

Review Article

Semiochemical Diversity in Practice: Anti-attractant Semiochemicals Reduce Bark Beetle Attacks on Standing Trees—A First Meta-Analysis

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Reduction of tree mortality caused by bark beetle attacks is not only important for forestry, but also essential for the preservation of biodiversity and forest carbon sinks in the face of climate change. While bark beetle mass trapping (a “pull” approach) is implemented in practice, few studies exist to estimate its effect. The more complex “push-pull” tactic has, in contrast, been repeatedly tested during the last decade. I analysed published data from 32 experiments in 9 papers published during 2000–2011 on *Ips typographus* and *Dendroctonus ponderosae*, to test if there was an overall effect of anti-attractant semiochemicals, that is, if treatments reduced the number of attacks on standing trees at the habitat or stand scale. This meta-analysis showed a substantial overall effect size (treatment-control means divided by their SD) of -0.96 , with some heterogeneity but little evidence of publication bias. There was no effect of beetle species or publication year. Heterogeneity resulted from different designs and beetle population levels (as year of study). The conventional “% Reduction” measure correlated well with effect size ($r^2 = 0.7$). Recommendations include more precise reporting of responses (avoiding dichotomous data), more unified experimental designs, and further meta-analyses that include “grey literature” and more beetle species.

1. Introduction

Strategies to reduce tree mortality caused by bark beetle attacks [1–5] are becoming urgent, not only for forest industry, but also for preservation of forest cover and forest carbon sinks in the face of climate change [6–9]. There is a need for quantitative reviews of management alternatives such as mass-trapping and push-pull [10]. While bark beetle mass trapping (a “pull” tactic) is partly implemented in practice, few replicated studies exist to estimate the efficacy of this approach [1–4]. The more complex “push-pull” (as defined by Cook et al. [11]) and “push” (as defined by Gillette and Munson [12]) tactics have, in contrast, been experimentally tested and reported in >10 papers in the last decade, so a review effort on the subject seems to be timely.

I chose the quantitative method of meta-analysis that uses the descriptive data obtained (means, standard deviations, sample sizes), rather than relying on the P values

and other analytical statistics which are heavily dependent on sample size when declaring an experiment “significant” or not. Meta-analysis is the method of choice for estimating interventions in complex systems such as clinical medicine, social work, and education [13–16], but also in resolving complex ecological issues [17–20], though less often in applied ecology [10, 21]. In principle, a meta-analysis describes the effect of a treatment among controlled experimental studies by analysing the distribution of effect sizes of the relevant studies [10, 22, 23]. The effect size measure in simple terms is the difference between control and treatment, gauged by the size of their standard deviations, which provides a common scale for the magnitude of effects for the experiments performed [24, 25]. A common “currency” such as the effect size is mandatory for any comparisons between experiments of different designs, sample sizes, and so forth, as measures dependent on sample size like P values cannot

be used. Effect sizes can be calculated in several ways; I use the simplest possible often referred to as Cohen's d [24]:

$$d = \frac{\text{Mean}_{\text{Control}} - \text{Mean}_{\text{Treatment}}}{\text{SD}_{\text{Pooled}}}, \quad (1)$$

where d above is (1) in [24] and $\text{SD}_{\text{Pooled}}$ is (2) in [24] which takes in account different sample sizes for control and treatment samples.

This meta-analytical review is limited to studies of standing trees at the plot or stand scale, with just two of the recently best studied bark beetle species, *Ips typographus* and *Dendroctonus ponderosae*, and published from 2000 and onwards in readily available international journals (thus excluding government reports, trade journals, and other so called "grey literature"). I keep to (1) only newer studies in order to concentrate on the latest development of semiochemicals representing "state of the art" and (2) stand or plot level tests, because they are the only type likely to give information for future practical applications. Tree scale experiments are nowadays essentially a thing of the past and do not provide essential information for forest management. The intended coverage of the literature is not the most comprehensive possible, but is clearly stated and thus open to future challenges.

In this first meta-analysis I hope to address the key question of whether there is any overall effect in reducing or stopping bark beetle attacks on standing trees by antiattractants. Distribution of effect sizes will be scrutinised for evidence of publication bias and heterogeneity. The latter will be studied for meaningful variation among results that may shed light on factors giving low or high effects of semiochemical interventions against beetle attacks.

The intended audience for this paper is not primarily those familiar with the workings of meta-analysis and its application to yet another field, but the colleagues involved in designing and performing field experiments with antiattractants against bark beetle attack on the stand or habitat scale and the forest managers interested in application of such tactics in forestry.

2. Materials and Methods

I have tried to adhere to the standards suggested by PRISMA and Cochrane collaborations [13, 15, 25–28], while acknowledging that these standards are primarily oriented to well-controlled clinical or laboratory studies. The somewhat less rigorous standards of ecological meta-analysis [10, 18, 19] must be used here, in particular to arrive at a sufficient number of experiments to allowing meaningful number for plots and tests for publication bias and sensitivity analysis [29, 30].

Studies were searched using references in published papers, including a review-like paper in the "grey literature" by Gillette and Munson 2009 [12], and "back-tracking" from these by consulting papers citing these first known papers in Google Scholar. This "centrifugal" multidimensional strategy was iterated by expanding to citing papers, and so forth, until no new relevant papers were discovered.

In some cases reports in noninternational sources were difficult to locate and in addition were sometimes partly overlapping with papers later published in international journals. Therefore, I choose to eliminate any studies that were not published in international journals.

A vast majority of recent papers located concerned either the mountain pine beetle of North America, *Dendroctonus ponderosae*, mostly on ponderosa and lodgepole pine (*Pinus ponderosae*, *P. contorta*) or the European spruce engraver, *Ips typographus*, on Norway spruce (*Picea abies*). Thus, I decided to concentrate only on these two species, while ignoring the earlier published works on the Southern pine beetle (*D. frontalis*) and the Western pine beetle (*D. frontalis*) and a few other spp with one paper each, in order to limit the overall size and heterogeneity of the material.

Numerical data sets were extracted from papers of various designs, by means and SD or frequencies when provided but sometimes from raw or nearly raw data depending on the presentation and were further summarised in MS Excel to avoid pseudoreplication [31–33]. Care was taken to ascertain the true number of replicates but to allow the different data sets to represent cases depending on variation in design, treatment, or time periods (season, year). In bark beetle population dynamics the variation over time and space is overwhelming and I could conclude after reading the experimental papers that multiple experimental outcomes (data points) are in most studies not autocorrelated. I did my best to avoid autocorrelated data, like from time series within a year as in Jakuš et al. [34] by using it as only one data point, or avoided pseudoreplications within experiments by pooling of data [35, 36].

Further analysis and plotting were done by SPSS 19 software package using command syntax (command files available on request) following suggested algorithms [23, 37, 38]. For a meta-analysis, an effect size for each study or experiment must be extracted from the central and secondary moments (means and a measure of variance, respectively) of the distributions of the treatment and control data (details on the data available are given in Table 1). Depending on the reporting and study design, data were often continuous (trees killed or attacked per plot or area, attack density etc.) allowing simple extraction of means and SDs [24, 25], but are sometime dichotomous (data from outcomes that can be divided into two categories), given as total trees killed/attacked versus alive/unattacked per treatment and experiment [39, 40]. In the latter case, a simple transformation of the ln (odds ratio) to Cohen's d is possible by $d = \ln(\text{OR})/(\pi/\sqrt{3})$ [41] which then allows a comparison of studies with both types of data. This transformation made it possible to use the Cohen's d also for the dichotomous data.

A random effect model was used, as there was no reason to assume that all studies were functionally identical, as in a fixed model where only a single effect plus error is estimated [38]. Instead the random model includes also variation due to heterogeneity, like different species and phases of the population dynamics were likely to influence results [37, 38] which lowers the magnitude of the estimated overall effect size (θ) and widens its associated confidence interval. Bootstrap re-sampling was not used.

TABLE 1: Input data for meta-analysis with basic effect size and standard error estimates and weights for individual studies.

Expt nr	Author	Year Publ	Year Expt	Location ¹	Beetle species	Treatment ²	Measure	Dichotomous	n Ctrl	Effect size (Cohen's <i>d</i>)	Standard error of <i>d</i>	Inverse SE	Z score of <i>d</i>	Standardised residual of <i>d</i>	Weighted <i>d</i> (by Inv. SE)	% Reduction
1	Borden	2006	03	BC	<i>D. ponderosae</i>	Vn 100 u/ha	% mass att.		10	-3.30	0.73	1.38	-2.80	-3.17	-4.54	85%
2	Borden	2006	03	BC	<i>D. ponderosae</i>	Vn + NHV 100 u/ha	% mass att.		10	-2.90	0.68	1.48	-2.30	-2.80	-4.28	83%
3	Jakuš	2011	08	SK	<i>I. typographus</i>	Vn + NHV	Freq tree kill		5	-1.81	0.85	1.17	-0.99	-0.96	-2.13	73%
4	Borden	2006	03	BC	<i>D. ponderosae</i>	NHV 100 u/ha	% mass att.		10	-1.79	0.56	1.79	-0.96	-1.41	-3.20	59%
5	Progar	2005	02	ID	<i>D. ponderosae</i>	Vn	% kill/Suit.		7	-1.68	0.68	1.48	-0.83	-1.01	-2.49	71%
6	Borden	2007	05	BC	<i>D. ponderosae</i>	Vn + tree rem.	Sum trees	Yes	4	-1.59	0.11	9.33	-0.72	-5.50	-14.82	85%
7	Progar	2005	00	ID	<i>D. ponderosae</i>	Vn	% kill/Suit.		7	-1.54	0.66	1.51	-0.66	-0.82	-2.33	83%
8	Jakuš	2003	00	PL	<i>I. typographus</i>	Šumava01	Sum trees	Yes		-1.45	0.81	1.23	-0.55	-0.55	-1.78	92%
9	Bentz	2005	01-03	ID, MT	<i>D. ponderosae</i>	Vn "High"	Att. trees/plot		38	-1.35	0.26	3.88	-0.43	-1.36	-5.24	78%
10	Progar	2005	01	ID	<i>D. ponderosae</i>	Vn	% kill/Suit.		7	-1.35	0.64	1.55	-0.42	-0.54	-2.09	68%
11	Gillette	2009	05	CA	<i>D. ponderosae</i>	Vn arial appl.	Att. trees/ha		5	-1.27	0.76	1.27	-0.33	-0.34	-1.61	69%
12	Jakuš	2003	01	CZ	<i>I. typographus</i>	Šumava03	Sum trees	Yes		-1.16	0.28	3.63	-0.19	-0.58	-4.20	84%
13	Jakuš	2003	00	CZ	<i>I. typographus</i>	Šumava02	Sum trees	Yes		-1.02	0.60	1.66	-0.02	-0.03	-1.69	83%
14	Borden	2003	01	BC	<i>D. ponderosae</i>	High Vn	Att. trees/plot		10	-0.94	0.50	2.01	0.07	0.12	-1.89	57%
15	Gillette	2009	05	ID	<i>D. ponderosae</i>	Vn arial appl.	Att. trees/ha		5	-0.94	0.76	1.32	0.07	0.08	-1.24	65%
16	Borden	2006	03	BC	<i>D. ponderosae</i>	Vn + NHV 400 u/ha	Freq tree kill		10	-0.93	0.50	2.01	0.09	0.15	-1.86	59%
17	Schiebe	2011	06	SK	<i>I. typographus</i>	Vn + NHV × 4	Prop tree kill		9	-0.88	0.67	1.50	0.14	0.18	-1.32	56%
18	Borden	2006	03	BC	<i>D. ponderosae</i>	Vn + NHV 100 u/ha	Freq tree kill		10	-0.87	0.49	2.02	0.15	0.25	-1.77	51%
19	Borden	2006	03	BC	<i>D. ponderosae</i>	Vn + NHV 178 u/ha	Freq tree kill		10	-0.85	0.49	2.03	0.18	0.30	-1.73	55%
20	Schiebe	2011	07	SK	<i>I. typographus</i>	Vn + NHV × 2	Prop tree kill		9	-0.82	0.66	1.51	0.22	0.28	-1.23	49%
21	Schiebe	2011	07	SK	<i>I. typographus</i>	Vn + NHV × 4	Prop tree kill		9	-0.76	0.66	1.51	0.29	0.36	-1.15	63%
22	Borden	2007	05	BC	<i>D. ponderosae</i>	Vn	Sum trees	Yes	3	-0.66	0.13	7.52	0.41	2.54	-4.96	55%
23	Jakuš	2003	00	CZ	<i>I. typographus</i>	Šumava01	Sum trees	Yes		-0.65	0.17	5.94	0.42	2.07	-3.86	52%
24	Schiebe	2011	06	SK	<i>I. typographus</i>	Vn + NHV × 1	Prop tree kill		9	-0.63	0.65	1.53	0.45	0.56	-0.97	34%
25	Borden	2003	01	BC	<i>D. ponderosae</i>	High Vn + NHV	Att. trees/plot		10	-0.44	0.48	2.09	0.68	1.16	-0.92	23%
26	Borden	2003	01	BC	<i>D. ponderosae</i>	Low Vn	Att. trees/plot		10	-0.40	0.48	2.09	0.72	1.25	-0.84	23%
27	Borden	2006	03	BC	<i>D. ponderosae</i>	Vn + NHV 114 u/ha	Freq mass att.		10	-0.39	0.48	2.10	0.74	1.27	-0.82	38%
28	Schiebe	2011	06	SK	<i>I. typographus</i>	Vn + NHV × 2	Prop tree kill		9	-0.32	0.64	1.56	0.82	1.05	-0.50	40%
29	Schiebe	2011	07	SK	<i>I. typographus</i>	Vn + NHV × 1	Prop tree kill		9	-0.27	0.64	1.56	0.88	1.13	-0.43	47%
30	Borden	2003	01	BC	<i>D. ponderosae</i>	Low Vn + NHV	Att. trees/plot		10	-0.27	0.47	2.11	0.89	1.53	-0.57	18%
31	Progar	2005	04	ID	<i>D. ponderosae</i>	Vn	% kill/Suit.		7	0.02	0.58	1.72	1.23	1.74	0.03	-2%
32	Progar	2005	03	ID	<i>D. ponderosae</i>	Vn	% kill/Suit.		7	1.26	0.64	1.57	2.74	3.55	1.97	-396%

¹ BC: British Columbia, Canada, SK: Slovak Republic, ID: Idaho, USA, MT: Montana, USA, CA: California, USA, CZ: Czech Republic.
² Vn: verbenone, NHV: nonhost volatiles (combination of green leaf volatiles and bark compounds), Šumava01-Šumava03: dispensers with Vn + NHV.

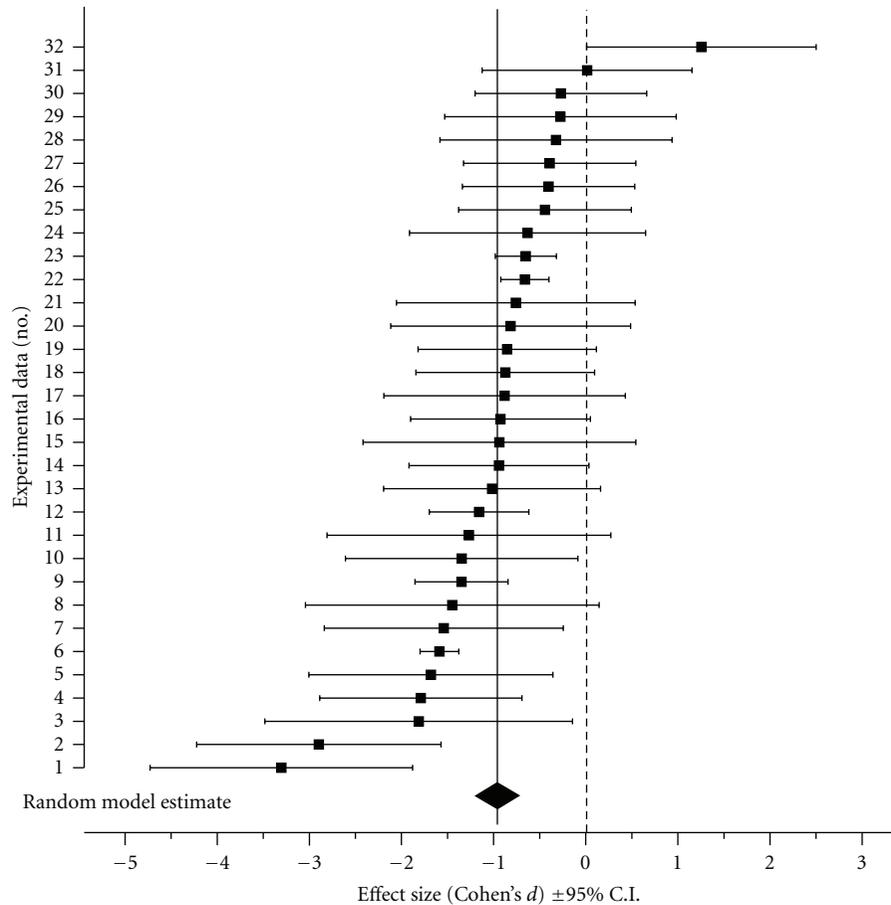


FIGURE 1: Ordered plot of individual study effect sizes and their $\pm 95\%$ confidence intervals; known as a “forest plot”. Vertical lines: — estimated overall effect size (θ), - - effect size = 0 or no effect. The “diamond” on last row shows the midpoint and width of the 95% CI of grand mean effect size by its location and width, based on a random model estimate [37, 38]. Numbers on the dependent axis correspond to the “Expt nr” in Table 1.

Heterogeneity in recorded effect size distributions may stem from several sources, including true biological variation as well as variation in study designs. Overall for the meta-analysis I followed the results and recommendations of Bax et al. [29] for use of more readily understandable plots for the applied ecologist in the assessment of reporting bias and heterogeneity, rather than the more arcane statistics of Q_T , I^2 , τ^2 , and so forth, [13, 22, 30, 42, 43]. Sensitivity plots and subgroup analysis as well as attempts of meta-regression, based on data of different quality, origin, and treatment levels, respectively, were included to explore heterogeneity and deviations from normality [13].

An important consideration for any review is the “file drawer problem” where a publication bias usually exists against the publication of negative outcomes with low effects. A notable exception is the combination of failures and successes by Jakuš et al. [40]. The subject of this paper, in particular may suffer from this problem, as applied experiments with unclear or negative results may often either not be submitted for publication (stays in the file drawer) or get hidden in the “grey literature” of various internal reports,

trade journals, and so forth. Fortunately, there exists graphical tools such as “funnel plots” to aid in detection of such publication biases [29].

3. Results

3.1. Effect Sizes. The analysis included 32 data points from 9 papers [35, 36, 39, 40, 44–48], where several papers reported experiments from different years or seasons and/or different semiochemical blends [36, 40, 47, 48] which were considered independent studies (Table 1). Overall, the effect sizes fell below zero, meaning that there was a lower density or number of attacks on trees in the treated plots, with only one exception (Figure 1). The effect size confidence intervals for individual studies, however, included zero for all but 12 cases (Figure 1). The overall estimate of effect was $\theta = -0.96 \pm 0.25$ (the midpoint and \pm the 95% CI of grand mean effect size based on a random model, $SE\{\theta\} = 0.126$). There was a narrow confidence interval for the grand mean compared to those of the individual studies (Figure 1, lowest point, “diamond”). The effect sizes followed in general a smooth

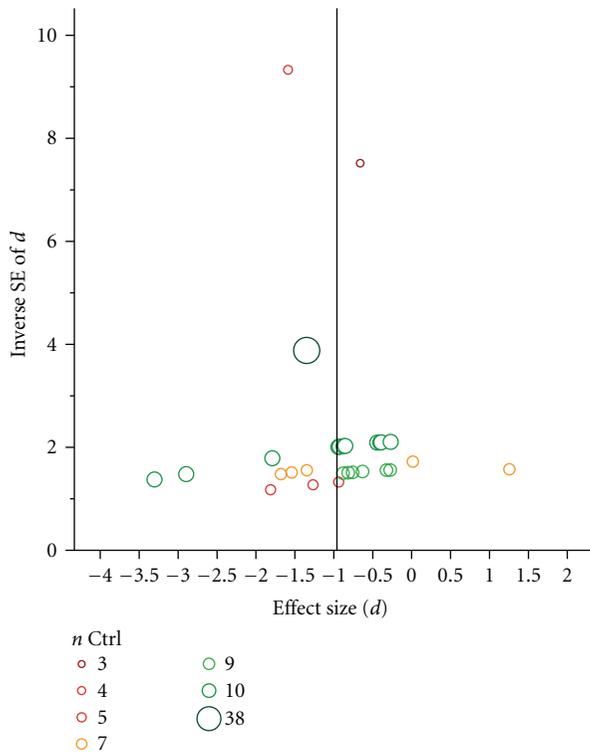


FIGURE 2: Funnel plot for dissemination or publication bias detection. — estimated overall mean effect size. Points distributed symmetrically around the mean effect size indicate little evidence of dissemination bias [29].

progression when ordered after size from low to high, while one study stood out with a reversed ($d > 0$) effect and two with large values ($|d| > 2$) (Figure 1).

3.2. Sensitivity Analysis

3.2.1. Publication Bias. This kind of field research, with highly variable forest conditions and bark beetle populations, and many factors outside the control of authors, might result in “failed studies” (negative or unclear results) that tend to remain unreported. An example to the contrary is the study of Jakuš et al. [40], reporting a string of “failures” before successes. Unfortunately, several of these “failures” could not be included here because they incorporated felled trees or logs, or did not provide sufficient details for estimation of d values. Still, the “funnel plot” (Figure 2) is reasonably symmetrical. If a strong bias existed against publication of unsuccessful studies, this plot would give very few points to the right of the mean d estimate of ≈ -1 and no points at or above $d = 0$. Interestingly, “good” studies with high n values or high inverse SE_d values do not have a clear bias to the left of $d \approx -1$, but have a rather symmetrical distribution (Figure 2).

There was no effect whatsoever of publication year on effect size ($R^2 = 0.002$).

3.2.2. Heterogeneity. The plots in Figure 3 indicate an overall moderate heterogeneity [29]. In Figure 3(a), the box plot of d values weighted by their inverse SE, there is one extreme value (from [39]) and one outlier (from [47]). The median d (middle line of box) falls lower than the mean d . The histogram of standardized residuals, Figure 3(b), shows no clear deviations from the normal distribution overlay (indicating a normal sample distribution) or any clumping of values indicating possible subpopulations (indicating little heterogeneity in the sample). Similarly, the normal quantile plots indicate a normal distribution (points close to a straight line) and little heterogeneity (no clustering of points).

Similarly, there was no variation between the effect sizes based on studies providing continuous data ($n = 26$) or dichotomous data ($n = 6$) in effect of antiattractants (continuous data d , mean \pm SE [median] = -0.98 ± 0.18 [-0.88], dichotomous ditto = -1.09 ± 0.16 [-1.09]; $F_{1,31} = 0.08$, $P \gg 10\%$).

3.3. Subgroup Analysis. There was little variation between the two species in overall effect of antiattractants (*Ips* mean \pm SE [median] = -0.89 ± 0.14 (-0.82), *Dendroctonus* ditto = -1.06 ± 0.21 [-0.94]; $F_{1,31} = 0.3$, $P \gg 10\%$).

From a practical point it would be of considerable interest to know if verbenone alone is as efficient as a blend of verbenone combined with sometimes more expensive non-host volatiles (NHV); however, the studies are not balanced in this respect. All *Ips* studies included an NHV blend plus verbenone, as the combination is known to be clearly needed [5, 40], but for *Dendroctonus* only one study included an NHV blend [36].

3.4. Meta-Regression

3.4.1. Year of Study. There was a relatively strong effect of year since the start of study (ANOVA, full corrected model: $F_{6,9} = 11.0$, $P = 3.8\%$, $\eta^2 = 0.96$) which most likely corresponds to an effect of beetle population variation between years (factor year-of-experiment: $F_{4,9} = 16.0$, $P = 2.3\%$, $\eta^2 = 0.96$). However, there was also some variation due to factor species ($F_{1,9} = 5.4$, $P = 10.2\%$, $\eta^2 = 0.64$) but there was no interaction due to year-of-experiment \times species ($F_{1,9} = 0.1$, $P \gg 10\%$, $\eta^2 = 0.24$).

3.4.2. Comparison to the Conventional “% Reduction” Measure. The conventional measure of inhibitory effect, “% Reduction”:

$$\% \text{ Reduction} = \frac{\text{Attacks (kills) in control group} - \text{Attacks (kills) in treatment group}}{\text{Attacks (kills) in control group} \cdot 100} \quad (2)$$

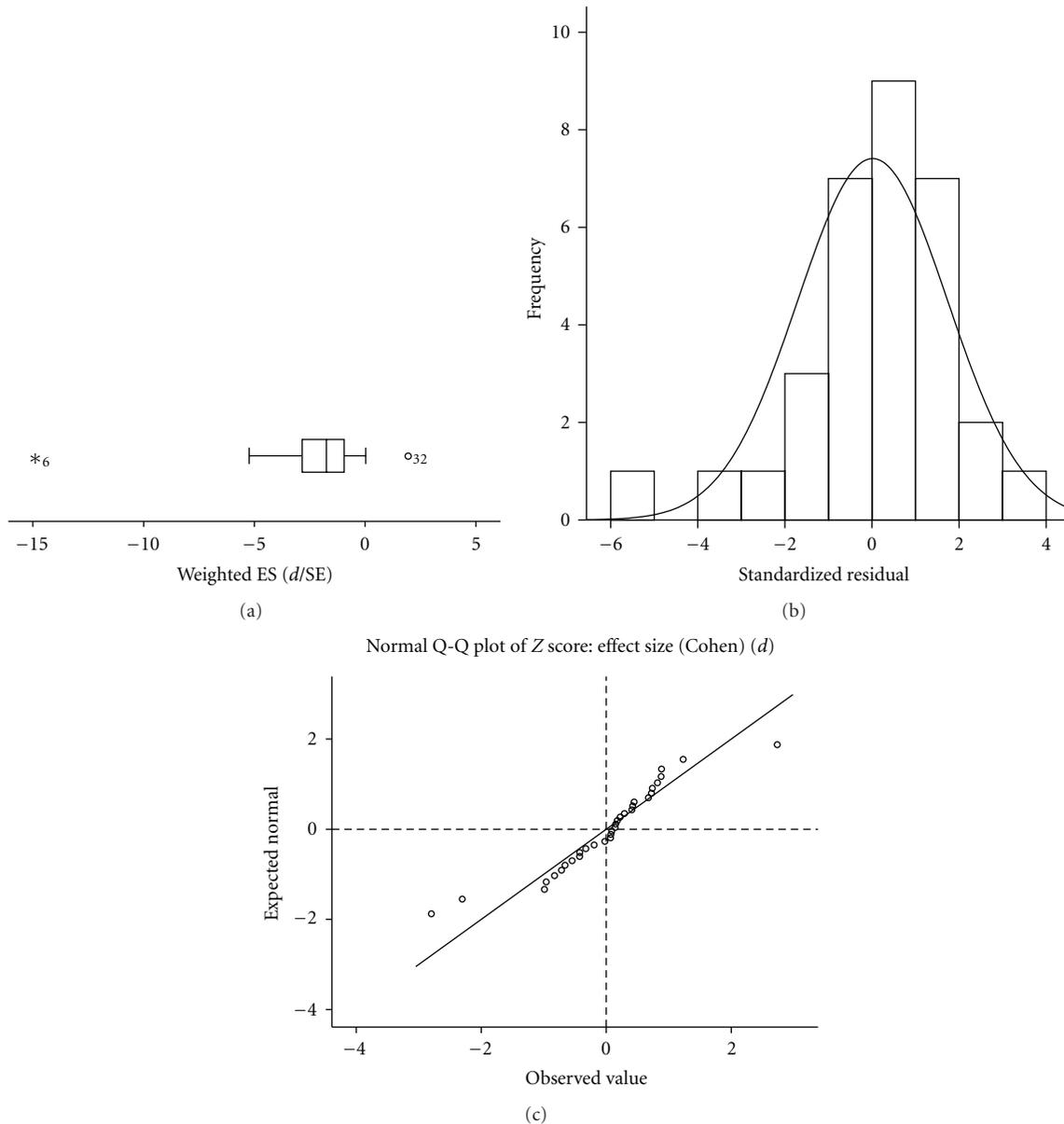


FIGURE 3: Plots to check normality and heterogeneity of effect size in the whole data set ($n = 32$) [29]. (a) Weighted box plot (data points used weighted by division of SE, vertical line is median, box enclose 50% of observations, whiskers 2 SD or 95% of observations, “o” are outliers not enclosed by whiskers, and “*” extremes), where asymmetry indicates heterogeneity and deviations from normality. Numbers near points correspond to the “Expt nr” in Table 1. (b) Histogram of residuals (data-grand mean)/SD allowing check of normality. (c) Normal Quantile Plot of Z-scores (normalised data by subtraction of mean and division by SD), allowing check of normality and of outliers contributing to heterogeneity.

is used in papers on reduction of trap catches, attack densities, or tree kills and is common in applied entomology. However, the stated “% reduction” probably has a wide SE (as it includes the subtraction of two variables both estimated with uncertainty, and then divided by one of them), but I have seen no attempts to quantify this uncertainty. Thus, there is a strong incentive to get a relation to the effect size and its well-defined uncertainty. “% Reduction” was regressed upon effect size and corresponded, as expected,

overall rather well ($R^2 = 0.68$) with effect size (Figure 4(a)), but only when omitting the three points that were >2 SDs away from the mean (the three deviates from line in Figure 3(c)). There was little variation between the slopes or the strength of correlation (R^2) based on studies providing continuous data or dichotomous data (Figure 4(a)). The *Ips* data points, which had a smaller spread along the independent axis (x -axis), had a weaker correspondence ($R^2 = 0.58$) than those for *Dendroctonus* ($R^2 = 0.79$) (Figure 4(b)).

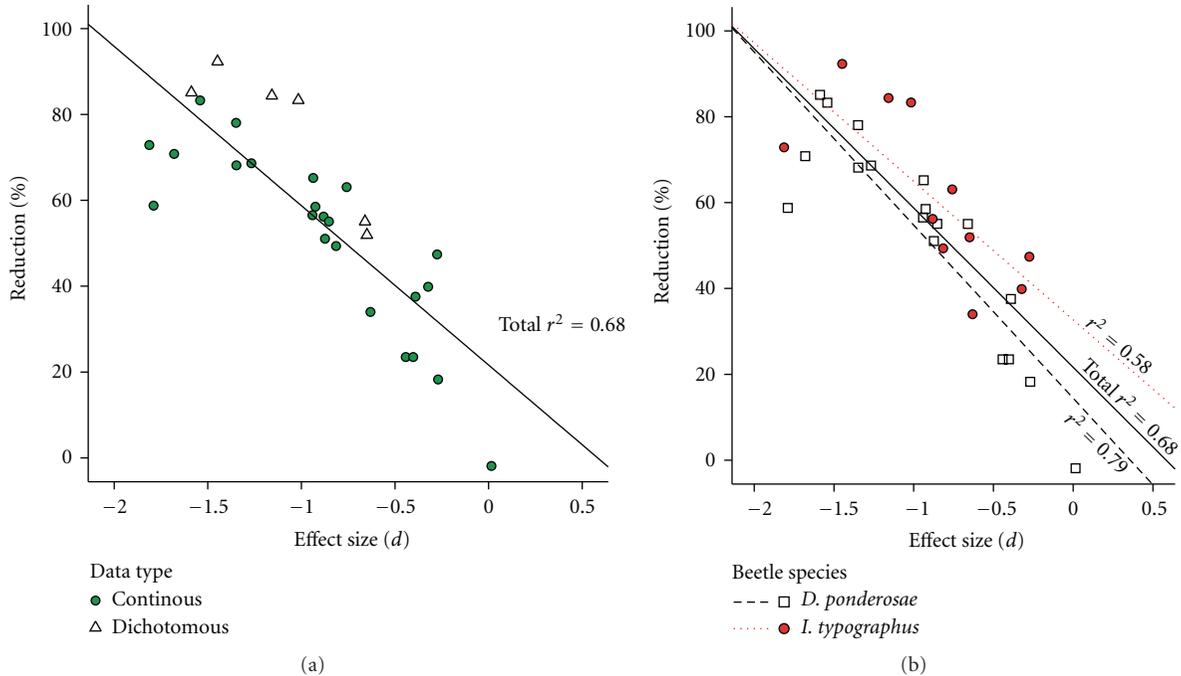


FIGURE 4: Correspondence between effect size and a standard measure of effect magnitude in applied entomology “% Reduction” ($[\text{attacked in control} - \text{attacked in treatment}/\text{attacked in control}] * 100$) for (a) different data types and (b) the two different species (*Ips/Dendroctonus*).

4. Discussion

In applied ecological applications such as forest entomology, critical reviews in the form of meta-analysis are not widespread [10] but see [7, 20, 21]. Sometimes titles of reviews may imply similarity in scope but, due to criteria set for included studies, have little overlap, as in [42], which covers semiochemical manipulation of pest insects but not insect pest management *per se*. Interestingly, the paper by Szendrei and Rodriguez-Saona [42] does not show a single experimental paper in common with the present review.

In principle, a meta-analysis describes the effect of a treatment among controlled experimental studies by analysing the distribution of effect sizes of the relevant studies [10, 22, 23]. By using results of many studies, it may allow detection of effects not easy to confirm by single studies [49].

The literature was screened by a “centrifugal” multidimensional strategy using citations to some core papers and then iterated by expanding to citing papers, and so forth, until no new papers turned up. This manual approach, based on my knowledge of the field, and the omission of a traditional one-dimensional database search step was justified by the finding that a single data base search may locate only 1/3 of relevant studies [50]. Back-tracking might have created an “inbreeding effect” of focus on papers by a possible citing bias, but I found no clear such indication and would leave this problem for a future discussion based on more studies.

Heterogeneity in effect size may come from several sources, including both true biological variation such as beetle population size and tree vigour in the field, as well as

variation in study design and treatment levels. Some papers present details of “different” experiments that are more of replications of the same design rather than different experiments, while others join or would allow joining of data of similar experiments conducted in different years under different conditions [47, 48]. A clear example is that of Progar [47] who clearly showed a reasonable variation in effect over the years of an outbreak, where in the beginning treated plots were protected from attacks by an escalating beetle population, but later became the victims of being the only remnants of mature trees left in the landscape, suitable to be attacked by the beetles at the peak of the outbreak [51].

An important consideration for any metastudy is the “file drawer problem” where a publication bias usually exists against the publication of negative outcomes with low effects. A notable exception is Jakuš et al. [40]. For the current analysis in particular, this aspect is an important consideration as the “grey literature” is not covered, which may cover some less successful experiments. The analysis of effect size distribution in this meta-analysis did, however, not detect any clear pattern of publication or dissemination bias.

The development of complete anti-attractant (verbenone) technology for the Southern Pine Beetle *Dendroctonus frontalis* was successfully finished in 1990s. The evaluation of treatments was based on growth rates of infestations. Clarke et al. [52] has shown that verbenone-only tactic completely suppressed 69% of infestation rate and verbenone-plus-felling tactic suppressed 86%, corresponding to an effect size of $|d| > 1$ and > 1.5 , respectively, based on the regression in this paper (Figure 4). If one may rely on the regression of % Reduction on effect size in this paper and on these

higher numbers for *D. frontalis* as representative, it is likely that the development of “push and pull” technology for *I. typographus* and *D. ponderosae* has some promise for future development. There is in my view a need for more complex anti-attractant mixture for both *I. typographus* and *D. ponderosae* (push) and for combinations with pheromone traps (pull) [34, 36, 40, 53–55]. It could be interesting to note that an effect size grand mean estimate in this paper $\theta \approx -1$ corresponds to a reduction of attacks of about 60%, a value found already in 2003 by Jakuš et al. [40] on data from 2000 and 2001 for *Ips*.

Patterns and mechanisms of the response by the tree to beetle attack are well researched in *Dendroctonus* [51, 56] and information is now becoming available for *Ips* [57, 58]. Contrarily, beetle response to signals from tree or beetle is in recent years better covered in *Ips*, especially at the antennal and single sensillum level of peripheral detection [59–62].

A deeper understanding of the olfactory interface with the environment for *D. ponderosae* will hopefully emerge from on-going study of the recently published transcriptomes [63, 64] and genome (Keeling et al., unpublished) and the transcriptome of antenna compared for the two species in progress (Andersson et al., unpublished). The present stage of analysis indicates a number of closely related pairs of antennal olfactory receptor genes (*OR*) that are not found in the other genomic coleopteran *Tribolium* [60]. Such understanding will in the future help in the study and manipulation of beetle olfaction and resulting behaviours.

This meta-analysis sets the basis that will further the development of antiattractants by quantitatively establishing a substantial overall effect of such interventions in the two species recently most studied. Such confirmed efficacy of antiattractants against attacks by these two “aggressive” bark beetles might encourage better designed and larger-scale applied studies on these and other economically important conifer bark beetle species in the future. The semiochemical-based “push-pull” tactic has played and will continue to play an important role in the pest management practices in agricultural, forestry, medical and urban settings [11]. Future meta-analysis and experimental studies on the subject would include more new study data points (more species) and “grey literature”, but also better reporting (clear provision of means and SDs [65], avoiding dichotomous data) of experimental responses and more of novel designs. Would it, for instance, be possible to use lower densities of dispensers, but with higher release rates as indicated by the distance effects noted in one study [48]?

When anti-attractant technology and treatment designs once comes of age, we will still have to keep in mind that we are not “protecting trees” in reality, but rather helping them to protect themselves. If we design forest landscapes for biodiversity and semiochemical diversity [11, 20, 66], we will in the long run help trees even better.

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