



Interactive Effects of Warming and Pollutants on Marine and Freshwater Invertebrates

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Accepted: 16 October 2022 / Published online: 1 December 2022
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Abstract

Purpose of Review Global warming and pollution are among the five major causes of global biodiversity loss, particularly in aquatic invertebrates which are highly diverse but understudied. In this review, we highlight advancements in current environmental studies investigating the interactive effects between warming and contaminants in freshwater and marine invertebrates. We not only focused on temperate regions but also synthesized information on the less studied Arctic/Antarctic and tropical regions.

Recent Findings In general, the same combination of warming and contaminants may result in either additive or non-additive interactive effects depending on taxa, the response variable, life stage, genotype, exposure level, duration and order of exposure, and the number of exposed generations. For traditional contaminants such as metals and pesticides, combined effects with warming at the individual level were generally synergistic. Growing evidence suggests that multigenerational exposure can shift the interaction between warming and contaminants toward antagonism, while contemporary evolution may change the interaction type.

Summary Our synthesis highlights the importance of temporal aspects in shaping interaction type, including order of exposure, ontogenetic effects, transgenerational effects, and evolution. The combination of laboratory experiments (to advance mechanistic understanding) and outdoor mesocosm studies or field observations (to increase realism) is needed to obtain comprehensive assessments of interactive effects of warming and pollutants from genes to ecosystems.

Keywords Aquatic insects · Climate change · Contemporary evolution · Copepods · Pesticides · Synergistic effects

Introduction

Aquatic invertebrates are among the most biologically diverse animal groups and play a crucial role in transferring energy and resources from algae and plants to higher trophic levels such as fish, birds, and mammals [1, 2]. They can also influence biogeochemical cycles, including carbon sequestration [3]. Globally, over 1.3 million invertebrate species have been identified, but many more have gone extinct before even being recorded [4]. Aquatic invertebrates are highly vulnerable to both warming and contaminants, and generally have a limited dispersal capacity to escape exposures to both stressors [5]. For example, the abundance of many crayfish, dragonflies, and damselflies in New South Wales, Australia, is projected to decline from 20% to over 50% by 2085 under warming due to their limited dispersal capacity [6]. Investigations of the combined effects of warming and contaminants have emerged as a major

This article is part of the Topical Collection on *Biology and Pollution*

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multidisciplinary research theme, bridging ecotoxicology and climatology, limnology, oceanography, ecology, and evolution [7, 8••].

Global warming and anthropogenic contaminants are among the five dominant threats that place ~1 million species at risk of extinction [9]. During the last 15 years, there have been several influential review articles, particularly emphasizing the synergistic effects of warming and contaminants on different biological levels of organization, from physiology to communities [10–14, 15••]. In this review, we discuss emerging research themes at the interface of global warming and traditional contaminants (metals, pesticides, herbicides, biocides), and emerging contaminants (pharmaceuticals, microplastics, and nanoparticles) on aquatic invertebrates focusing on the period 2017–2022 (see Supplementary material S1). The interaction between warming and contaminants is considered synergistic, additive, or antagonistic when their combined effect is greater, equal, or smaller than the sum of the individual effects on a biological response, respectively [16]. In the next sections, we will discuss how contaminant effects on marine and freshwater invertebrates may depend on (i) different aspects of warming, including elevated temperatures, heat waves, and daily temperature fluctuations; (ii) the number of exposed generations (transgenerational effects); (iii) the evolution of increased tolerance; and (iv) argue the importance of studying the interaction between the two stressors in mesocosm experiments. In each of the sections, we highlight understudied aspects to inspire future studies.

Interactive Effects Between Contaminants and Different Aspects of Warming

Interactive Effects of Contaminants and Elevated Mean Temperatures

Most experiments tested the interaction of contaminants with a relatively small step-increase in temperature within a range of 10–30 °C; some of these were specifically based on scenarios of the Intergovernmental Panel on Climate Change [17]. These studies are relevant for the reproductive and growing seasons of marine and freshwater invertebrates, particularly in temperate regions. At the individual level, the combined effect of warming and traditional contaminants (pesticides, metals, oil substances) is mainly synergistic within this temperature range (Table 1, Fig. 1, Wald $\chi^2 = 26.94$, $P < 0.01$) and this pattern was not statistically different between marine and freshwater studies (Wald $\chi^2 = 5.06$, $P = 0.08$). Most studies on interactive effects, and all those summarized in Table 1, are laboratory experiments that focused on life history, with behavioural responses understudied. Nevertheless, the latter can be important in linking individual responses to community-level responses. For example, when tested at a higher temperature, the pesticide

chlorpyrifos reduced food intake of the predatory larvae of the damselfly *Ischnura elegans* more, while negative effects of the pesticide on their antipredator behaviour were not temperature-dependent [18]. This suggests the overall pesticide-induced changes in interactions with lower and higher trophic levels can be differentially temperature-dependent [19].

Studies listed in Table 1 mainly focused on traditional contaminants. In contrast, information on the combined effects of warming and emerging contaminants of global concern, such as microplastics [20, 21] remains limited to a handful of studies on a few aquatic invertebrates (e.g., bivalves, cladocerans, and corals, Table 2 [22–24]). In general, these studies found that warming had a much greater effects on the life history and physiological traits than microplastics, whereby the total effect of the two stressors was mostly equal to the effect of warming alone [22, 23]. Nevertheless, synergistic effects have been observed in the coral *Pocillopora verrucosa*, with microplastics increasing the susceptibility to bleaching under warming, possibly due to the need to spend more energy on coping with the microplastics [23]. In addition, microplastics can also be a carrier of various contaminants, and therefore, studies on how microplastics interact with these and warming are urgently needed.

Very few experiments have tested the toxicity of contaminants on aquatic invertebrates of the thermally more extreme regions of our planet: Arctic [25] and Antarctic [26•], and tropics [27, 28]. Polar invertebrates are typically stenothermic with a very slow development and long generation time, and limited plasticity. Just a few degrees increase in water temperature can take temperatures beyond the optimal range of these species. For example, the Arctic marine copepods *Calanus glacialis* and *C. hyperboreus* have a peak distribution at a seawater temperature of 1–2 °C and the upper range of the thermal niche for both species is around 7 °C [29]. Similar thermal adaptations to low temperatures are found in Antarctic invertebrates, e.g. the upper critical thermal limit is ~2 °C for the Weddell Sea bivalve *Limopsis marionensis* and ~4 °C for the brachiopod *Liothyrella uva* [30]. Most Antarctic marine invertebrates cannot survive after a short exposure to temperatures of 5–10 °C (reviewed in [30]) that can be linked to the limited response to thermal stress. For example, the Arctic copepod *C. glacialis* shows no upregulation of genes encoding heat shock proteins when exposed to temperatures from 0 to 15 °C [31].

Only few exposure studies have tested the interaction of warming and contaminants on polar marine invertebrates at relevant temperatures [25, 26•]. These studies found weak interactive effects which depended on the response variable, species, warming level, and the exposure concentration (Table 1). For instance, the lethal effect of the polycyclic aromatic hydrocarbon pyrene on *C. glacialis* was only evident at 0 °C, but not at higher temperature (5 °C and 10 °C) [32]. This result suggests that high thermal stress overshadowed the

Table 1 Summary of major findings of the interactive effects of warming and traditional contaminants (pesticides, metals, polycyclic aromatic hydrocarbons) on freshwater and marine invertebrates in laboratory experiments

Regions	Taxa	Species	Exposed life stage	Response variables	Type of warming	Temperature range	Contaminants	Interaction type	Ref.
Freshwater invertebrates									
Temperate	Diptera	<i>Culex pipiens</i>	Final larval stage (L4)	Survival, development time (♀), wing length (♀)	DTF 13.0–27.0 °C Constant 20 °C	16.5–23.5 °C	Pesticide Chlorpyrifos Pesticide <i>Bacillus thuringiensis israelensis</i> Mixture	Chlorpyrifos and 7 °C DTF Additive (mortality, development time) Synergistic (wing length) Chlorpyrifos and 14 °C DTF Additive (mortality, development time) Synergistic (wing length) Bti and 7 °C DTF Additive (mortality, development time, wing length) Bti and 14 °C DTF Additive (mortality, development time, wing length) Pesticide mixture at 7 °C DTF Additive (mortality) Antagonistic (development time and wing length) Pesticide mixture at 14 °C DTF Synergistic (mortality) Additive (development time & wing length)	[91]
Temperate	Diptera	<i>Culex pipiens</i>	Final larval stage (L4)	Survival, heat tolerance (CTmax)	DTF 13.0–27.0 °C Constant 20 °C	16.5–23.5 °C	Pesticide Chlorpyrifos	Synergistic (survival); antagonistic (CTmax)	[57]

Table 1 (continued)

Regions	Taxa	Species	Exposed life stage	Response variables	Type of warming	Temperature range	Contaminants	Interaction type	Ref.
Temperate	Diptera	<i>Culex pipiens</i>	Final larval stage (L4)	Survival, development time, pupal mass	DTF 20 °C Constant	15.0–25.0 °C	Pesticide Chlorpyrifos	Antagonistic	[59]
Temperate	Odonata	<i>Ischnura elegans</i>	Final larval instar (F0)	Survival, growth rate, fat content, activity of acetylcholinesterase and cytochrome P450 monoxygenase	DTF 15.0–25.0 °C DTF 20 °C Constant	17.5–22.5 °C	Pesticide Chlorpyrifos	Synergistic (strongest chlorpyrifos-induced growth ↓ and survival ↓ under DTF) Additive (fat content, activities of acetylcholinesterase and cytochrome P450 monoxygenase)	[58]
Temperate	Odonata	<i>Ischnura elegans</i>	Final larval instar (F0)	Survival, growth rate, heat tolerance (CTmax)	DTF 15.0–25.0 °C 20 °C Constant 21.5–26.5 °C DTF 19.0–29.0 °C DTF 24 °C Constant	17.5–29 °C	Pesticide Chlorpyrifos	Synergistic (stronger chlorpyrifos-induced survival ↓ and heat tolerance ↓ under 10 °C DTF) Additive (growth rate)	[92••]
Temperate	Odonata	<i>Ischnura elegans</i>	Final larval instar (F0)	Survival, growth rate, malondialdehyde	Warming and 24 °C Constant, DTF 15.0–25.0 °C DTF 20 °C Constant 21.5–26.5 °C DTF 19.0–29.0 °C DTF	17.5–22.5 °C	Pesticide Chlorpyrifos	Synergistic (survival): strongest under warming and DTF increase (at 24 °C & 10 °C DTF) (Stronger chlorpyrifos-induced growth ↓ and malondialdehyde ↑ under 10 °C DTF)	[60]

Table 1 (continued)

Regions	Taxa	Species	Exposed life stage	Response variables	Type of warming	Temperature range	Contaminants	Interaction type	Ref.
Temperate	Odonata	<i>Ischnura elegans</i>	Final larval instar (F0)	Energy availability, energy consumption, energy budget	DTF 15.0–25.0 °C DTF 20 °C Constant 21.5–26.5 °C DTF 19.0–29.0 °C DTF 24 °C Constant	15–29 °C	Pesticide Chlorpyrifos	Synergistic (strongest chlorpyrifos-induced energy budget ↓ (–18%) and energy availability ↓ (–16%) under warming and DTF increase (at 24 °C & 10 °C DTF))	[61]
Temperate	Isopoda	<i>Asellus aquaticus</i>	Individuals with similar mass (mean ± SE: 14.76 ± 0.19 mg)	Survival, growth rate, feeding rate	DTF 18 °C Constant 18.0–26.0 °C DTF 22 °C Constant	14.0–22.0 °C	Pesticide Chlorpyrifos	No effect on survival Synergistic (strongest chlorpyrifos-induced growth ↓ under warming and DTF increase (at 22 °C & DTF)) Chlorpyrifos and 4 °C warming DTF Antagonistic (feeding rate) Chlorpyrifos and DTF at 18 °C Additive (feeding rate) Chlorpyrifos and DTF at 22 °C Synergistic (feeding rate)	[93]
Temperate	Amphipoda	<i>Gammarus pulex</i>	Adult stage	Survival, molecular responses	DTF: (Average: 16 °C) 18–22 °C DTF (Average: 20 °C)	14–22 °C	Inorganic chemical Mercury(II) chloride	Additive (survival, stronger effects of Mercury(II) chloride under warmer DTF)	[94]
Marine invertebrates									
Temperate	Mysida	<i>Neomysis awatschensis</i>	Juveniles and adults	Survival, antioxidant defenses	3 °C warming, stable temperatures	22–25 °C	Metals: arsenic, cadmium, copper, lead, zinc	Synergistic	[95]
Temperate	Harpacticoida	<i>Tigriopus japonicus</i>	Adults	Survival and accumulation, gene expressions	3 °C warming, stable temperatures	22–25 °C	Metal mercury	Synergistic	[96]

Table 1 (continued)

Regions	Taxa	Species	Exposed life stage	Response variables	Type of warming	Temperature range	Contaminants	Interaction type	Ref.
Tropics	Ostreida	<i>Crassostrea brasiliana</i>	Adult	Accumulation, gene expressions (HSP70, HSP90, fatty acid binding protein, biotransformation)	6 and 8 °C warming, stable temperatures	18–32	Polycyclic aromatic hydrocarbon: phenanthrene	Antagonistic for accumulation, additive for gene expressions	[28]
Temperate	Mytiloidea	<i>Mytilus galloprovincialis</i>	Embryo and juveniles	Malformation, DNA damage, gene expression (DNA repairmen)	2 °C warming, stable temperatures	18–22 °C	Metals copper, silver, and mixture	Synergistic	[97]
Temperate	Neogastropoda	<i>Tritia neritea</i>	Adults	Survival, foraging success, searching time, feeding time	6 °C warming, stable temperatures	15–21 °C	Lithium	Synergistic (survival), additive (foraging success and feeding time), and antagonistic (searching time)	[98]
Temperate	Mytiloidea	<i>Mytilus galloprovincialis</i>	Adults	Accumulation, antioxidant defenses, cellular damage	5 °C warming, stable temperature	20–25 °C	Metal cadmium	Additive (accumulation) Synergistic (antioxidant defenses and cellular damage)	[99]
Subantarctica	Harpacticoida	<i>Harpacticus</i> sp.	Adult	Survival	2–3 °C warming, stable temperature	6–11 °C	Metal copper	Synergistic	[26•]
Subantarctica	Isopoda	<i>Limnoria stephenseni</i>	Adult	Survival	2 °C warming, stable temperature	6–10 °C	Metal copper	Synergistic	[26•]
Subantarctica	Tricladida	<i>Obrimoposthia ohlmi</i>	Adult	Survival	4 °C warming, stable temperature	6–10 °C	Metal copper	Addictive	[26•]
Subantarctica	Veneroidea	<i>Gaimardia trapesina</i>	Adult	Survival	3 °C warming, stable temperature	5.5–8.5 °C	Metal copper	Synergistic	[26•]
Subarctic	Calanoidea	<i>Calanus finmarchicus</i>	Adult males and females	Fecal pellet production	4 °C warming, stable temperature	10–14 °C	Polycyclic aromatic hydrocarbon Pyrene	Additive	[100]
Tropics	Scleractinia	<i>Acropora formosa</i>	Adults	Bleaching: colour, chlorophyll content, zooxanthellae cell division	3 °C warming, stable temperature	28–31 °C	Pesticides	Antagonistic (bleaching colour and chlorophyll content), additive (zooxanthellae cell division)	[101]

Table 1 (continued)

Regions	Taxa	Species	Exposed life stage	Response variables	Type of warming	Temperature range	Contaminants	Interaction type	Ref.
Tropics	Scleractinia	<i>Mussismilia hartii</i>	Adults	Trophic behaviours; lipid peroxidation (LPO) and total antioxidant capacity (TAC)	1–1.5 °C warming, stable temperature	25–27.5 °C	Metal copper	No effect after 4 days of exposure Additive effects of warming and copper on LPO of corals	[40]
Tropics	Calanoida	<i>Centropages velificatus</i>	Adults	Survival, egg production, specific fecal pellet production	2–3 °C warming, stable temperatures	24.5–29.5 °C	Pyrene	Synergistic (survival, specific fecal pellet production at 100 nM) Antagonistic (specific fecal pellet production at 300 nM) Additive (egg production)	[50]

DTF daily temperature fluctuations, Ref. references

pyrene effects as indicated by a high mortality in the pyrene-free treatment at 10 °C [32]. Pyrene-exposed *C. finmarchicus* showed stronger decreases in egg production at both lower (0.5 °C) and higher (8 °C) temperatures than at an intermediate temperature (5 °C) [25]. The interactive effects of warming and trace metals on the survival of polar invertebrates are more consistent and generally synergistic (Table 1). For example, the lethal toxicity of copper on the sub-Antarctic marine copepod *Harpacticus* sp., the isopod *Limnoria stephenseni*, and the bivalve *Gaimardia trapesina* increased when the temperature increased from 6 to 8 °C or 10 °C [26•].

In tropical ecosystems, aquatic invertebrates are hyper-diverse [33] and are highly sensitive to contaminants, particularly when the temperature is above 25 °C [34]. Furthermore, tropical aquatic invertebrates occur close to their upper thermal limit and are therefore highly susceptible to warming [35–38]. A small increase in the water temperature may result in great ecological consequences [35] and this is expected to be more severe in contaminated environments. For example, the tropical copepod *Pseudodiaptomus annandalei* lives in coastal areas with a seawater temperature of 24–30 °C; an increase of 4 °C in temperature may severely impair its growth, development, and reproduction [39]. Exposure to copper (26.5 µg/L) reduced the survival of *P. annandalei* males and females with 32% and 62% at 30 °C, and considerably more so at 34 °C (74% and 95%, respectively) [27]. At the sublethal level, Cu-exposed females produced eight times fewer nauplii at 34 °C than at 30 °C [27].

Another study on a tropical species highlighted how exposure duration may result in different single and additive effects of warming and the metal copper on the physiology of the reef-building coral *Mussismilia hartii* and its photosynthetic symbionts [40]. There was no change in either corals or symbionts in cellular damage (e.g., lipid peroxidation) or total antioxidant capacity after 4 days of exposure to thermal stress. After 12 days of exposure, however, the symbiont had reduced lipid peroxidation under thermal stress, and increased total antioxidant capacity under both stressors [40]. The coral showed an increase in cellular damage under thermal stress or copper exposure, but there was no interaction between the two stressors [40].

Interactive Effects of Contaminants and Heat Extremes

Heat waves (duration ≥ 5 days) and heat spikes (duration < 5 days) can be defined as discrete periods of abnormally high temperatures above the 90th percentile of temperatures recorded in a 30 year timespan at a given locality [41]. Invertebrates typically respond negatively to heat waves [42], including mass coral bleaching (e.g., along ~2,300 km of the Great Barrier Reef in 2017 [43]) and mass mortality of freshwater and coastal marine invertebrates (e.g. Cnidaria,

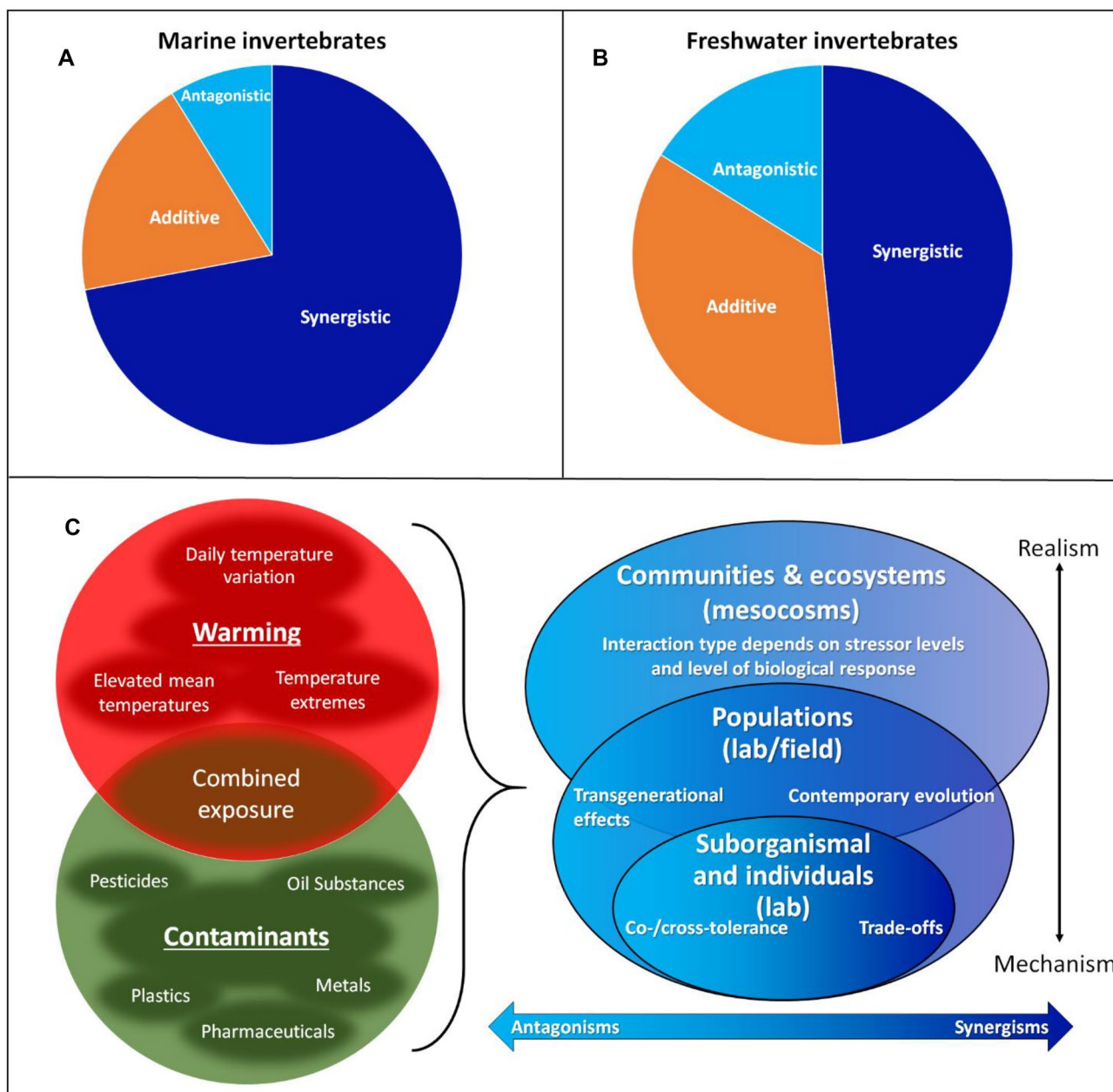


Fig. 1 Summary of the proportion of each type of interactive effects between warming and contaminants on marine (A) and freshwater (B) invertebrates, and (C) schematic overview how the combined

effects of warming and contaminants depend on the aspects of warming and contaminant type, the intensity of stressors being manipulated, and the level of biological organization studied

Porifera, Bryozoa, Bivalvia, Annelida, Chlorophyta, Echinodermata in the Mediterranean Sea [44]). Episodes of heat waves occur at a higher frequency and have a longer duration and greater intensity under global warming, particularly in Arctic and tropical ecosystems [45].

The few studies on combined effects of heat waves/spikes and contaminants showed interactive effects with pesticides in temperate freshwater invertebrates [46, 47, 48••], and with metals and oil substances in tropical marine copepods [49, 50]. Life history traits of

contaminant-exposed invertebrates are generally severely impacted under heat waves, which can be linked to metabolic depression, and an associated reduced protein synthesis, and to increased oxidative damage [46]. While a heat wave may be lethal in itself [46], contaminant exposure may reduce heat tolerance [51], further increasing the mortality risk under heat stress [46]. Synergistic effects between heat waves/spikes and contaminants have indeed been reported [46], yet a study on water fleas revealed that within a set of six *Daphnia magna* clones of a single

Table 2 Summary of major findings of the interactive effects of warming and emerging contaminants including pharmaceuticals, nanoparticles, and microplastics on freshwater and marine invertebrates in laboratory experiments

Regions	Taxa	Species	Exposed life stage	Response variables	Type of warming	Temperature range	Contaminants	Interaction type	Ref.
Freshwater invertebrates									
Temperate	Diplostroaca	<i>Daphnia magna</i>	4th brood neonates	Survival, total lifetime reproductive success, population growth rate	DTF 20 °C Constant 25 °C Constant	10.0–25.0 °C	Pharmaceutical Fluoxetine	Synergistic (greater fitness costs under fluoxetine & DTF exposure: –37% in lifetime reproductive success; –17.9% in population growth rate)	[102]
Temperate	Diplostroaca	<i>Daphnia magna</i>		Age at maturity, fecundity, growth rate, physiology, heartbeat rate, and swimming speed	Stable temperatures (20 and 24 °C) and DTF ()	17.5–29 °C	Microplastics	Synergistic (under DTF) Additive (under increasing mean temperatures) Effects of warming were generally much greater than microplastics	[24]
Marine invertebrates									
Temperate	Mytiloidea	<i>Mytilus edulis</i>	Adults	Gene expressions (apoptosis-related: <i>HSP70</i> , <i>CASP8</i> , <i>BCL2</i> , and <i>FAS</i>)	10 °C warming, stable temperature	10–20 °C	Pharmaceutical Metformin	HSP70: antagonistic caused by the dominant stress of warming; <i>CASP8</i> , <i>BCL2</i> , and <i>FAS</i> : synergistic, but the responses to temperature, metformin, and their combinations were in different directions	[103]
Temperate	Harpacticoida	<i>Tigriopus japonicus</i>	Adults	Survival, antioxidant defenses	10 °C warming, stable temperatures	15–35 °C	Metal zinc oxide nanoparticles	Synergistic	[104]
Temperate	Anostraca	<i>Artemia salina</i>	Instars I and II	Immobilization rate	5 °C warming, stable temperatures	25–30 °C	Metal silver nanoparticles	Synergistic	[105]
Temperate	Camarodonta	<i>Paracentrotus lividus</i>	Larvae	Larval growth and development	4 °C warming, stable temperatures	20–24 °C	Microplastics	Additive	[22]

Table 2 (continued)

Regions	Taxa	Species	Exposed life stage	Response variables	Type of warming	Temperature range	Contaminants	Interaction type	Ref.
Tropics	Scleractinia	<i>Pocillopora verrucosa</i>	Adults	Mortality, bleaching, photosynthetic efficiency, tissue necrosis	6 °C warming, elevated mean temperatures, DTF	27–33 °C	Microplastics	Experiment 1: under elevated mean temperature Additive (mortality, bleaching, survival) Experiment 2: under elevated mean temperature Synergistic (bleaching) Antagonistic (maximum photosynthetic efficiency) Experiment 3: DTF Additive (photosynthetic efficiency, bleaching, tissue necrosis, microplastics had minor effect compared to heat stress)	[23]

Table 2 (continued)

Regions	Taxa	Species	Exposed life stage	Response variables	Type of warming	Temperature range	Contaminants	Interaction type	Ref.
Tropics	Scleractinia	<i>Stylophora pistillata</i>	Adults	Mortality, photosynthetic efficiency, bleaching, tissue necrosis	6 °C warming, elevated mean temperatures, DTF	27–33 °C	Microplastics	Experiment 1: under elevated mean temperatures Antagonistic (mortality, bleaching, photosynthetic efficiency) Experiment 2: under elevated mean temperatures Additive (photosynthetic efficiency, bleaching, tissue necrosis, microplastics had minor effect compared to heat stress) Experiment 3: DTF Additive (photosynthetic efficiency, bleaching, tissue necrosis, microplastics had minor effect compared to heat stress)	[23]
Tropics	Scleractinia	<i>Acropora muricata</i>	Adults	Bleaching, photosynthetic efficiency, tissue necrosis	6 °C warming, elevated mean temperatures	26–32 °C	Microplastics	Additive (microplastics had minor effect compared to heat stress)	[23]
Tropics	Scleractinia	<i>Montipora digitata</i>	Adults	Bleaching, photosynthetic efficiency, tissue necrosis	6 °C warming, elevated mean temperatures	26–32 °C	Microplastics	Additive (microplastics had minor effect compared to heat stress)	[23]
Tropics	Scleractinia	<i>Porites cylindrica</i>	Adults	Bleaching, photosynthetic efficiency, tissue necrosis	6 °C warming, elevated mean temperatures	26–32 °C	Microplastics	Additive (microplastics had minor effect compared to heat stress)	[23]

DTF daily temperature fluctuations, Ref. references

population, the interaction type could vary between a synergism to an antagonism, whereby the more pesticide-tolerant clones showed a stronger synergism [47].

In marine ecosystems, heat waves occur in 25% of the world oceans [52], yet the investigations on the interactive effects of heat waves and contaminants on marine species are very limited. In the tropical marine copepod *Centropages velificatus*, effects of a short-term exposure (5 days) to pyrene and heat waves on survival, reproduction, and grazing were synergistic, antagonistic, or additive depending on the life history trait measured and the intensity of the stressors [50]. Indeed, at the control temperature (24.5 °C), pyrene exposure only reduced the survival at a concentration of ~300 nM, but under a simulated heat wave, the lethal effect of pyrene already occurred at a concentration of 100 nM, indicating a synergistic effect [50]. There was also a synergistic effect for fecal pellet production, whereby exposure to the heat wave or to 100 nM pyrene alone did not reduce this variable, while it was reduced by 86% when the two stressors were combined [50]. In contrast, the highest pyrene exposure concentration (~300 nM) also caused a strong reduction in pellet production, which was not reduced further under a heat wave, suggesting an antagonistic effect and highlighting the role of pyrene as a dominant stressor in this system [53] and the importance of stressor magnitude in determining interactive effects.

No studies tested for the combined effect of heat waves or heat spikes and emerging contaminants on marine and freshwater invertebrates.

Interactive Effects of Contaminants and Daily Temperature Fluctuations

One limitation in current studies on the interactive effects of warming and contaminants is that experiments have been conducted under constantly elevated temperatures. In nature, however, ambient temperatures fluctuate on a daily basis, which may be more challenging for ectotherms compared to exposure to increased average temperatures [54]. Exposure to daily temperature fluctuations (DTF) is energetically costly [55] and may therefore shape how organisms deal with contaminants [56]. In the majority of studies, daily temperature fluctuations and contaminants reinforced each other's effects, resulting in synergisms, which has been mostly observed in terms of reduced survival rates (Tables 1, 2). For example, larval survival of *C. pipiens* mosquitoes under chlorpyrifos exposure was ~15% lower in the presence of 7 and 14 °C DTF than at the constant temperature of 20 °C [57]. A similar pattern has been observed for *I. elegans* damselflies, where chlorpyrifos exposure decreased larval survival (–25%) and growth rate (–100%), yet only under 5 and 10 °C DTF and not at a constant temperature of 20 °C [58]. Notably, the synergistic effect between warming and a contaminant was stronger under the more realistic global

warming scenario in which both higher average temperatures and higher daily temperature fluctuations are combined [58], yet antagonistic interactions between pesticides and daily temperature fluctuations have also been observed. For example, while chlorpyrifos exposure reduced larval survival of *C. pipiens* mosquitoes with ~40% at a constant temperature of 20 °C, chlorpyrifos did not affect larval survival under 10 °C DTF, which was explained by a faster chlorpyrifos degradation rate under DTF [59]. Although physiological responses are important for mechanistic insights to explain observed patterns in life history traits, they are understudied and mostly show no interaction patterns [56] (Table 1), yet few studies have found that daily temperature fluctuations increased the impact of chlorpyrifos at the physiological level, in terms of increased levels of oxidative damage to lipids [60] and reduced energy budget levels [61].

Only two studies tested the effects of emerging contaminants in the presence of DTF. A study on reef building corals found additive effects of microplastics and DTF [23], whereby the effects of realistic microplastics concentrations were weakly positive while those of DTF were strongly negative [23]. For the freshwater invertebrate *D. magna*, exposure to microplastics increased fecundity and intrinsic growth rate, but only under 5 °C DTF and not under a constant optimal temperature, likely because of an associated increase in food ingestion [24].

In summary, there is a need for improving our understanding of how aquatic invertebrates, particularly those occurring in extreme thermal environments such as polar and tropical regions cope with contaminants under warming, and especially under realistic daily temperature fluctuations and heatwaves. Investigations considering different stress levels, exposure durations, and temporal aspects of stressors on different life stages are particularly needed.

Multigenerational Effects Shaping the Interaction Type Between Contaminants and Warming

Recent studies on aquatic invertebrates revealed that the interaction effects between warming and contaminants may depend on exposure of the parental generation, highlighting the role of transgenerational effects in shaping the susceptibility of aquatic invertebrates to human-induced rapid environmental change [62]. Parental exposure to warming or contaminants can have two contrasting outcomes that may eventually shape their interaction type. Parental exposure can, through acclimation, alleviate in the offspring the negative effects of single stressors such as warming [63], and contaminants [64]. This was shown in the mosquito *C. pipiens*, the chlorpyrifos-induced lethal and sublethal effects in the offspring were smaller when parents had also been exposed to chlorpyrifos [64]. Similarly, when the parental generation

of the mosquito *C. pipiens* was exposed to warming, warming no longer reduced diving times in the offspring [63], yet generally, our review indicates that parental exposure to warming or a contaminant increased the vulnerability of offspring to warming [65], and to contaminants such as metals (e.g. copper [49], and lead [66•]) and pesticides (e.g. chlorpyrifos [65]) and this pattern was observed across marine and freshwater invertebrates. This can be explained by poor maternal provisioning and/or the transfer of contaminants or metabolites from mothers to offspring [67].

Such transgenerational shaping of the offspring's tolerance to single stressors may eventually affect the interaction type in the offspring. In freshwater invertebrates, a series of studies on the mosquito *C. pipiens* demonstrated evidence for this but at the same time showed it to be case-specific. Two studies showed that the increased sensitivity to the pesticide chlorpyrifos under warming was less pronounced when also the parental generation had been exposed to warming [64, 68]. This could be explained by the observation that only in the latter case warming caused no reduction in the net energy budget [64]. Furthermore, the synergism between warming and the pesticide chlorpyrifos shifted toward an additive effect in offspring whose parents were exposed to both warming and the pesticide because in this condition the pesticide was already more lethal at the lower temperature [65]. In the same species, the interaction type between warming and the pesticide chlorpyrifos changed from an antagonism (caused by increased degradation of the pesticide) when parents were not exposed to warming toward an additive pattern when parents experienced warming [63], yet some studies found no effect of the parental exposure history on the interactions between warming and contaminants in the offspring. For example, a heat spike enhanced the toxicity of chlorpyrifos on the survival of *C. pipiens* in both parental and offspring generations, and the magnitude of the interactive effects remained the same in the offspring [64].

A few studies went a step further and tested for interactive effects between warming and a contaminants after many generations of exposure. These experiments have been limited to species with relatively short generation times, mainly marine copepods and water fleas, mosquitoes, and rotifers. These studies so far indicate that such multigenerational exposure may strengthen as well as weaken the interaction type. In the tropical marine copepods *Pseudodiaptomus annandalei* and *P. incisus* the interaction between copper and a heat wave was synergistic, additive, or antagonistic depending on the life history trait and the number of exposed generations [27, 49]. Heat waves typically magnified the lethal and sublethal effects of copper in the parental generation [27, 49]. Interestingly, the interaction between copper and a heat wave on the clutch size, the nauplii and fecal pellet production was synergistic in the parental generation, but became additive in the offspring generations [49]. In the freshwater water

flea *Moina dubia*, the interaction effect between warming and the metal lead was antagonistic, and this antagonistic effect increased gradually across 10 exposed generations and levelled off in the 11th exposed generation [66•].

In summary, transgenerational effects of warming and contaminants tend to shift the interaction type from synergistic in the parental generations toward antagonistic in the offspring generation(s), likely due to the poor maternal provisioning of exposed parents.

Evolution Shaping the Interaction Type Between Contaminants and Warming

While transgenerational effects are reflecting plastic changes, also, evolutionary (genetic) changes may shape the interaction type between contaminants and warming in aquatic invertebrates. Recent studies have shown that aquatic invertebrates can rapidly evolve adaptations to warming (e.g., [69, 70, 71••]) and contaminants (e.g., metal copper [72]). Such evolution of tolerance to a single stressor may eventually shape the interaction type with a second stressor. In marine ecosystems, rapid evolution of the copepod *Acartia tonsa* to warming and CO₂-induced ocean acidification changed the interaction type between both stressors [71••]. Indeed, the synergistic negative effects of warming and ocean acidification on egg production rate and hatching success in the first generation disappeared in generations 3–25 as both traits recovered [71••] caused by rapid genetic adaptation [73]. Furthermore, the combined effects of these stressors on survival and development time shifted from additive (no interaction) toward antagonistic, particularly after 15 generations caused by increased survival in the warming treatment, but not in the selection treatment where both stressors were combined [71••]. The genome-wide analyses showed substantial allelic frequency changes in response to warming (57%), ocean acidification (20%), and their combination (63%) whereby warming was the dominant stressor in driving the interactive effects [74••].

In freshwater ecosystems, two studies in the water flea *D. magna* showed contrasting effects of how thermal evolution can shape the interaction effects between warming and zinc oxide nanoparticles. A resurrection study of a natural population showed that the old “ancestral” subpopulation, which were obtained from resting eggs in lake sediments, showed a synergism for intrinsic growth rate, metabolic activity, and energy reserves which disappeared in the recent “derived” subpopulation that evolved a lower sensitivity to the nanoparticles at 24 °C [75]. This indicates that thermal evolution could offset the elevated toxicity of nano-zinc particles under warming. Instead, experimental evolution trials in heated mesocosms showed that nano-zinc particles were more toxic at 20 °C than at 24 °C due to a higher accumulated zinc burden at 20 °C than at 24 °C, and this did not change

after thermal evolution [76]. This suggests that the ecological context may critically shape the evolutionary outcome of the stressor interaction type. In an experimental evolution trial with the rotifer *Brachionus calyciflorus*, animals evolved to both single and combined exposure to contaminants (salt and copper) and a lower temperature [77]. Here, rapid evolution to contaminants and a lower temperature shifted their interactive effect toward a synergism [78••].

From the limited number of evolutionary experiments, no pattern seems to emerge as rapid evolution to warming and contaminants may both enhance antagonisms, and enhance or reduce synergisms.

Mesocosm Studies Testing Higher-Level Effects of the Interaction Between Warming and Contaminants

All studies discussed above are indoor laboratory experiments, and while these are highly relevant for providing detailed and mechanistic insights into the interactive effects of warming and contaminants (see e.g., [46, 79]), their limited environmental realism limits extrapolation of their findings to real-world systems. Only few freshwater studies have empirically attempted to link the combined effects of warming and contaminants from the individual to the ecosystem levels in a single study (see [48••, 80, 81]). Such studies are important for demonstrating how individual trophic level studies are predictive of multitrophic community responses, where biotic interactions such as competition, predation, and parasitism can modify how effects manifest throughout the food web [15••]. The costly nature of manipulating water temperature in semi-natural conditions and challenge of controlling treatments that follow the natural fluctuations of the ambient, environmental temperature are reasons for the rarity of these studies. These manipulations of thermal regimes are more achievable in smaller, closed mesocosm systems mimicking pond systems [80–84]. By contrast, achieving these in open stream mesocosm systems (e.g. [48••, 85, 86]) is considerably more challenging due to the constant, yet varying input of heated water required to maintain the desired temperature difference. Measuring and processing samples across multiple trophic levels (as achieved by Van de Perre et al. [80] in indoor laboratory microcosms, see below) are also costly and time-consuming.

Recent meta-analyses have shown that the combined effects of two stressors are more often antagonistic at the community and ecosystem levels [53, 87]. This might be caused by increased functional redundancy or species acclimating to similar stressors so exposure to additional stress has a less-than-additive effect [53]. There have been two published outdoor aquatic mesocosm studies to investigate the combined effects of raised water temperature

and contaminants; one each in pond mesocosms [82] and in flow-through circular stream channels [48••]. The pond mesocosm study found no effects of three simulated heat waves on the effect of a single pulse of the insecticide esfenvalerate on the zooplankton community. However, pesticide effects on the common and sensitive taxon, *Daphnia* spp., lasted twice as long under warming compared to constant ambient temperatures, likely increased interspecific competition under warming prolonged *Daphnia* spp. recovery. The second study simulated climate warming and reduced flow velocity and pulsed exposure of the neonicotinoid imidacloprid in flow-through stream mesocosms [48••]. Owing in part to a natural heat wave that occurred during the experiment, only antagonistic interactions between imidacloprid exposure and raised water temperature were observed, where the negative effects of imidacloprid on the macroinvertebrate community were the strongest at ambient temperatures. These results resemble those observed in a laboratory microcosm study, where negative effects of chronic imidacloprid exposure only manifested in mayfly nymphs that had had no prior exposure to simulated heat waves [79]. By contrast, short-term laboratory exposures with freshwater macroinvertebrates to imidacloprid at higher concentrations over a wider temperature gradient had previously shown synergism between these two stressors, demonstrating temperature-enhanced toxicity of imidacloprid [19]. Taken together, these findings suggest that the observed interaction type can be heavily dependent on the level (and environmental realism) of each manipulated stressor.

Two further studies have investigated the combined effects of temperature and contaminants at the community level using indoor microcosm experiments [80, 81]. A first study [80] found that interactions between raised water temperature and zinc on freshwater zooplankton, phytoplankton, and protozoan communities were far more prevalent at the community level than at the species population level. Most of these interactions were antagonistic where the effect of zinc (at the highest concentration applied) was smaller at the higher temperature. A second study [81] observed both synergistic and antagonistic interactions between raised water temperatures and the insecticide lufenuron for different zooplankton taxa. Overall, increased temperature did not affect the sensitivity of the community to the insecticide but it did reduce the time to onset of toxic effects (likely due to increased chemical uptake as a result of raised metabolic rates [11]) and subsequent recovery from low-level insecticide exposure (likely because of increased pesticide degradation [88]).

In future research, there is a need for more studies to address the important question of how contaminant and temperature interactions affect whole ecosystems with multiple trophic levels and higher levels of biological organization in environmentally realistic scenarios [15••]. With continually

improving methods of manipulating temperature in semi-natural mesocosm studies (e.g. [83]), such studies will likely become more common. Mesocosms are an ideal tool for assessing the impacts of contaminants at the ecosystem-level, in combination with other climate-related stressors that are not easily manipulated in situ [48••, 89]. By replicating the trophic diversity of natural ecosystems, maintaining environmentally realistic physicochemical conditions and biotic interactions, and allowing the manipulation of toxic substances in controlled, yet realistic environments, mesocosm experiments represent a promising opportunity for providing the empirical data needed to improve our understanding in this field.

Summary Remarks

Global warming and heat extremes continue to be among the most pressing threats for global invertebrate biodiversity [90]. In addition, continued and increased use and release of chemical contaminants in the environment poses another threat. Our review highlights that the interaction type between an increase in mean temperature and contaminants is mainly synergistic but also indicates the type and strength of the interaction between both stressors depends on taxa, the response variable, life stage, genotype, exposure level, duration and order of exposure, and the number of exposed generations (Tables 1, 2). The combined effects of warming and contaminants also need to be assessed under more realistic thermal scenarios of temperature fluctuations, particularly in mesocosms to increase the environmental realism. Linking laboratory experiments and mesocosm studies are essential for understanding field observations of the combined effects of the two stressors. This information will be crucial for managing and mitigating the combined risk of global warming and pollutants in natural systems.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s40726-022-00245-4>.

Funding Open access funding provided by University of Oslo (incl Oslo University Hospital). K.V.D., K.B., and K.H. received grants from The Nansen Legacy (RCN#276730) and Researcher Project for Young Talents (RCN#325334) of the Research Council of Norway. S.J.M. and M.C.J received funding from UK's Natural Environment Research Council (NE/V001396/1). R.S. was supported by grants from the Fund for Scientific Research Flanders (FWO) and KU Leuven C1 grant C16/17/002.

Compliance with Ethical Standards

Conflict of Interest The authors declare no competing interests.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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