020). Teflon-treated traps caught more cerambycids than traps that were not treated, but replacing dirty traps with clean traps every 2 weeks did not affect overall catch. However, when traps were left in the field and cleaned every other week, overall mean catch of bark and ambrosia beetles (including individuals captured from three species) and one cerambycid species were significantly higher than in traps that were not cleaned. This cleaning probably provided a more slippery surface reducing the beetles' ability to land on and then take flight from the trap. Regardless of how often traps are cleaned during the season, an argument can be made for cleaning traps between field seasons, as this process should increase the lifespan and efficacy of the traps. Glue-coated surfaces are more susceptible to the detrimental effects of saturation with dust and debris that can reduce trap efficacy. In the USA, A. planipennis guidelines (USDA APHIS PPQ 2023) for prism traps promote the removal of the debrisfilled glue followed by a subsequent re-coating of the surface with glue in order to maintain the "sticky" glue surface. While these references are mostly anecdotal and promote preventative maintenance to avoid problems, there has been a paucity of research to compare the effects of cleaning traps on the traps' abilities to capture and retain beetles.

Trap killing agent

Early traps for BBWB used a variety of killing agents in nonglue-coated flight intercept traps, from isopropanol-filled bottles or cups (Wilkening et al. 1981) to adding a wetting

agent or detergent to a water-filled collection trough or cup (Chapman and Kinghorn 1955; Lindgren 1983; Lindgren et al. 1983). As multiple-funnel trap use expanded, a "dry" trap option that relied on a plastic strip with the insecticide dichlorvos (2,2-dichlorovinyl dimethyl phosphate) to kill trapped insects became available. However, as target taxa broadened, a concern grew that dry traps may be allowing escape of larger more agile insects (e.g., cerambycids and siricids) before the pesticide could act, and that wet traps filled with liquid killing agent would catch more BBWB (e.g., Morewood et al. 2002; de Groot and Nott 2003). Subsequent studies confirmed wet cups were superior to dry cups for many BBWB species (Sweeney et al. 2006; Miller and Duerr 2008). Various collection liquids have been used, including saturated salt solution (Graham and Poland 2012; Lyons et al. 2012; Webster et al. 2012a; Petrice and Haack 2015; Wong et al. 2017; Marchioro et al. 2020) or ethylene glycol (Rassati et al. 2019; Cavaletto et al. 2020, 2021; Marchioro et al. 2020). Propylene glycol (generally RV-style antifreeze with 25-30% propylene glycol) is a common trapping agent and preservative used in North America (Miller and Duerr 2008; Francese et al. 2011; Miller and Crowe 2011; Dodds et al. 2015; among others) and has the added benefit of low toxicity to vertebrates compared to ethylene glycol that is deadly. At times, soap or other additives may be added to the collection liquid to reduce surface tension and/or increase bitterness of the solution, thereby warding off vertebrates that might find the solution appealing to drink or insects palatable to eat.

Most trapping surveys are conducted with insect mortality being a goal. However, there are times when capturing live insects is important. Hanks et al. (2007) used a modified intercept panel trap to collect live cerambycid beetles for volatile collection and identification of sex-aggregation pheromones. Francese et al. (2019) suggested that following the addition of an internal, fluon-coated funnel with a long stem (6.9 cm) that decreased the diameter of the bottom funnel of a multiple-funnel trap from 5.0 to 3.9 cm, the multiple-funnel trap had the potential for use as a live trap. This method was utilized by Gould et al. (2018) to collect native non-target cerambycids for host-specificity testing with potential parasitoids of *Anoplophora glabripennis* (Motschulsky).

Trap color

For some BBWB, trap color is an important consideration when establishing surveys. In early behavioral Y-tube assays, several bark beetle species displayed an affinity for wavelengths in the visible section of the electromagnetic spectrum relating to ultraviolet (426 nm), blue (476 nm), blue/green (500–525 nm), and red (600–625 nm) (Groberman and Borden 1981). However, when Lindgren et al. (1983) incorporated some of these colors (blue, green, red, and clear) into their multiple-funnel trap, black traps caught more beetles. This pattern was further reinforced in subsequent studies (Dubbel et al. 1985; de Groot and Zylstra 1995; Strom and Goyer 2001; Campbell and Borden 2005). Dubbel et al. (1985) suggested that black traps should be used as a standard for the group, and this has been the case for the past 40 years. Interestingly, trapping of European and Canadian scolytines (Marchioro et al. 2020) using purple and green multiple-funnel traps revealed several species that were attracted to traps of these colors, however, no black trap comparison was included in the study. Cavaletto et al. (2020) compared several trap colors against black and found attraction to the novel colors in the species Hylesinus oleiperda (blue and purple) and Scolytus multistriatus (blue and gray). However, these beetles may be outliers and several other species tested were attracted more to black traps. With the exception of yellow and white sticky panel traps catching lower numbers of ambrosia beetles, trap color was mostly unimportant for general surveys of these communities (Werle et al. 2016).

Studies to determine optimal traps for cerambycids relied primarily on variations of black multiple-funnel and intercept panel traps (de Groot and Nott 2001, 2003; McIntosh et al. 2001; Morewood et al. 2002). During these studies, traps would occasionally capture larger buprestid genera (e.g., Chalcophora, Buprestis, Dicerca), but in general this family was much rarer in traps than cerambycids or bark beetles. Studies conducted by Oliver et al. (2002) and later published in Perkovich et al. (2022) showed that purple traps were attractive to Chrysobothris spp., an observation that led to the development of colored traps for A. planipennis (Francese et al. 2005, 2008). Electroretinogram assays demonstrated the ability of A. planipennis to see color in four regions-ultraviolet, blue, green, and red, and when tested in the field, green and purple sticky prism traps outperformed all other colors tested, and green were more attractive than purple (Crook et al. 2009). Colors were later refined based on tests comparing variations in the wavelength and reflectance of the green as well as the red and blue peaks (Francese et al. 2010a, 2010b) and incorporated into commercially available green and purple sticky prism traps and later into double decker traps (Poland et al. 2011) and nonsticky multiple-funnel traps (Francese et al. 2011, 2013). Green multiple-funnel traps and prism traps placed in the canopy caught more beetles (Francese et al. 2011), and with the addition of fluon had higher detection rates in low density areas, than purple prism traps (Crook et al. 2014; Tobin et al. 2021). Additionally, green multiple-funnels, green prism traps, and purple and green and purple double-decker traps exhibited higher catch and detection rates than single purple, canopy prism traps (Tobin et al. 2021). Green traps of varying shades (multiple-funnels, intercept panels and

other trap types) also catch high numbers of other Agrilus species (Domingue et al. 2013; Petrice et al. 2013; Petrice and Haack 2015; Rassati et al. 2019; Cavaletto et al. 2020), with the exception of the goldspotted oak borer, Agrilus auroguttatus Schaeffer (Coleman et al. 2014) and Agrilus viridis (L.) (Rhainds et al. 2017) which preferred purple over green traps. For Chrysobothris and Dicerca species, which do not tend to visit flowers or the tree canopy, the preferred trapping color is purple (Petrice and Haack 2015; Cavaletto et al. 2020; Perkovich et al. 2022, 2023). Within the Cerambycidae, trends tend to follow a similar pattern, that is attraction to yellow, green and blue traps by flower-visiting beetles (usually in the subfamily Lepturinae) and to darker colors (red, brown, black) for beetles that do not visit flowers, usually in the Cerambycinae and Lamiinae (de Groot and Nott 2001; Campbell and Borden 2009; Rassati et al. 2019; Cavaletto et al. 2021; Marchioro et al. 2020). With the incorporation of these colors into traps based on the targets sought, there is a greater chance for successful surveys.

Extrinsic factors

Type of habitat

Site and habitat selection is often predicated by survey objectives. For nonnative BBWB survey traps, the proximity to high-risk environs is the most important consideration. These include coastal ports of entry, inland ports, high density warehouse concentrations, and anywhere large concentrations of freight or solid wood packing material and pallets may be stored (Brockerhoff et al. 2006; Rassati et al. 2015a, 2015b; Meurisse et al. 2019). It also includes forests, parks, or arboreta adjacent to these areas (Rassati et al. 2015a; Rabaglia et al. 2019; DiGirolomo et al. 2022; Mas et al. 2023). The goal of this trap placement is to detect any BBWB that may have arrived in products or packing material subsequently discarded within or adjacent to ports, either as the insects disperse from brood material or early in the establishment phase in the adjacent forests. Selection of which site to trap should be adjusted based on risk of BBWB introduction or known threat of a specific species introduction. Previous studies indicated that ports importing large amounts of commodities and surrounded by broadleafdominated forest patches should be prioritized over small ports or even big ports surrounded by conifer-dominated forests when generally surveying for nonnative BBWB (Rassati et al. 2015b).

Besides proximity to high-risk environs, other factors can affect site selection when targeting native and nonnative BBWB. Many lessons learned from studies estimating arthropod species diversity in forests may be applied to the design of surveys for detection of nonnative species. For example, biodiversity studies using insecticide fogging of tree canopies have shown that beetle species composition can vary significantly among forest habitats (Guilbert 1997), among different tree species (Davies et al. 1997), among trees of the same tree species (Allison et al. 1997), and even between north and south aspects of the same tree (Richardson et al. 1997). Thus, the selection of survey sites and the tree species in or near where traps are placed may significantly affect the number and composition of species detected. Depending on habitat preference and life history traits, stands in poor condition (i.e., overstocked, declining trees) are often targeted for some species that typically colonize stressed trees and behave as secondary species. North American detection efforts for S. noctilio focused on surveying stands that contained host trees under stress (Dodds and de Groot 2012). Alternatively, healthy stands may also be implemented as survey sites, especially when the target insect is a primary tree killer or associated with living hosts, such as A. glabripennis, Xyleborus glabratus (Eichhoff), and Pityophthorus juglandis Blackman (Formby et al. 2012; Nehme et al. 2014; Wiggins et al. 2014; Fraedrich et al. 2015; Marchioro and Faccoli 2021).

Trap proximity to host trees

Since the foraging behavior of BBWB may be influenced by olfactory and visual stimuli from both host- and non-host trees (Bruce et al. 2005), it follows that efficacy of survey traps may be influenced by the tree species in which they are placed, especially for canopy traps. For example, Uly-shen and Hanula (2007) collected more beetles (but not more beetle species) in unbaited flight intercept traps that were placed in sycamore trees, *Platanus occidentalis* L., compared to traps placed in the canopies of *Quercus phellos* L., *Liquidambar styriciflua* L., or *Pinus taeda* L., and mean catch of the citrus longhorn beetle, *Anoplophora chinensis* (Forster), was greater in traps that were placed in the crowns of host trees than in traps hung from wooden poles in openings (Marchioro et al. 2022a).

Host volatile lures that attempt to simulate the blend of volatiles emitted from host trees have proven effective for surveys of *A. planipennis* (Crook et al. 2008) and *Tetropium fuscum* (F.) (Sweeney et al. 2004). However, for BBWB species for which we currently have no effective long distance semiochemical attractants (e.g., most species of Buprestidae) it may be worth considering the tree in which traps are placed as the "host volatile lure". Because the BBWB species assemblages attracted to the vicinity of trees should vary among tree species, it follows that species richness of BBWB in traps should increase when traps are placed in a greater diversity of tree species. However, this is largely hypothetical and is a topic for further research.

Presence of disturbances

Dispersal and host selection in BBWB is understudied for most species. Some species respond positively to disturbance and host presence (Wermelinger et al. 2002; Park and Reid 2007), while others have not shown strong responses (Sanchez-Martinez and Wagner 2002; Gossner et al. 2019). In general, forest disturbances influence wood-inhabiting BBWB in two ways. First, BBWB often respond to damaged, stressed, downed, or dead trees in an area after a disturbance such as tornadoes, straight-line winds, fire, drought, defoliation, pathogens, or silvicultural treatments (Dunbar and Stephens 1975; Muzika et al. 2000; Gandhi et al. 2009; Dodds 2011; Furniss 2014; Kelsey et al. 2014; Sierota and Grodzki 2020; Cours et al. 2022; Miller et al. 2023). Stressed trees and damaged or downed tree material release host volatiles like terpenes and ethanol (Kelsey 2001; Böröczky et al. 2012) that attract insects dispersing and seeking ephemeral reproductive habitat. Sites that have been repeatedly disturbed may have a diversity of downed wood species and decay classes, providing habitat for a larger BBWB community (Økland et al. 1996). The resulting structurally diverse forests also often contain higher species richness of insects than more uniform forests (Storch et al. 2023).

The second way disturbances influence BBWB occurs after colonization of host material when habitat becomes a source of insects that may be captured in detection traps as they disperse away from the habitat (Wichmann and Ravn 2001; Feldhaar and Schauer 2018; Potterf et al. 2019). A potential downside of trapping within disturbed habitats and one cited at times by surveyors is a concern for reduced captures because of competition with reproductive habitat that likely is a stronger source of attraction than a trap. While not studied specifically, this concern does not seem to be warranted. More or equal numbers of insects and species are commonly captured in disturbed habitats compared to controls (Gandhi et al. 2009; Morin et al. 2015; Dodds et al. 2023; Miller et al. 2023).

Crown cover/understory light

While stand disturbance influences local beetle populations, localized crown disturbances resulting in changes to lighting conditions may also influence BBWB at smaller spatial scales. Less is known about this factor as it directly relates to the use of survey traps. However, there is evidence that canopy openness and microhabitat light conditions can influence the broader saproxylic insect community (Bouget and Duelli 2004; Lindhe et al. 2005; Koch Widerberg et al. 2012; Bouget et al. 2013; Seibold et al. 2016; Lettenmaier et al. 2022), suggesting more open conditions could yield better trapping results. Insects are more active in warmer conditions, increasing chances to capture them in traps (Taylor 1963), especially in early spring and late fall. Nonetheless, increased sunlight is not always associated with increased species richness and abundance. For example, ambrosia beetle abundance and species richness has been positively associated with higher canopy coverage estimates (Holuša et al. 2021; Menocal et al. 2022). It is also likely that higher temperatures on traps under more direct sunlight results in increased semiochemical release rates (Nielsen et al. 2019) and potentially a stronger attractive source compared to cooler shaded conditions.

Horizontal and vertical placement

The position of a survey trap relative to its surroundings can significantly affect the community of BBWB captured. Proximity to a forest edge, along either a horizontal- (forest opening-edge-interior) or vertical gradient (understory-mid canopy-upper canopy) can influence climatic variables (temperature, humidity, sunlight, windspeed), plant species diversity and composition, and ultimately resource availability (food, mates, oviposition sites) for herbivorous insects (Murcia 1995; Basset et al. 2003; Lindhe et al. 2005; Vodka et al. 2009; Domingue et al. 2011; Lelito et al. 2011; Ulyshen 2011; Vodka and Cizek 2013; Normann et al. 2016). In a meta-analysis, De Carvalho Guimarães et al. (2014) reported that species richness of insect herbivores was 65% greater along forest edges compared to forest interiors and that the effect was strongest for generalist herbivores in the Lepidoptera and Orthoptera. Significant variation in abundance, species richness, or species composition of beetles (Ulyshen et al. 2004; Wermelinger et al. 2007; Ewers and Didham 2008; Normann et al. 2016) and more specifically BBWB (Igeta et al. 2004; Francese et al. 2008, 2010b; Dodds 2011; Allison et al. 2019; Sweeney et al. 2020) has been observed among traps placed in openings vs. forest edges vs. forest interiors. Similarly, vertical stratification (understory vs. mid- or upper canopy) has been observed for beetles (Sutton et al. 1983; Kato et al. 1995; Preisser et al. 1998; Su and Woods 2001; Hirao et al. 2009; Schroeder et al. 2009; Bouget et al. 2011; Normann et al. 2016; Stork et al. 2016; Weiss et al. 2016) and BBWB in particular (Vance et al. 2003; Igeta et al. 2004; Leksono et al. 2006; Ulyshen and Hanula 2007; Wermelinger et al. 2007; Francese et al. 2008, 2010b; Vodka et al. 2009; Reding et al. 2010; Hanula et al. 2011; Graham et al. 2012; Vodka and Cizek 2013; Dodds 2014; Hardersen et al. 2014; Maguire et al. 2014; Schmeelk et al. 2016; Wong and Hanks 2016; Li et al. 2017; Procházka et al. 2018; Flaherty et al. 2019; Foit et al. 2019; Rassati et al. 2019; Sheehan et al. 2019; Ulyshen and Sheehan 2019; Miller et al. 2020; Sweeney et al. 2020; Meng et al. 2022).

Trends along these gradients vary among and within BBWB families (Ulyshen et al. 2004; Wermelinger et al. 2007; Normann et al. 2016; Allison et al. 2019; Sweeney

et al. 2020) and feeding guilds (Sheehan et al. 2019; Ulyshen and Sheehan 2019). Buprestids were often more abundant and/or species rich in the tree canopy than the understory (Francese et al. 2008, 2010b; Rassati et al. 2019; Sheehan et al. 2019; Sweeney et al. 2020) whereas in Scolytinae there was the opposite trend (Ulyshen and Hanula 2007; Hanula et al. 2011; Dodds 2014; Hardersen et al. 2014; Flaherty et al. 2019; Sheehan et al. 2019; Ulyshen and Sheehan 2019; Meng et al. 2022) or no trend (Wermelinger et al. 2007; Maguire et al. 2014; Meng et al. 2022). Inconsistency in vertical distribution of Scolytinae is partly because the subfamily consists of more than one feeding guild. Species richness of ambrosia beetles tends to decrease with trap height, due to greater humidity and other conditions favoring fungal growth in the understory (Ulyshen 2011) whereas the opposite trend has been observed for phloem/wood feeders (Procházka et al. 2018; Sheehan et al. 2019; Ulyshen and Sheehan 2019). Similar differences in feeding patterns may partially explain why species richness of longhorn beetles is sometimes greater (Ulyshen and Hanula 2007; Maguire et al. 2014; Flaherty et al. 2019; Rassati et al. 2019; Ulyshen and Sheehan 2019; Sweeney et al. 2020; Meng et al. 2022), similar (Vance et al. 2003; Graham et al. 2012; Hardersen et al. 2014; Schmeelk et al. 2016; Wong and Hanks 2016; Flaherty et al. 2019; Meng et al. 2022), or lower (Wermelinger et al. 2007; Dodds 2014) in the canopy than the understory. Species that preferentially breed in large diameter stems, stumps or downed trees are usually more active in the understory (Brar et al. 2012; Procházka et al. 2018; Flaherty et al. 2019; Miller et al. 2020) whereas species that breed in small branches and twigs are more active in the canopy (Vance et al. 2003; Ulyshen and Hanula 2007).

Abundance of all three BBWB families tended to be greater along forest edges or in openings than inside the forest but there were exceptions for individual species of scolytines and cerambycids. For example, catch of Acmaeops proteus proteus (Kirby) was greatest along the forest edge whereas catches of Euderces pini (Fabr.), Neoclytus acuminatus (F.), and Anelaphus pumilus (Newman) were greatest in the forest interior, and catches of Monochamus mutator LeConte and M. scutellatus (Say) were greatest in a clearing (Allison et al. 2019). In studies that simultaneously tested effects of horizontal and vertical trap position, Scolytinae were more abundant in the canopy than the understory in traps placed inside the forest but not along the forest edge (Sweeney et al. 2020) and BBWB species composition differed between mid- and upper canopy traps inside the forest but not at the forest edge (Sheehan et al. 2019). Effects of trap height on catch of buprestids (Wermelinger et al. 2007) and other saproxylic beetles (Vodka and Cizek 2013) were less pronounced or absent when traps were placed along a forest edge vs. the forest interior, suggesting that degree of sun exposure is associated with vertical stratification of some species.

The effects of horizontal or vertical trap placement is often context dependent, varying among forest types (Procházka et al. 2018; Meng et al. 2022), silvicultural treatments (Su and Woods 2001), size and age of forest clearings (Ulyshen et al. 2004; Allison et al. 2019; Sweeney et al. 2020), seasons (Hardersen et al. 2014), degree of slope (Sutton et al. 1983), dominant tree species (Vance et al. 2003), and the semiochemical lure used to bait traps (Flaherty et al. 2019). Depending on the attraction range of an attractant, baited traps may reduce the effects of horizontal and vertical placement on catch of certain species (Ulyshen and Sheehan 2019). In spite of inconsistency in trends of species richness or abundance of BBWB along horizontal or vertical gradients, most studies have shown that species composition differs between strata, and that many species are captured solely or predominantly in the canopy or understory, edge or interior (Vance et al. 2003; Leksono et al. 2006; Wermelinger et al. 2007; Vodka et al. 2009; Graham et al. 2012; Dodds 2014; Hardersen et al. 2014; Schmeelk et al. 2016; Webster et al. 2016; Wong and Hanks 2016; Procházka et al. 2018; Flaherty et al. 2019; Ulyshen and Sheehan 2019; Miller et al. 2020; Sweeney et al. 2020; Meng et al. 2022). Therefore, when the objective is to detect as many species as possible of BBWB present at a site, traps should ideally be deployed in both the canopy and understory, and along forest edges as well as inside the forest.

BBWB species composition in mid-canopy traps has reflected that in both canopy and understory traps suggesting it may be a good compromise when budgets or logistical limitations make it impractical to sample at more than one trap height (Weiss et al. 2016; Procházka et al. 2018; Ulyshen and Sheehan 2019). However, Sheehan et al. (2019) suggested that traps deployed at an intermediate height of 5 m would fail to detect certain species active in the upper canopy.

Using knowledge on factors affecting trap efficacy to improve surveillance programs

As described above, many factors influence BBWB behavior and response to semiochemical-baited traps. It is often difficult to address all factors when deploying traps due to budget constraints and logistical realities. However, there are several considerations to be mindful of when developing surveys that can help improve results. First, there is rarely a perfect survey, but a sub-optimal trap deployed in only one vertical or horizontal strata is better than no survey at a location. Placing traps in almost any location is informative but placing traps in more than one vertical or horizontal strata (e.g., canopy and understory, forest edge and interior) often increases the number of BBWB species detected and is recommended if budgets allow. Second, baiting traps with multiple pheromones can increase the number of species detected with little or no negative effect on catch of other BBWB, an approach that is especially useful for generic surveillance. Third, using more than one trap color, e.g., green or purple traps, as well as black traps, can increase detection efficacy of longhorn beetles and jewel beetles. Treating these traps with a lubricant and conducting regular maintenance and cleaning can help improve trap efficacy. Finally, simply increasing the number of traps per site and using multiple trap types usually increases the numbers of BBWB species detected. In general, our review has found that, for generic surveys, the greater the diversity in trapping methods used (e.g., more than one type of lure blend, trap height, trap color) the more BBWB species are detected and the greater the chances of detecting nonnative species that may be present. However, with limited budgets these considerations must be weighed against the number of sites that can be surveyed per year. One way in which increased costs of diversifying trapping methods may be offset is by using a different suite of lure blends, trap colors, etc. in alternating years, as done by the Canadian Food Inspection Agency for nonnative BBWB surveillance (Thurston et al. 2022). For surveillance of individual target species during a specific survey, trap type, lure, color, height, etc. should follow established protocols that have proven most efficacious in terms of mean catch or detecting the species at sites with low population densities. If no protocols exist, using methodology developed for closely related insects in the same genus or family is an appropriate starting point.

A practical example of how to use these considerations and the available knowledge can be illustrated by two case studies (Fig. 3). For a generic survey for nonnative BBWB (Fig. 3A), efforts should concentrate on coastal or inland ports and surrounding forests with traps deployed across available sites (Rassati et al. 2015a, b). The number of traps strongly depends on the budget, but even a low number of traps can lead to important results (Mas et al. 2023). In forested areas adjacent to ports, black intercept panel traps set up in the understory should be coupled with green multiple funnel traps set up in the canopy to increase likelihood of intercepting jewel beetles as well as other BBWB species active in the latter forest stratum (Rassati et al. 2019; Marchioro et al. 2020). Ideally, traps should be placed in the interior of the forested area and along the edge to account for different BBWB foraging preferences of species that may be present (Ulyshen et al. 2004; Wermelinger et al. 2007; Allison et al. 2019; Sweeney et al. 2020). The same trap combination (i.e., black intercept and green multi-funnel traps) should be attached to available supports at a height of 1.5-2 m in areas of the active port where timber is stored before being sent to the destination, or where containers are opened for visual inspections (Rassati et al. 2014). Traps within the port environs and in adjacent forested areas should be baited with a multi-lure blend composed of pheromones and kairomones that are known to attract a wide array of taxa without affecting catches of jewel beetles (e.g., Roques et al. 2023). When budget permits, black intercept traps should be coupled with traps of different colors, for example yellow or blue, to also attract longhorned beetle species that are not attracted by semiochemicals used in the survey (e.g., Lepturinae). All traps should be treated with fluon or other lubricants (Allison et al. 2011; Graham and Poland 2012) and the collector cup should be filled with propylene glycol or other liquids rather than left dry with an insecticide (Allison and Redak 2017).

As an example of a specific surveillance program, native and non-native Monochamus spp. pose a serious risk in some areas because they vector the destructive pine wood nematode [Bursaphelenchus xylophilus (Steiner & Bührer) Nickle] (Mamiya 1988). A surveillance program targeting Monochamus spp. should also be concentrated in ports and surrounding forested areas (Fig. 3B). Black intercept panel traps are optimal for *Monochamus* spp. and should be baited with a blend of pheromones and kairomones that are efficient for several species in the genus (Allison et al. 2012; Miller et al. 2016; Boone et al. 2019; Foit et al. 2019). There may be some benefit of having traps in tree canopies when available (Foit et al. 2019), but Monochamus spp. have also been frequently captured in understory traps (de Groot and Nott 2004; Dodds 2014; Allison et al. 2019). Traps should be treated with a lubricant, such as fluon (Jaworski et al. 2022; Dong et al. 2023), and a wet collection cup should be used with propylene glycol as the liquid preservative (Allison and Redak 2017). Possibly, traps should be set up both on the forest edge and in the forest interior as different Monochamus spp. prefer either the former or latter habitat (Allison et al. 2019), and any areas of recent disturbance may also help improve trapping results (Dodds 2011; Dodds et al. 2019).

Concluding remarks and future research

Despite the large amount of existing research, our understanding of factors affecting the efficacy of BBWB surveys is still incomplete. Additional studies are necessary to further understand species-specific responses and to elucidate whether general patterns can be described. In addition, while there has been much research on the effects of trap types, lures, colors, etc., on the relative abundance of BBWB captured in traps, there are very few papers that describe the relationship between trap catch and actual population or attack density of the target BBWB species (but see Hanula et al. 2011). Greater understanding of these relationships

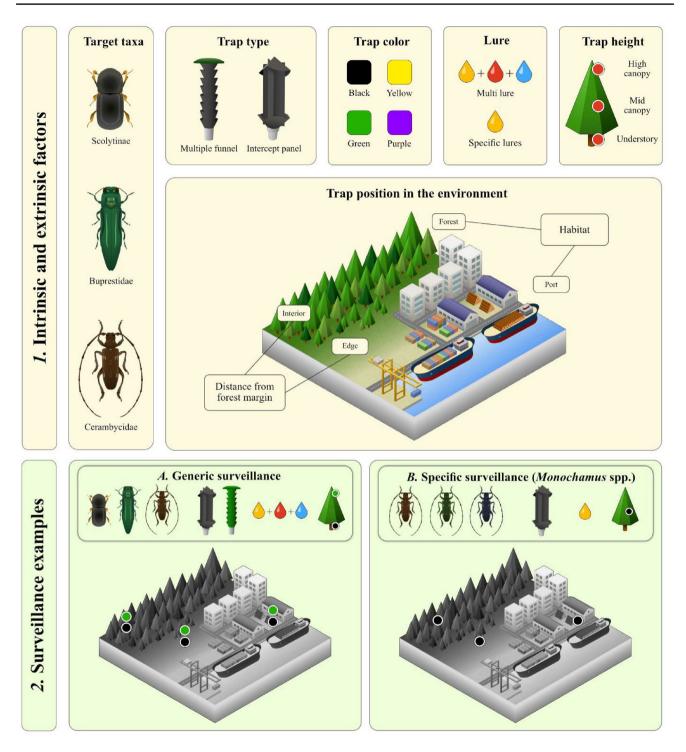


Fig. 3 Example of how to exploit available knowledge on intrinsic and extrinsic factors affecting trap efficacy in surveillance programs. Here we use as case studies a generic surveillance targeting bark and ambrosia beetles, longhorn beetles and jewel beetles (\mathbf{A}) and a specific surveillance targeting longhorn beetles of the genus *Monocha*-

mus (**B**) carried out in a port area and its surrounding natural area (e.g., a forest). For each of them, information on the best trap type, trap color, lure (multi-lure blend vs. specific lure), trap height, and horizontal position of the traps are provided. Black or green dots on the black and white landscapes represent the traps

will improve our interpretation of trap catches in determining risk and monitoring spread of invasive BBWB, especially during specific surveys. Furthermore, a rapid increase in cerambycid pheromone chemistry knowledge over the last 2 decades has greatly increased our ability to detect many of these species in surveys (Hanks and Millar 2016; Roques et al. 2023). New information on the role of fungal volatiles (Hulcr et al. 2011; Kuhns et al. 2014) for attracting some ambrosia beetles offers opportunities to narrow survey efforts for these species. Unfortunately, knowledge of buprestid pheromones and attractive semiochemicals is much more limited at this time (Silk et al. 2019). Further research in this area may lead to improved lures and greater detection efficacy of Buprestidae. Lastly, innovative technologies to reproduce the most attractive visual cues on trap panels [e.g., the microstructures present on elytra of jewel beetles which are responsible for the light scattering effect used to locate mates (Domingue et al. 2014)] can strongly improve trap attractiveness, especially toward species for which pheromones are not yet known.

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Declarations

Conflict of interest The authors declare no financial or non-financial conflict of interests.

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