Environmental Toxicology and Chemistry, Vol. 28, No. 6, pp. 1111–1119, 2009

Printed in the USA
0730-7268/09 $12.00 + .00

Critical Review

EFFECTS OF TERRESTRIAL POLLUTANTS ON INSECT PARASITOIDS

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(*Received* 8 *September* 2008; *Accepted* 5 *January* 2009)

Abstract—Parasitoids are important organisms in the regulation of insect herbivores in natural, urban, and agricultural ecosystems. The impact of pollutants acting on parasitoids has not been extensively reviewed. This prompted us to propose a falsifiable null hypothesis (pollutants have no effects on parasitoids) and two alternative hypotheses (pollution negatively or positively affects parasitoids) to assess in the available literature the effects of pollutants acting on parasitoids. We found 26 studies examining 39 biological systems that met our criteria for inclusion. Of these studies, 18 of the 39 biological systems (46.2%) supported the null hypothesis while 18 (46.2%) supported the first alternative hypothesis in which pollutants exhibited negative effects on parasitoids. Only a small percentage of the studies (7.6%, 3 of 39) supported the second alternative hypothesis suggesting that pollutants had positive effects on parasitoids. We provide a synthesis of the available data by pollution type, summarize trends for different pollutants, and suggest future areas of research.

Keywords—Pollution Parasitoids Air pollutants Heavy metals Metalloids

INTRODUCTION

Insect parasitoids (insects living parasitically as larvae that kill their hosts) represent a large group of arthropods that are major selective forces regulating herbivore populations in both natural and managed habitats [1]. Here we review the impacts of pollutants on parasitoids. Human-induced pollution is an old and increasing problem that has modified insect population structures and ecosystems [2,3]. Covering the entire topic of pollution in all ecosystems is beyond the scope of this review, so we focus on terrestrial ecosystems and their most relevant pollutants. (The effects of pesticides and dusts as pollutants affecting parasitoids are not discussed, as this topic has been extensively reviewed elsewhere [4–9].) Specifically, we cover contaminants that affect parasitoids in terrestrial environments, including the air pollutants ozone (O_3), sulfur oxides (SO_x), nitrogen oxides (NO_x), and carbon oxides (CO_x) and soil pollutants such as metalloids and heavy metals. These atmospheric and soil pollutants are released into the environment mostly through anthropogenic activities such as the burning of fossil fuels from vehicles and various industrial, mining, and agricultural processes [10–16]. Pollution-induced environmental changes have effects that can disrupt tritrophic (i.e., three trophic levels such as the plant, the herbivore, and the natural enemy) interactions in terrestrial systems [2,6,17–19]; however, most reviews only briefly mention parasitoids.

Observations of pollution effects on parasitoids date back to 1961 [20]. The study by Wentzel and Ohnesorge [20], and subsequent publications [21–27], documented reduced parasitism rates, reduced parasitoid population density, and decreased activity of parasitoids along gradients from pristine habitats toward industrial sources, urban environments, or roadsides [28–30]. Fuhrer [31] noted susceptibility of natural enemies to pollutants and considered parasitoids more sensitive to anthropogenic toxicants than herbivorous hosts. In contrast, studies by Villemant [32], as well as Braun and Fluckiger [28], showed unchanged parasitism rates in polluted or roadside environments despite an elevation of host populations (as cited by Gate et al. [29]). Not surprisingly, clarifying trends in surveying the impact of pollutants on parasitoids in the field has proved difficult.

Research on insect parasitoids has been driven by their critical importance in the functioning of both natural and agriculturally managed ecosystems. Estimates suggest that up to 20% of the described insect species are parasitoids [33], and numerous species have been used in biological control of insect pests worldwide [34]. Thus, understanding how environmental factors such as pollution may affect these organisms is important. The present study comprehensively analyzes the literature to summarize the responses of parasitoids to terrestrial pollutants and to suggest directions for future research.

METHODOLOGY

The impact of pollutants on parasitoids was examined by determining the numerical response in the peer-reviewed literature to a falsifiable null hypothesis. This hypothesis (H_0) states that the effects of pollutants on parasitoids (e.g., percent parasitism, behavioral responses, fitness correlates, population density in the field) are equal in polluted compared to in nonpolluted environments. The alternative hypotheses (H_{a1} and H_{a2}) provide that pollutants have differential effects on parasitoids. For H_{a1} the effects are reduced when pollutants are present, and in H_{a2} the effects are enhanced when pollutants are present. Pollutants were categorized by chemical type in regards to their effect on parasitoids, and in some studies more than one pollutant was examined.

References were searched using the University of California's Melvyl System®, PubMed®, Web of Science®, and AGRICultural OnLine Access® databases, as well as examining the references of acquired papers. The surveyed literature included both laboratory and field studies. Each study had to meet three criteria for inclusion in this review: (1) parasitoids had to be exposed to pollutants (either indirectly to the parasitoid

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Published on the Web 1/8/2009.

through contamination of the hosts or directly to the parasitoid through inhalation by fumigations or oral administration of the contaminant in the diet or water) and there had to be an uncontaminated control; (2) at least one aspect of the parasitoid's fitness, behavior, or population density was measured; (3) appropriate statistical tests were included to determine whether the effects of pollutants on the parasitoids were significantly different than otherwise could occur by chance alone.

RESULTS

We found 26 studies examining 39 biological systems that met the criteria for inclusion. In all, these studies included parasitoids in the orders Hymenoptera and Diptera across nine families, 35 genera, and 37 species (Table 1). In a few cases, the taxonomic information for parasitoids was not provided and the authors only reported levels of parasitism in the field for the hosts [35–37]. A nearly equal number of studies that met the criteria for inclusion were completed in the field (14) compared to the laboratory (12). In addition, 7 of the studies directly exposed parasitoids to pollutants, while only 6 studies indirectly exposed parasitoids to pollutants through the host. A majority of the studies (13) did not provide the necessary information to determine whether the parasitoids were exposed directly or indirectly to pollutants. Two types of atmospheric pollutants, acidic precipitation and fluorides, have not been examined in regards to their effect on parasitoids.

The concentrations of pollutants used in the studies we evaluated were examined at currently relevant levels or at concentrations expected in the next few decades. For example, the gaseous pollutant sulfur dioxide (SO_2) is often reported at a concentration of up to 0.2 parts per million (ppm = μl/ml) in polluted air [38]. Only one of the studies that examined SO_2 impacts on parasitoids included concentrations above this level [39], but the concentrations were at levels found near anthropogenic sources. Likewise, the pollutant nitrogen dioxide (NO_2) has a concentration of up to 0.2 ppm in polluted air [38], and the concentrations of NO_2 examined were below this level as well [29]. For O_3, the most commonly reported levels found in polluted air extend up to 0.5 ppm [38], with concentrations of this pollutant predicted to increase in the upcoming decades [40]. Most studies that examined O_3 impacts on parasitoids were below the 0.5-ppm level [29,40,41], but one study examined a level of O_3 at the higher levels found near some large cities [36]. For carbon dioxide (CO_2), the current level in the atmosphere is 379 ppm, with some models predicting CO_2 concentrations reaching up to 790 ppm in future decades (www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr.pdf). All of the studies mentioned in this manuscript that examined CO_2 impacts on parasitoids did not exceed 710 ppm. For the heavy metals, concentrations can vary depending on the element involved, but concentrations up to 167, 413, 400, and 1,600 ppm (ppm = mg/kg) of cadmium (Cd), copper (Cu), lead (Pb), and zinc (Zn), respectively, have been reported [42,43]. Only one of the studies that examined Cd impacts on parasitoids included concentrations above this level [44]; the other studies examined the effects of much lower doses [45–48]. For the metalloid selenium (Se), levels in the soil can reach 110 ppm [49]. The level used to examine parasitoid responses mentioned was substantially below this concentration [50]. Studies involving combinations of pollutants were typically conducted in the field with the exception of two studies that examined the combination of the heavy metals Cd and Pb, but again the levels examined were below those reported to occur in the environment [45,46].

Studies on 18 of the 39 pollutants (46.2%) supported the null hypothesis that parasitoids were unaffected by pollutants. In contrast, 18 of the 39 pollutant systems (46.2%) supported the first alternative hypothesis and exhibited negative effects on parasitoids. Only a small percentage of the studies (7.6%, 3 of 39) supported the second alternative hypothesis: pollutant positively affected parasitoids. In surveying impacts of pollutants on parasitoids, the following patterns emerged.

Sulfur dioxide

Studies assessing the effect of SO_2 on parasitoids have not documented consistent negative effects. A variety of fitness correlates were assessed by Petters and Mettus [39] following acute exposure of SO_2 (i.e., 3 ppm for a 3- or 5-h period). Their results indicated that eclosion rates of the ectoparasitoid *Bracon hebetor* larvae from eggs were variable, with some experiments showing a reduction while others showed an increase [39]. The searching efficiency of the braconid parasitoid *Asobara tabida* (the proportion of hosts attacked per unit of search time) was not significantly affected by SO_2 fumigations at 0.1 ppm for 5 h [29]. In a field study by Amino-Kano et al. [35], rates of percentage parasitism did not show a statistically significant trend with increasing SO_2 concentrations (0.007–0.057 ppm). Overall, the impact of moderate SO_2 pollution appears to be minimal on those parasitoids examined.

Nitrogen dioxide

Only one study examined the impact of NO_2 on parasitoids. This study was conducted in the laboratory and focused on searching behavior [29]. Gate et al. [29] found that NO_2 fumigations at 0.1 ppm for 5 h did not significantly affect searching efficiency or proportion of hosts parasitized by the parasitoid *A. tabida*.

Ozone

Ozone appears to have predominantly negative effects on parasitoids. Only three studies have examined O_3 effects on parasitoids, and two of these showed negative effects. In the study by Gate et al. [29], 0.1 ppm fumigations of O_3 for 5 h resulted in a significant 10% reduction in the number of hosts parasitized and a significant reduction in searching efficiency by *A. tabida*. This study is particularly important because relatively few experiments have been published that document the potential changes in parasitoid behavior in the presence of gaseous pollutants. Results of a similar study by Pinto et al. [41] added information. They revealed that O_3 fumigations of 0.06 and 0.12 ppm did not affect the ability of the parasitoid *Cotesia plutella* to find herbivore-damaged plants when compared to controls [41]. In a field study, Holton et al. [40] found that chronic exposure to O_3 at concentrations 1.5 times above ambient levels (estimated to be 0.09–0.1 ppm) resulted in significant declines in larval survivorship of the tachinid fly parasitoid, *Compsilura concinnata*.

Carbon dioxide

The effects of CO_2 on parasitoids are equivocal. Cases occurred in which there were no effects [40,51,52], negative impacts [53], and positive fitness responses [37,42]. In three of the six studies, elevated CO_2 levels (550–600 ppm) did not affect percent parasitism, survival, or development times of parasitoids. Negative results of elevated CO_2 concentrations

(700 ppm) were reported in only one study; significant decreases were documented in metatibia length and increased mortality of the braconid parasitoid *Cotesia melanoscela* [53]. Most interesting are the studies by Stiling et al. [37,54] which found significantly greater mortality of host larvae (in one study, 80% higher mortality rates [37]) caused by parasitoids attacking lepidopteran leafminers hosts (Table 1) in elevated CO_2 treatments (700–710 ppm). Stiling et al. [54] proposed that the increased mortality was the result of an indirect trophic cascade. Because of reduced nitrogen availability in elevated CO_2, leafminer mines increased in size as larvae ate more in order to ingest enough nitrogen. These mines were easier for parasitoids to discover because of increased mine surface area, and the reduced nutritional quality extended exposure times of suitable host stages and potentially weakened the leafminer larvae, making them more vulnerable to parasitoid attack.

Heavy metals

Four heavy metals, Cd, Cu, Pb, and Zn, have been examined in regards to effects on parasitoids. These studies represent a range of contamination regimes: The soil was contaminated (the heavy metal was absorbed by the roots of the plant and then ingested by the host [44]), the heavy metal was given to the hosts in an artificial diet [47,48], or the heavy metal was administered directly to the parasitoid adults in the food or water [45,46]. In nearly all cases, there were either no effects or significant negative impacts on parasitoids [44–48]. All studies investigating heavy metals were conducted in the laboratory.

Cadmium has consistently resulted in negative effects on parasitoids at concentrations exceeding 10 ppm (μg/g). Ortel and Vogel [45] found that adult males and females of the ichneumonid wasp *Pimpla turionellae* exposed to 33 ppm of Cd in contaminated food and water exhibited significant declines in life span compared to uncontaminated controls. They also demonstrated that both sexes of this parasitoid had significantly lower oxygen consumption when compared to controls, suggesting their metabolic activity was adversely affected [45]. Reduction in metabolic activity may have important implications across pollutants as even gaseous contaminants such as SO_2 pollution have been shown in nonparasitic Hymenoptera to reduce flight activity [55]. In a subsequent study, Ortel [46] examined *P. turionellae* and found that the percentage of total body protein was significantly lower for males when exposed to 33 ppm of Cd and that the percentages of lipids in adult males and females were also lower than levels detected in unexposed controls.

The response to Cd for the parasitoid *Glytapanteles lipardis* was less consistent, but the concentrations of Cd used were substantially lower than in the aforementioned studies [47]. When exposed to 2 ppm of Cd, there was a significant increase in the mean number of adult parasitoids eclosing per host larva than in controls, but significantly fewer adults eclosed per host larva at 10 ppm of Cd as compared to controls [47], which might be a hormetic response. This study also determined that the development of *G. lipardis* was significantly longer in Cd-contaminated hosts [47].

At least some parasitoids cannot distinguish between contaminated and uncontaminated hosts. The diapriid parasitoid *Coptera occidentalis* did not discriminate between Cd-contaminated hosts (or hosts contaminated with Cu and Pb, for that matter) at 50 ppm and uncontaminated hosts [48]. This inability of parasitoids to detect contaminated hosts suggests that hosts in polluted sites may act as sinks that reduce population densities of parasitoids. Kazimirova et al. [48] also reported that Cd contamination resulted in a significant decrease in the percentage of female offspring produced, but there was a significant increase in life span of adult parasitoids compared to controls. Similarly, there was a significant reduction in the instantaneous growth rate of the parasitoid *Aphidius ervi* when exposed to 400 ppm of Cd compared to cohorts exposed to the control level (0 ppm of Cd) or 200 ppm of Cd [44].

Only two studies have examined Cu in relation to effects on parasitoids, and both show detrimental impacts on parasitoid fitness correlates. Ortel et al. [47] found the number of adults that successfully emerged from hosts contaminated with 10 and 50 ppm of Cu were significantly lower compared to controls. Also, Ortel et al. [47] and Kazimirova et al. [48] showed that development rates of parasitoids were significantly slower when compared to controls. In addition, Kazimirova et al. [48] found that the percentage of female offspring of *C. occidentalis* emerging from contaminated hosts was significantly reduced.

For the heavy metal Pb, four reports suggest that parasitoids may be able to tolerate increased concentrations as compared to other heavy metals. For example, *P. turionellae* females did not exhibit significant differences in life span or oxygen respiration rates at 82 ppm of Pb as compared to uncontaminated controls [45]. Also, percent protein and lipid content for *P. turionellae* at 82 ppm of Pb was not significantly different from controls [46]. For *G. lipardis*, there were no significant differences in the number of adults that emerged at 0 or 4 ppm or in developmental times from hosts contaminated with 0, 4, or 20 ppm of Pb [47]. In a study by Kazimirova et al. [48] with contamination levels reaching 400 ppm, there were no significant differences for a variety of fitness correlates of the parasitoid *C. occidentalis*, such as development time, oviposition time, number of progeny emerging from host, and percentage of female offspring. However, reductions did exist for some fitness correlates and in one case a positive affect was noted; for example, male *P. turionellae* did exhibit significant declines in life span and respiration rates at 82 ppm of Pb [45], the number of eclosed adults was significantly reduced for *G. lipardis* at 4 ppm of Pb [47] and, female life spans of *C. occidentalis* that emerged from metal-contaminated hosts at 400 ppm of Pb were significantly longer than controls [48].

Only one study examined the effects of Zn on parasitoids [47]. This study demonstrated the negative effects of this metal on the parasitoid *G. lipardis*. The number of adults that emerged from hosts contaminated with Zn at 100 and 500 ppm was significantly less than controls, and parasitoid development time at the same concentrations took significantly longer than at control concentrations.

Metalloids

Metalloids are elements that have metal and nonmetal properties. Only one study has examined the impact of the metalloid Se on parasitoids. This particular study was conducted in the laboratory and focused on a variety of fitness correlates of the braconid *Cotesia marginiventris* [50]. They demonstrated that Se can have harmful impacts on this parasitoid's development time and weight compared to wasps emerging from hosts on unpolluted control plants [50].

Table 1. Published reports of effects of pollutants on parasitoids

	Pollutant/ concentration	Parasitoid/host	Experimental setting	Exposure, administration, stage	Effects	Hypothesis	Reference
1	SO_x, heavy metals/not available	*Telenomus aradi* (Hymenoptera: Scelionidae)/*Aradus cinnamomeus* (Hemiptera: Aradidae)	Field	Not available	Significant negative correlation occurred of percent parasitism with distance from pollution source.	H_{a1}	[62]
2	SO_2/3 ppm for 3 or 5 h	*Bracon hebetor* (Hymenoptera: Braconidae)/*Ephestia kuehniella* (Lepidoptera: Pyralidae)	Laboratory	Direct, fumigation, adults	No significant direct effect of SO_2 was seen on female life span and reproductive performance.	H_0	[39]
3	SO_x, heavy metals/not available	*Macrocentrus* spp. (Hymenoptera: Braconidae), *Liotryphon* spp. (Hymenoptera: Ichneumonidae), Hymenoptera: Chalcididae, Diptera: Tachinidae/*Petrova resinella* (Lepidoptera: Tortricidae)	Field	Not available	Proportion of galls parasitized was not significantly different with distance from source of pollution.	H_0	[57]
4	Pb, Cd, Pb + Cd/82 ppm of Pb, 33 ppm of Cd, 82 ppm of Pb + 33 ppm of Cd all in food or water	*Pimpla turionellae* (Hymenoptera: Ichneumonidae)/*Galleria mellonella* (Lepidoptera: Pyralidae)	Laboratory	Direct, oral, adults	Life span and respiration rates were significantly affected depending on sex of parasitoid, metal, and level of exposure.	H_0, H_{a1}	[45]
5	SO_2/0.007–0.057 ppm	Not available/*Sitobion avenae* (Hemiptera: Aphididae)	Field	Direct, fumigation, adults	No significant differences occurred of percentage parasitized with pollution level.	H_0	[35]
6	SO_x, heavy metals/not available	*Synomelix scutulata* (Hymenoptera: Ichneumonidae), *Lamachus eques* (Hymenoptera: Ichneumonidae), *Olesicampa* spp. (Hymenoptera: Ichneumonidae), *Diplostichus janithrix* (Diptera: Tachinidae)/*Neodiprion sertifer, Diprion pini, Gilpinia pallida* (Hymenoptera: Diprionidae)	Field	Not available	No significant differences were seen of percentage of hosts parasitized with pollution level. No visible difference appeared in parasitoid species composition in relation to air pollution level.	H_0	[58]
7	Pb, Cd, Pb + Cd/82 ppm of Pb, 33 ppm of Cd, 82 ppm of Pb + 33 ppm of Cd all in food or water	*P. turionellae* (Hymenoptera: Ichneumonidae)/*G. mellonella* (Lepidoptera: Pyralidae)	Laboratory	Direct, fumigation, adults	No effect to significant decrease was seen in total lipid and protein content with increasing levels of metal contamination.	H_0, H_{a1}	[46]
8	Cd, Pb, Cu, Zn/2 and 10 ppm of Cd, 4 and 20 ppm of Pb, 10 and 50 ppm of Cu, 100 and 500 ppm of Zn	*Glytapanteles liparidis* (Hymenoptera: Ichneumonidae)/*Lymantria dispar* (Lepidoptera: Lymantriidae)	Laboratory	Indirect, —, egg/larvae	No correlation was found between extent of metal contamination and parasitoid success.	H_0	[47]
9	SO_x, heavy metals/not available	*Pnigalio longulus* (Hymenoptera: Eulophidae), *Chrysocharis nephereus* (Hymenoptera: Eulophidae), *Minotetrastichus ecus* (Hymenoptera: Eulophidae)/*Eriocrania* spp. (Lepidoptera: Eriocraniidae)	Field	Not available	*Eriocrania* parasitism rates were not significantly affected by emission from the factory source.	H_0	[59]
10	SO_2, NO_2, O_3/100 nl/L	*Asobara tabida* (Hymenoptera: Braconidae)/*Drosophila subobscura* (Diptera: Drosophilidae)	Laboratory	Direct, fumigation, adults	Proportion of parasitism and searching efficiency were significantly decreased in O_3 but not in other treatments.	H_0, H_{a1}	[29]
11	Gases, Pb/0.06 ppm of Pb	*Eurytoma gigantean* (Hymenoptera: Eurytomidae), *Eurytoma obtusiventris* (Hymenoptera: Eurytomidae)/*Eurosta solidaginis* (Diptera: Tephritidae), *Epiblema scudderiana* (Lepidoptera: Tortricidae)	Field	Not available	Mortality by parasitoids did not affect gall-formers close to roadside pollution.	H_0	[64]
12	CO_2/700 ppm	*Cotesia melanoscela* (Hymenoptera: Braconidae)/*L. dispar* (Lepidoptera: Lymantriidae)	Laboratory	Indirect, fumigations, eggs/larvae	Parasitoid mortality increased and adult female size decreased in elevated CO_2.	H_{a1}	[53]
13	SO_x, heavy metals/not available	*Cleonice nitiduscula* (Diptera: Tachinidae), *Megaselia rubricornis* (Diptera: Phoridae)/*Melasoma lapponica* (Coleoptera: Chrysomelidae)	Field	Not available	Parasitism rate depended neither on pollution nor on population density of the host.	H_0	[60]

Table 1. Continued

	Pollutant/ concentration	Parasitoid/host	Experimental setting	Exposure, administration, stage	Effects	Hypothesis	Reference
14	SO_x, heavy metals/<200 ppm of Ni, <200 ppm of Cu	*Cotesia jucunda* (Hymenoptera: Braconidae), *Aleiodes gastritor* (Hymenoptera: Braconidae), *Phobocambe neglecta* (Hyemenoptera: Ichneumonidae)/*Epirrita autumnata* (Lepidoptera: Geometridae)	Field	Not available	Rates of parasitism were not associated with pollution level.	H_0	[61]
15	O_3/<0.08 ppm	Not available/*Dendroctonus brevicomis* (Coleoptera: Scolytidae)	Field	Not available	Significantly lower parasitoid density occurred in the polluted site compared to nonpolluted sites that persisted for two generations.	H_{a1}	[36]
16	Cu, Cd, Pb/400 ppm of Cu, 50 ppm of Cd, 400 ppm of Pb	*Coptera occidentalis* (Hymenoptera: Diapriidae)/*Ceratitis capitata* (Diptera: Tephritidae)	Laboratory	Indirect, —, eggs/larvae	Parasitoids did not discriminate between contaminated and uncontaminated hosts. Development time, proportion of females, life span, and reproductive performance depended on metal involved.	H_0, H_{a1}	[48]
17	CO_2/550–600 µmol/mol	*Aphidius matricariae* (Hymenoptera: Braconidae)/*Myzus persicae* (Hemiptera: Aphididae)	Laboratory	Direct, fumigations, pupae/adults	Parasitism rates were not changed in CO_2 elevated treatments.	H_0	[51]
18	CO_2/700 µl/L	*Zagrammosoma multilineatum* (Hymenoptera: Eulophidae), *Chrysonotomysia* sp. (Hymenoptera: Eulophidae), *Anachrysocharoides* sp. (Hymenoptera: Eulophidae), *Closterocercus trincinctus* (Hymenoptera: Eulophidae), *Elasmus* sp. (Hymenoptera: Eulophidae), *Chrysocharis* sp. (Hymenoptera: Eulophidae), *Chelonus cosmopteridis* (Hymenoptera: Braconidae)/*Stigmella* spp. (Lepidoptera: Nepticulidae), *Cameraria* spp. (Lepidoptera: Gracillariidae), *Stilbosis* spp. (Lepidoptera: Cosmopterigidae)	Field	Not available	Significantly greater mortality was inflicted by parasitoids on hosts in elevated CO_2 treatments.	H_{a2}	[54]
19	SO_x, heavy metals/not available	*Cheonice nitidiuscula* (Diptera: Tachinidae), *Megaselia opacicornis* (Diptera: Phoridae), *Schizonotus sieboldy* (Hymenoptera: Chalcidoidae), *Mesochorus confusus* (Hymenoptera: Ichneumonidae), *Aspilota* sp. (Hymenoptera: Braconidae)/*M. lapponica* (Coleoptera: Chrysomelidae)	Field	Not available	Mortality caused by parasitoids was lower at clean sites than at polluted sites. Total parasitism increased with pollution load.	H_{a2}	[30]
20	CO_2/660 ppm	*Diaeretiella rapae* (Hymenoptera: Braconidae)/*M. persicae* (Hemiptera: Aphididae), *Brevicoryne brassicae* (Hemiptera: Aphididae)	Laboratory	Direct/indirect, fumigation, eggs/larvae/adults	Number of aphids parasitized for both species in this experiment did not change in elevated CO_2.	H_0	[52]
21	CO_2/710 µl/L	Not available/*Acerocercops* sp. (Lepidoptera: Cosmopterigidae), *Buccalatrix* sp. (Lepidoptera: Lyonetidae), *Cameraria* sp. (Lepidoptera: Gracillariidae), *Stigmella* sp. (Lepidoptera: Nepticulidae), *Stilbosis* sp. (Lepidoptera: Cosmopterigidae), *Tischeria* sp. (Lepidoptera: Tischeridae)	Field	Not available	Mortality caused by parasitoids of leafminers increased significantly, by more than 80%, in elevated CO_2 treatments.	H_{a2}	[37]
22	CO_2, O_3/560 µl/L of CO_2, <100 nl/L of O_3, <100 nl/L of CO_2 + O_3	*Compsilura concinnata* (Diptera: Tachinidae)/*Malacosoma disstria* (Lepidoptera: Lasiocampidae)	Field	Indirect, fumigation, larvae	Parasitoid larval survivorship decreased under elevated O_3 but not for CO_2 and a combination of gases.	H_0, H_{a1}	[40]
23	Cd/0, 200, 400 ppm	*Aphidius ervi* (Hymenoptera: Aphelinidae)/*Acyrthosiphon pisum* (Hemiptera: Aphididae)	Laboratory	Indirect, —, eggs/larvae	Cd had a significant negative impact on *A. ervi* population growth rate.	H_{a1}	[44]

Table 1. Continued

	Pollutant/concentration	Parasitoid/host	Experimental setting	Exposure, administration, stage	Effects	Hypothesis	Reference
24	Se/31 ppm	*Cotesia marginiventris* (Hymenoptera: Braconidae)/*Spodoptera exigua* (Lepidoptera: Noctuidae)	Laboratory	Indirect, —, eggs/larvae	Adults did not discriminate between Se-containing and control plants, but parasitoids did exhibit significant increases in development time and decreased pupal weight.	H_{a1}	[50]
25	SO_x, heavy metals/not available	*P. longulus* (Hymenoptera: Eulophidae), *C. nephereus* (Hymenoptera: Eulophidae), *Minotetrastichus frontalis* (Hymenoptera: Eulophidae), *Cirrospilus vittatus* (Hymenoptera: Eulophidae), *Pnigalio agraules* (Hymenoptera: Eulophidae), *Neochrysocharis formosa* (Hymenoptera: Eulophidae), *Cirrospilus lyncus* (Hymenoptera: Eulophidae)/*Eriocrania* spp. (Lepidoptera: Eriocraniidae)	Field	Not available	In undisturbed forests rate of population change of *Eriocrania* leafminers was correlated negatively with previous-year parasitism, but in polluted forests no correlation was found.	H_{a1}	[63]
26	O_3/120 nl/L	*Cotesia plutellae* (Hymenoptera: Braconidae)/*Plutella xylostella* (Lepidoptera: Plutellidae)	Laboratory	Direct, fumigation, adults	Parasitoid was still able to find herbivore-damaged plants in elevated O_3.	H_0	[41]

Combinations of pollutants

Although most studies examined individual pollutants, contaminants often occur in mixtures [56]. Of the 13 studies that have examined combinations of pollutants, 11 were conducted in the field. One of the most common combinations studied (8 of 13 studies) was SO_x and heavy metals. These studies occurred in either southwestern Finland or northwestern Russia. Results mostly indicate a pattern of no effects on parasitoids, but negative effects, and in one case a positive effect, have been documented. Five studies showed the levels of parasitism in the field were not significantly different between polluted and nonpolluted sites [57–61]. In contrast, significant negative effects on parasitoids adjacent to a pollution source and a significant disruption of parasitism (as compared to unpolluted forests) have been noted [62,63]. In the only study to find a positive effect of multiple pollutants, parasitism rates by the dipteran parasitoids *Megaselia opacicornis* and *Cleonice nitidiuscula* were significantly higher near polluted sites compared to nonpolluted sites [30]. Zvereva and Kozlov [30] hypothesized that dipteran parasitoids may have greater innate tolerance of pollutants than hymenopteran parasitoids. An objective analysis of this interesting hypothesis is not possible due to the limited numbers of dipteran parasitoids examined to date.

Combinations of other mixtures of pollutants have found either negative effects or no impacts on parasitoids. Two studies dealing strictly with combinations of heavy metals were conducted in the laboratory [45,46]. These studies illustrate that combinations of heavy metals (i.e., Cd + Pb) have significant negative effects on life span, oxygen respiration rates, and percentage of protein and lipid contents of parasitoids. From these studies, the results are unclear regarding whether combinations of metals have additive, synergistic, or potentiating interactions. However, studies with combinations of roadside gaseous pollutants and heavy metals found that mortality caused by parasitoids of gall-makers was not significantly different in clean environments versus polluted environments [64]. For combinations of gaseous pollutants, two studies have examined the effects on parasitoids. One study found no effects of elevated atmospheric CO_2 plus O_3 on *C. concinnata* survival, development time, and adult mass [40]. In a field study, western pine beetle (*Dendroctonus ponderosae*) parasitoid densities were significantly lower in polluted ponderosa pines (*Pinus ponderosa*) when compared to nonpolluted environments [36]. These differences persisted for two generations in areas where O_3 concentration exceeded 0.8 ppm for more than an average of 7.3 h per day [36].

DISCUSSION

Trends in pollutant impacts

Predicting patterns and the primary and interactive effects of pollutants on parasitoids remains problematic. Some trends from the literature suggest pollutants such as O_3, the heavy metal Cd, and combinations of heavy metals generally have negative effects on parasitoid searching behavior, physiology, and fitness, although the number of studies is still too low to conclude these effects with certainty. For other pollutants, the patterns are even less clear and vary with the system being examined. In particular, no clear patterns were evident for SO_2, CO_2, the heavy metal Pb, and combinations of pollutants that contain SO_x and heavy metals. For these pollutants, researchers have documented systems with no effects, negative effects, or positive impacts on parasitoids that manifest in a variety of measures, such as parasitoid development, survival, life span, parasitoid physiology, and percent parasitism of the host population. However, caution should be used in papers that report percent parasitism in the field because host and parasitoid phenologies per generation can influence samples, making them poor indicators of the actual impact of pollutants on parasitoids and hosts [65].

Also, the search for patterns is complicated by the number of studies that do not report pollutant concentrations in the environment or the hosts (Table 1). Host insects can acquire contaminants from their food and their environment. Herbivorous insects rely on plants that may change the chemical form of the contaminant, which is often not investigated [50]. Host insects may sequester the pollutant nonlinearly, so the concentration in the environment may not reflect the concentrations to which the parasitoid is exposed. Another caveat is that reports of no effects may reflect that only the concentrations tested were below the sensitivity threshold of the parasitoid. Also, while it appears that some pollutants may have hormetic effects on insect parasitoids (positive effects at low concentrations), the manuscripts cited here were not designed to specifically test this type of dose–response relationship and these papers do not offer conclusive evidence. Further research is required before any definitive statements can be made. Thus, testing a wide range of concentrations is required to fully assess the dose–response relationship and impacts of pollutants on a given parasitoid species.

In most cases, scientists report parasitoid responses in three categories: positive, negative, and no effects. This would appear to provide a logical interpretation of the results of most studies. However, this simple categorization may not accurately indicate the impact on ecosystem function. For example, Vickerman et al. [50] documented a negative effect of Se on the parasitoid *C. marginiventris*. Therefore, the reader would normally assume that Se-contaminated environments would not be advantageous to the parasitoid. Because Se contamination has reached toxic levels in most of the irrigated areas of the San Joaquin Valley in California, USA [66], an obvious concern is that the parasitoids would be severely impacted. However, while the Se-containing plants in the study allowed for the survival of *Spodoptera exigua* at suitable stages for parasitization but did not allow complete development of the host insect, some *C. marginiventris* still completed development and survived. Thus, the Se-accumulating plants would reduce populations of the pest insect (host) while allowing populations of parasitoids to persist. For a phytoremediation agricultural system, this is nearly an ideal outcome.

Research priorities for the future

This review has identified a number of critical areas worthy of additional research. Relatively few parasitoid taxa have been studied, and data are needed for a diverse set of parasitoid groups in both natural and agricultural settings. Parasitoids are a large group of insects that include species not only in the orders Hymenoptera (64,000 described species in 10 superfamilies) and Diptera (~15,000 parasitoid species in 9 families) but also in the orders Coleoptera (~3400 parasitoid species in 4 families), Lepidoptera (~11 species in 2 families), Neuroptera (~50 species in 1 family), Strepsiptera (~440 species in 8 families), and Trichoptera (1 species in 1 family) [33,67–69]. Thus, more research on other groups is critical. However, as illustrated in this review, only two orders of parasitoids have been examined that include 37 species. In some studies, taxonomic detail even at the level of order was not included. In addition, there was difficulty in determining whether the species mentioned in these studies were endoparasitoids or ectoparasitoids, koinobionts or idiobionts, primary or secondary (hyperparasitoids) parasitoids, or solitary or gregarious parasitoids or whether these parasitoids had been used in biological control programs or occurred predominately in natural ecosystems. Hence, at the least, inclusion of additional detail allowing examination of these aspects of the parasitoid life history in relation to pollutants should be a priority in future research.

Furthermore, it is unknown whether hosts exposed to pollutants are more vulnerable or less susceptible (e.g., pollutants induce resistance) to parasitism and whether changes in the immune responses of the host have impacts on parasitoid fitness and population dynamics. For example, the effects of heavy metals, as well as Se, appear to generally increase the immunocompetence, encapsulation rates, and phenoloxidase enzyme activity of insect hosts compared to prey insects monitored in unpolluted controls [70–73]. However, the encapsulation rate by the ant *Formica aquilonia* initially increased with increased heavy metal concentrations but then decreased at higher heavy metal concentrations [74]. Thus, in polluted environments hosts may have altered immune functions, and this may have repercussions for the fitness of parasitoids. In addition, insect responses obviously vary with pollutant concentrations (possible hormetic responses), and experiments using a single concentration cannot be assumed to provide a complete response profile. Obviously, the dose range tested is critical.

Parasitoids also have endosymbionts such as polydnaviruses *Wolbachia*, *Rickettsia*, and *Cardinium* that can affect oviposition success and life history characteristics, including sex ratios [75,76]. So far, reports are not available that test whether pollutants can affect these symbionts or whether any resulting effects occur related to parasitoid fitness or competitive interactions within and between parasitoid species. In addition, an examination of the potential lethal and sublethal effects of pollutants on parasitoid mating success, development success, and life span of the F_1 generation of parasitoids have not been undertaken. Sublethal effects of pesticides, for example, are significant factors to consider when drawing conclusions about their impacts on pestiferous and beneficial arthropods [9]. As noted earlier, relatively few studies have been conducted on behavioral responses of parasitoids to pollutants, including habitat location, host location, and host acceptance. Modifications of any of these behaviors could reasonably be expected to have major effects on ecosystem function.

In addition, this review has raised an interesting question regarding dipteran tolerance to metals. Previous research has hypothesized that the detritivore lifestyle may be able to tolerate toxicants as indicated with the model research species *Megaselia scalaris* (Loew), both a detritivore and a facultative parasitoid in some cases [77]. This species was not as sensitive to the pollutant Se as compared to an herbivore [78]. However, the order Diptera itself may possibly be able to tolerate pollutants. Dipteran parasitoids in the study by Zvereva and Kozlov [30] were better able to withstand environmental SO_x and heavy metal pollution. Future research may look to examine the mechanisms for physiological tolerance to heavy metal pollutants in flies and to contrast dipterans with other orders.

This review has also emphasized the dearth of information available for many pollutants. Specifically, reports are nonexistent for acidic precipitation and fluorides. Only one study is available for other pollutants such as NO_2, the heavy metal Zn, the metalloid Se, gases (other than SO_x) in combination with heavy metals, and combinations of gases (e.g., CO_2 + O_3). There are two other studies examining CO_2 + O_3, but these combined parasitoids with other natural enemy groups [79,80].

CONCLUSION

Overall, more research in both the laboratory and the field is needed before patterns of parasitoid responses can be predicted with accuracy. Information on the environmental effects of pollutants on parasitoids is important not only for fostering successful biological control in agriculture and forestry but also for understanding ecological processes in anthropogenically altered natural habitats.

Acknowledgement—We thank T. Paine, J. Li, B. Carson, G. Kund, and K. Hladun whose comments and suggestions greatly improved an earlier version of this manuscript.

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