



Review

Alain Thill*, Marie-Claire Cammaerts and Alfonso Balmori

Biological effects of electromagnetic fields on insects: a systematic review and meta-analysis

<https://doi.org/10.1515/reveh-2023-0072>

Received June 1, 2023; accepted October 4, 2023;

published online November 23, 2023

Keywords: electromagnetic radiation; high frequency; low frequency; mobile phone; *Drosophila*; honey bee

Abstract: Worldwide, insects are declining at an alarming rate. Among other causes, the use of pesticides and modern agricultural practices play a major role in this. Cumulative effects of multiple low-dose toxins and the distribution of toxicants in nature have only started to be investigated in a methodical way. Existing research indicates another factor of anthropogenic origin that could have subtle harmful effects: the increasingly frequent use of electromagnetic fields (EMF) from man-made technologies. This systematic review summarizes the results of studies investigating the toxicity of electromagnetic fields in insects. The main objective of this review is to weigh the evidence regarding detrimental effects on insects from the increasing technological infrastructure, with a particular focus on power lines and the cellular network. The next generation of mobile communication technologies, 5G, is being deployed – without having been tested in respect of potential toxic effects. With humanity’s quest for pervasiveness of technology, even modest effects of electromagnetic fields on organisms could eventually reach a saturation level that can no longer be ignored. An overview of reported effects and biological mechanisms of exposure to electromagnetic fields, which addresses new findings in cell biology, is included. Biological effects of non-thermal EMF on insects are clearly proven in the laboratory, but only partly in the field, thus the wider ecological implications are still unknown. There is a need for more field studies, but extrapolating from the laboratory, as is common practice in ecotoxicology, already warrants increasing the threat level of environmental EMF impact on insects.

Introduction

Insects are an integral part of all ecosystems. It is estimated that over 80 % of flowering plants require pollinators [1]. In the absence of pollinating insects, around one-third of all wild plant species would produce no seeds at all, and half would experience an 80 % reduction in fertility [2]. Pollinators contribute to the productivity of most agricultural crops, and their lack could only be compensated by costly substitutes [3]. In addition, insects contribute to seed dispersal, nutrient cycling, decomposition of detritus and constitute an essential stage in food chains [4]. Many amphibian, reptile and bird species rely on insects for their diet, at least during critical periods of growth [5, 6]. The loss of pollinators could increase human global deaths yearly by about 1.4 million, which corresponds to a 2.7 % increase [7, 8].

The decline of insects began several decades ago and is caused by a multitude of factors with cumulative effects [9–11]. The main causes are the use of pesticides and the destruction, degradation, or fragmentation of natural habitats, and to a lesser extent, invasive species, climate change and overexploitation [12]. Pollutants whose occurrence in nature has drastically increased in recent decades are also likely implicated: endocrine disruptors, heavy metals and electromagnetic fields [13–15]. Agrochemicals have synergistic toxic effects: two pesticides, each administered at a dose that kills 10 % of test animals, can kill up to 90 % when administered simultaneously [16].

This systematic review following PRISMA guidelines [17] addresses the effects of low- and high-frequency electromagnetic fields on insects. Electromagnetic fields (EMF) are non-quantum fields produced by moving electrical charges, that exert forces on any charged object in their vicinity. They consist of two distinct but inseparable field components (electric and magnetic) perpendicular to each other, as described in Maxwell’s equations [18]. Natural EM radiation (EMR), e.g. sunlight and resonances within the atmosphere caused by lightning discharge (Schumann resonances),

***Corresponding author: Alain Thill**, MSc Env Sciences, Independent Researcher, Brouch, Luxembourg, E-mail: alain.thill@protonmail.com

Marie-Claire Cammaerts, Independent Researcher, Retired from the University of Brussels, Brussels, Belgium

Alfonso Balmori, Independent Researcher, Valladolid, Spain, E-mail: abalmorimartinez@gmail.com. <https://orcid.org/0000-0002-4118-0912>

differ from man-made EMFs. Anthropogenic EMFs are coherent, polarized and stronger than natural ones [19]. A distinction is made between extremely low frequency electromagnetic fields (LF-EMFs), mainly high-voltage power line and mains current with 50- or 60-Hz frequency, and “radiofrequency”, i.e. high frequency EMFs (HF-EMFs), e.g. WiFi and mobile telephony, but also Radar, mostly in the range of a few GHz [20]. Technically, the currently commonplace HF-EMFs of anthropogenic origin fall into the categories of ultra or super high frequencies, i.e. microwaves (300 MHz–300 GHz), but will here be denoted as HF [20]. HF-EMFs propagate in a wave-like manner, as radiation (i.e. far-field behavior), but LF-EMFs from power lines are better described as bound to these power lines (i.e. near-field behavior). Technological HF-EMFs are in general pulsed or pulse-modulated, meaning that the carrier frequency (a sine wave) is emitted, cut-off and re-emitted many times per second. Typical values are 10 Hz (WiFi), 100 Hz (DECT), 217 Hz (GSM) up to 1,000 Hz and above (4G and 5G). The widespread use of newer technologies that use HF-EMFs, i.e. WiFi and cell phones, started from *ca* 1990 on. In general, a distinction is made between thermal and non-thermal effects of HF-EMFs. The thermal effect is based on direct heating of tissue (as in a microwave oven), and is biologically relevant for an increase of more than 1 °C. Below the intensities where tissue heating is substantial, several non-thermal effects have been described, e.g. parametric resonance and microwave hearing in humans (Frey effect) [21, 22]. Recent findings from cell biology point towards the implication of multiple mechanisms or pathways to explain the experimentally observed biological effects of EMF, as discussed below.

Ephaptic coupling and perception of EMF through ion channels for synchronization of neuronal activity

Animals have stable rhythms in their brains, measurable by electroencephalogram (EEG) or electrodes, for example. For honeybees and locusts, a main frequency of 18 Hz or 20 Hz was observed, and 20–30 Hz in *Drosophila* fruit flies [23–25]. Parametric resonance describes the change of the human or animal EEG observed upon exposure to pulsed EMFs [26, 27]. EMFs pulsed at brain frequencies cause considerably stronger effects than continuous, non-pulsed EMF. This is likely a by-product of the mode of operation of voltage-gated ion channels (VGICs) responsible for relaying nerve impulses, and therefore might affect all animals and plants [22, 28]. VGICs, e.g. Na⁺, K⁺, Ca²⁺ channels, as well as the N-methyl-D-aspartate (NMDA) receptor, are sensitive to

non-thermal (i.e. very low) endogenous EMF strengths. The perception of surrounding EMF arising from neuronal activity can lead to coupling of nerve fibers as a result of local electric fields [29–31]. This so-called “ephaptic coupling” influences the synchronization and timing of action potential firing in neurons, and appears to play an active role in the heart, hippocampus, cerebellum and olfactory or antennal nerves [30, 32, 33, 34, 35]. VGICs have been shown to respond to LF-EMF [36–39].

The activation of voltage-gated sodium or potassium channels or NMDA receptors indirectly leads to increased activation of synaptic voltage-gated calcium channels (VGCC) and release of calcium [40]. Calcium is an important secondary messenger in all organisms, and elevated levels of calcium have a stimulating effect, e.g., on the respiratory chain and muscle [41, 42]. An overactivation of calcium-dependent neurotransmission leads to the production of reactive oxygen species (ROS) such as peroxyinitrite, i.e. to oxidative stress. Chronic oxidative stress has a toxic effect on organisms, e.g., by blocking the respiratory chain, damaging mitochondria, misactivating the immune system and increasing the mutation rate [43, 44].

Geomagnetic storms caused by solar flares have been shown to cause stress in animals, a fact well documented in fish and *Daphnia*, migratory birds, and honeybees [45–47]. During solar flares impacting the Earth, the distance of the ionosphere to the ground changes, which in turn changes the Schumann resonances [48]. It may be that the perception of the stable frequencies of the Schumann resonances (7.83 Hz, 14 Hz, 20 Hz) was a key step in evolutionary history that enabled stable biorhythms [49, 50]. The rat heart responds to very weak magnetic fields in the range of the first Schumann resonance (7.6–8 Hz) [51]. This may be mediated by VGCCs and sarco/endoplasmic reticulum Ca²⁺-pumps (SERCAs), since specific blockers abolish the effect [52]. This is in accordance with theoretical calculations by Panagopoulos and Balmori, and may be the way animals perceive upcoming earthquakes, since earthquakes are preceded by geomagnetic field and ionospheric perturbations [53, 54]. The hypothesis that VGCCs are the main conduit by which biological effects of EMFs are produced is based on observations that EMFs cause calcium release (leading to oxidative stress), that calcium channel blockers protect from adverse effects as well as on theoretical grounds [55, 56].

Magnetic sense

A magnetic sense has been described in most insect orders, e.g. in butterflies, beetles, flies, ants and bees,

termites and cockroaches [57–61]. It has not yet been conclusively elucidated, and there are at least two mechanisms for perceiving the geomagnetic field: cryptochrome and magnetite, both found in vertebrates and insects [62, 63]. Also, some fish and insects (e.g. the electric eel and the hornet) have specialized organs or cells for sensing electric fields [64].

Cryptochrome

Cryptochrome (CRY), a molecule from the blue light receptor family, regulates the circadian rhythm in insects. In addition, cryptochrome is magnetosensitive once it has been activated by high-energy light via the radical pair mechanism [65]. CRY is found in the eyes and brains of most insects and vertebrates, where it acts as a molecular clock (see [66]). Using cryptochrome mutant *Drosophila*, Fedele et al. showed that cryptochrome is necessary for light- and EMF-induced delay of circadian rhythmicity [67]. Fogle et al. showed that CRY, by the intermediary of free radicals (ROS), opens the voltage-gated potassium channel $Kv\beta$ in the pacemaker neurons of *Drosophila*, leading to an increased action potential firing rate [36].

Sherrard et al. examined free radical production in *Drosophila* [68]. PEMF (“pulsed electromagnetic field”) devices are coils with medical applications, e.g. faster healing of wounds or bone fractures [40]. Wild-type *Drosophila* showed an aversion response and ROS formation after irradiation with a 10 Hz PEMF. This was not the case in mutant CRY-deficient *Drosophila*. An effect in the wild type was found only when blue or white light was present, since insect cryptochrome requires high-energy blue photons for its activation. In contrast, *Pyrrhocoris* firebugs seem to possess a mechanism to keep Cryptochrome in the activated state for more than a day after exposure to light, and it remains to be seen how comparable various insect orders are in this respect [69]. Using cell cultures of the owl butterfly, it was shown, that CRY is necessary for free radical formation when treated with PEMF coils, and this may apply to all LF-EMF sources [68]. Activation of cryptochrome by EMF, proven and largely elucidated in birds and insects, leads to opening of VGCCs in the clock neurons in *Drosophila* (Figure S1). Since these neurons regulate cell division throughout the body, this implies a cancer-promoting effect, which has been shown *in vitro* [70–72].

Magnetite

All insects possess cryptochromes in their eyes and brain. Ocular cryptochromes only function as magnetosensors

under blue light (red light in the case of birds). Insects that are active in the dark seem to use a magnetite-based magnetic sense instead; this has been experimentally confirmed in bees, ants and termites [60, 73, 74]. In honeybees, changes in the size of magnetite crystals cause a release of calcium [75]. Termites and cockroaches use a combination of CRY and magnetite for their orientation – CRY during the day, magnetite at night or in the dark [76–79].

Previous reviews whose references were included in this review

Cucurachi’s review: “Insects are a useful target system for the study of HF-EMF due to their limited size, short life cycle and the possibility to easily detect developmental errors [80].”

Balmori’s review: Balmori mentions that insects have long been shown to respond to (non-thermal) electromagnetic radiation in the microwave range, since this was first described 50 years ago by Carpenter and Livstone [81, 82]. Pulsed microwave radiation from cell phones or WiFi disrupts the development of *Drosophila* fruit flies and leads to reduced fecundity and increased mutation rate; these effects have been documented by several research groups [83–85].

Levitt et al.’s review: Levitt et al. is a three-part review of EMF effects on flora and fauna [86]. Part two discusses the effects of EMFs on animals and lists 140 references dealing with insects. Quote: “Many behavioral aspects in biology are thought to be synchronized with both the Earth’s natural fields and Schumann resonances. But now, for the first time in evolutionary history, we have covered the Earth’s surface with a blanket of artificial energy fields without knowing what the consequences might be.”

EKLIPSE Report and Vanbergen et al. review: A detailed report was written at the request of the English NGO “Bug-Life” [87, 88]. 39 studies were evaluated according to ecological aspects, 26 of which were additionally evaluated according to technical aspects. Vanbergen et al., contributors to the EKLIPSE report, evaluated the risk to pollinating insects only, thus excluding most EMF studies in insects [89]. The authors emphasize the proven harmfulness of “artificial light at night”, and claim, that the only clearly proven effect of man-made electromagnetic radiation to date is disruption of orientation [90–92]. This is a mere opinion of the authors not supported by science, as discussed below.

Methods

Literature search

A literature search was performed on the EMF-Portal database [93], using the following search terms: “insect drosophila bee apis pollinator ant termite locust cockroach” (separated by “Or”). The references of the reviews listed above were extracted and integrated into a common bibliography. A Google Scholar and Pubmed Central Search of the years 2012–2022 was made separately, using the following search terms: one of each: “insect; drosophila; bee; apis; pollinator; ant; termite; locust; cockroach” and all the following (separated by “Or”): “EMR; EMF; electromagnetic field; electromagnetic radiation; electromagnetic; high frequency; HF; low frequency; LF; WiFi”.

Methodology for selection of studies

The titles and abstracts of all entries were read and entries not in English nor German, or not related to the topic, were excluded. Then, full-text articles were viewed, and only those describing experiments with EMF on insects, not older than 1980, and considering non-thermal effects, were kept. Studies were categorized as non-thermal based on provided tissue temperature measurements, or on the declared power densities used in experiments, if they were below ICNIRP limits [94]. Some of the magnetic sense studies were used for the introduction, but were not used for further analysis.

Quality assessment

Studies underwent quality assessment before being included in the review. The review criteria checklist published by the Task Force of Academic Medicine and the GEA-RIME Committee was used for this purpose, as adapted by Bertagna et al. [55, 95]. All studies relevant to the topic were reviewed by the lead author for quality using 13 prespecified criteria, and those meeting at least 11 of the 13 criteria were retained [55].

Data extraction and processing

All studies included in the review were evaluated and data was recorded (by the lead author) in one spreadsheet each for HF- and LF-EMF. The data format of the Oceania Radiofrequency Scientific Advisory Association (ORSAA) database was used to record both the EMF sources used, field strengths and duration of experiments, as well as biological findings [96]. Supplementary columns for effect size (as percent change compared to control) and direction of effect (detrimental, beneficial, uncertain, none) were added. Direction of effect was determined based on the judgment of the respective study authors, or on common sense understanding of biology (such as increased mortality or occurrence of mutations being detrimental), or on corollary variables that the study authors had measured. E.g., increased oxidative stress was usually classified as “uncertain”, unless co-occurring reduced reproductive capacity or DNA damage was also observed, in which case it was classified as “detrimental”. When possible, extracted data were compared with values already recorded in the ORSAA database. Exposure times were converted to hours, and field strengths or power densities to V/m, when possible, using the formulas listed in the Appendix. Estimates of effect

size were obtained and normalized by converting percentage changes to ratios of means (ROM), and inverting the ratio of means in case of a diminution. Thus, a decrease of 50 % was counted as a ROM of 0.5, and the inverse of this, 2, was noted as the effect size estimate. In this way, positive toxicity measures, such as increased DNA damage in the ovaries, could be compared to negative changes, like reduced reproductive capacity [97]. Effect sizes of experiments finding beneficial outcomes were inverted, so that all detrimental outcomes would have a ROM > 1, and all beneficial outcomes a ROM < 1. Observed bioeffects were classified into the following categories: reduced reproductive capacity (damage to egg or sperm cells, reduced number of eggs laid or offspring), developmental effects (delayed or accelerated larval development, occurrence of mutations), DNA damage, altered DNA or DNA transcription, altered enzyme activity or metabolism, oxidative stress, altered behavior (speed of locomotion, reaction speed, orientation, response to pheromones), impaired memory, other. Disturbance of sense of direction or orientation was included in “altered behavior” [89]. Data was plotted in RStudio.

Data synthesis and statistical analysis

A minority of studies did have complete statistical information needed for meta-analysis, and it was possible to infer standard errors from p values for a wider number of studies (R package “dmetar”). Experiments that provided an effect size but were declared as “not statistically significant” or “no effect” were assigned a p value of 0.5. A meta-analysis was performed for all HF-EMF studies that found reproductive effects in *Drosophila*, this being the subgroup with the highest number of studies. Also, for the devices most often used in studies, it was possible to derive estimates of pooled effect sizes by meta-analysis, using the R packages “meta” and “bayesmeta” [98, 99]. RStudio was used for data synthesis, analysis and plots.

Results

The literature search in EMF-Portal yielded 413 results. The bibliographies of previous reviews and the literature search in Pubmed and Google Scholar together yielded 291 studies. After removing duplicates, a total of 587 entries resulted, which were treated as follows and as described in the PRISMA flowchart (Figure 1).

Selection of studies

One hundred and thirty studies relating experiments with EMF in insects, published after 1980, underwent quality appraisal. Three HF studies that are computer simulations were treated separately [100–102]. These studies are prospective in nature, and did not provide data points for the graphs, but did provide information on impacts to be expected in the future. 11 studies were excluded because of qualitative deficiencies (lacking EMF measurements, bad experimental procedure, inadequate design of experiments,

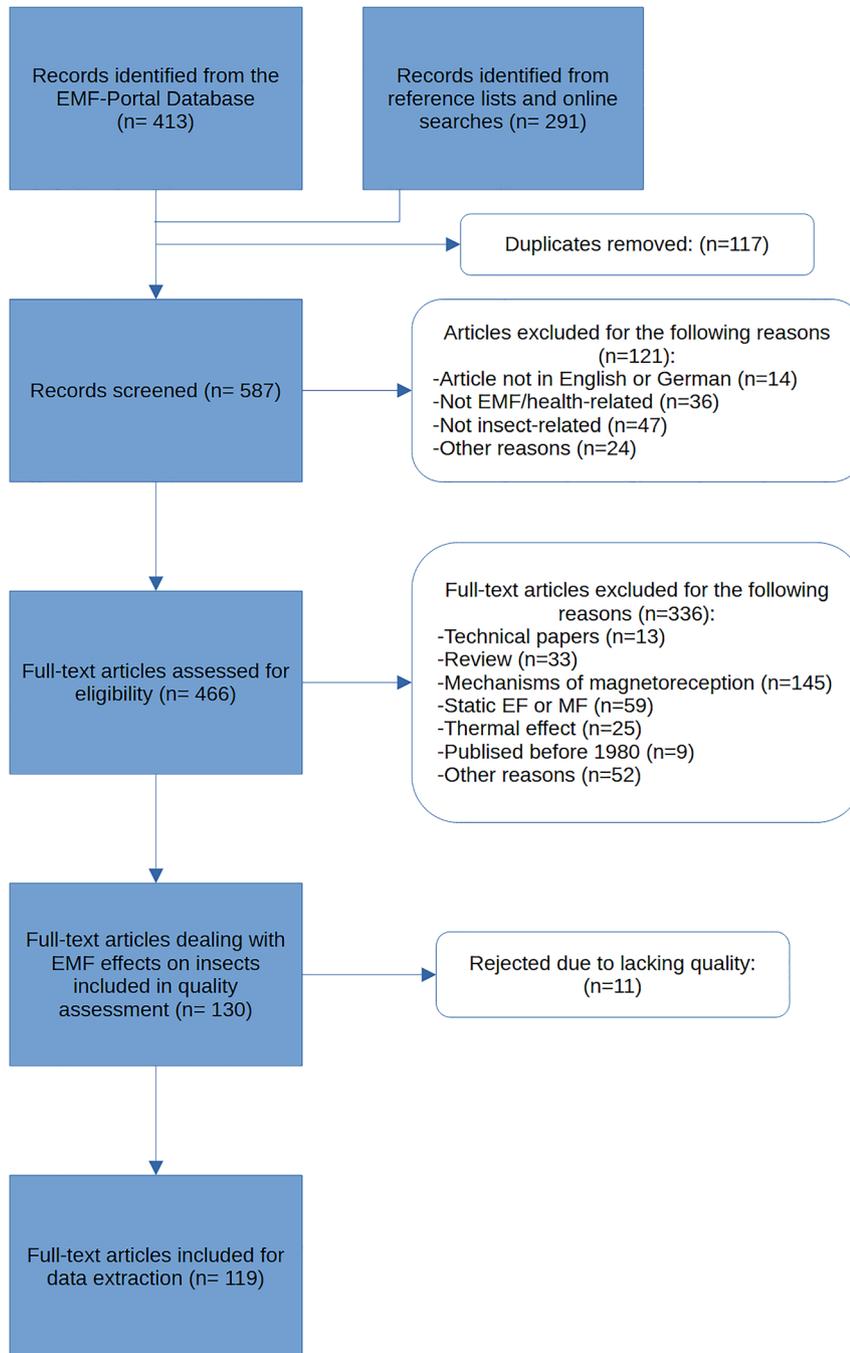


Figure 1: PRISMA flow diagram for selection of studies.

poor data handling or lack of reporting of statistical analyses) (cf. Supplementary Tables 1 and 2). 119 studies (64 LF studies, 55 HF studies) involving experiments with EMF in insects were subjected to data extraction and included in summary tables (cf. Supplementary Tables 3–6).

Trends

One hundred and eighty five papers (including reviews) on the effects of EMF on insects, and 145 studies on insect

magnetic sensing, have been published since 1980 (Figure 2). Trends indicate a slight increase of interest in the subject, but there is probably a lack of awareness for biological effects of EMF in general, since it is not a part of most university curricula and requires knowledge in multiple fields. In addition, the field of bioelectromagnetics is underfinanced and considered controversial.

The majority of the studies were conducted with *Drosophila* fruit flies or honey bees (Figure 3A). Generally, cell phones, coil systems or signal generators were used

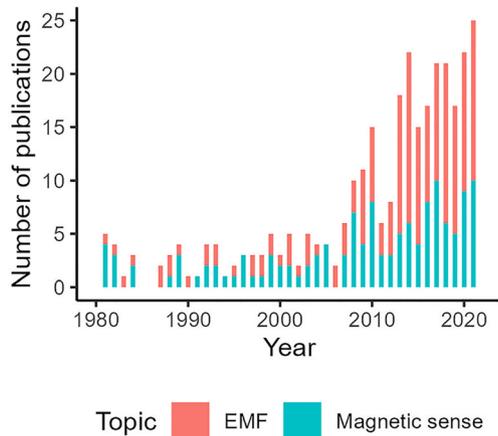


Figure 2: Number of publications on insects per year by topic.

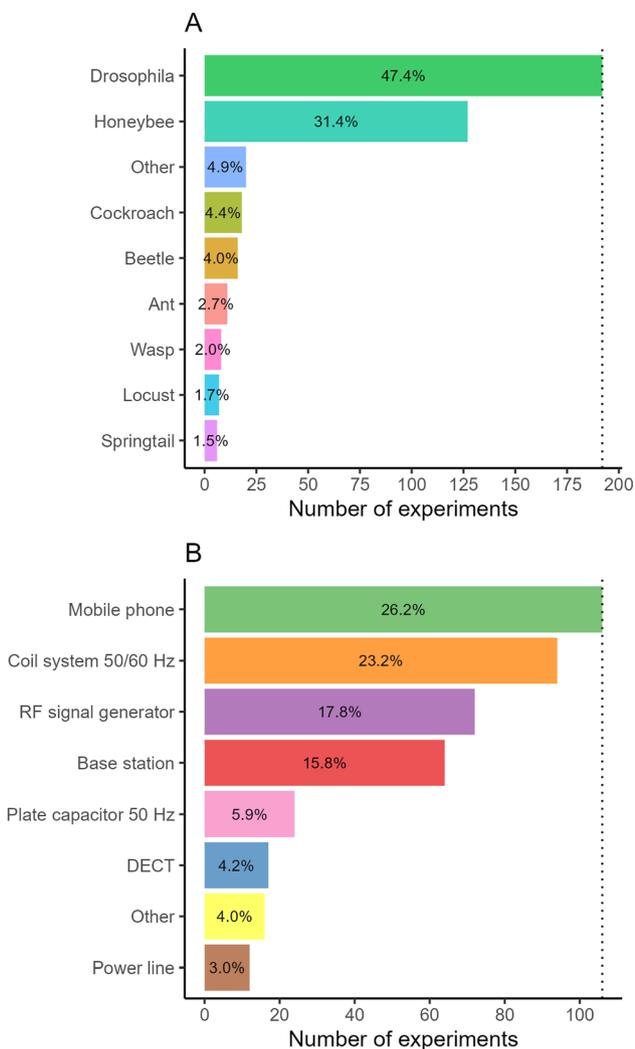


Figure 3: Number and percentage of published experimental findings by insect species or group (A) and EMF sources (B) used in experiments.

(Figure 3B). Helmholtz coils are wire coils powered by line current, and emit 50 Hz low-frequency EMF. In 70 % of studies using a coil system, Helmholtz coils were used. Nevertheless, a minority of studies used Merritt coils, solenoids or single electromagnetic coils: all these studies were grouped under the category “coil system”. Signal generators are, in the simplest case, oscilloscopes configured to produce high-frequency signals, with similar signal characteristics as wireless communications systems (WiFi, cellular 1G to 5G, etc.). The signal is usually fed to a horn antenna to radiate HF-EMF.

In the HF-EMF studies, radiation intensities (or electric field strengths) ranged from 0.00005 to 38,200 mW/m², respectively 0.0043–120 V/m (Figure 4). The duration of exposure of the insects ranged from 30 s to 8.5 months. 64 % of experiments indicated an effect size, 51 % of experiments also indicated a p-value, while 23 % furthermore indicated standard deviations or standard errors (SEs). By deriving SEs from p-values, 53 % of experiments, or 39 % of studies could be included in the meta-analysis. Almost none of the included studies are randomized controlled trials (RCT). However, a 2014 meta-analysis comparing RCTs with observational-only studies concludes that such studies are as good as RCTs at finding and gauging real-world effects [103].

Estimates of effect size of toxicity

Regarding the toxicity of various EMF sources (Figure 5), the HF devices cordless phone (DECT), cell phone, and signal generator appear to be similarly toxic. Base stations seemed to be less harmful than cell phones, although both use the same technology. This discrepancy is probably due to the fact that studies on cell phones usually are laboratory studies in a controlled environment at relatively high field strengths, whereas the studies on base stations are field experiments, usually at much lower field strengths or with exposure duration too short to find long-term effects. The field strength of the signal from the cellular towers was in the range of 0.56 V/m on average (median value 0.32 V/m), whereas the field strength from cell phones was 18.7 V/m on average (median value 16.2 V/m) (Figure 4). Converted into power densities (median values), the quantitative difference is easier to grasp. Cellular tower: 0.27 mW/m²; cell phone: 695 mW/m². Current typical field strengths of cellular towers (used in experiments) are less harmful than those of cell phones, DECT and WiFi. The current experimental evidence from base station studies should not be interpreted in the way that effects are weak *per se*, but that in general the

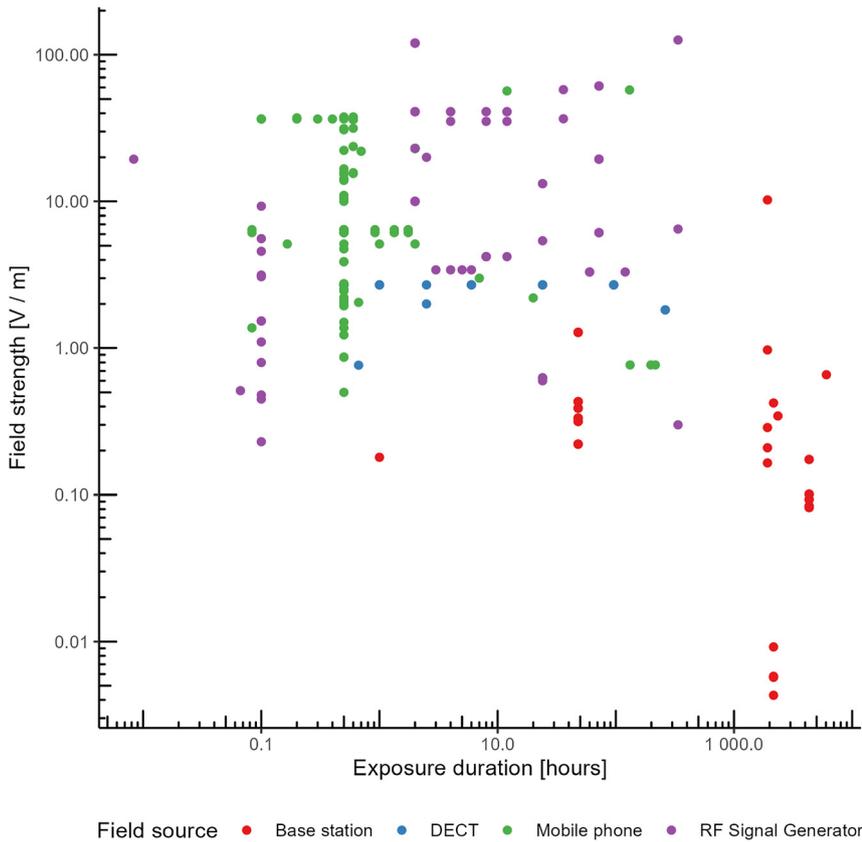


Figure 4: EMF field strength in relation to the duration of exposure (data points from 239 experiments or experimental groups in 48 HF-EMF studies).

experimental setup was such that only relatively weak power densities were tested (typically at 100–500 m from emitter), while insects can be subject to much higher power densities if they get nearer to the antennae. Experiments using cell phones often found detrimental effects within 10 min of irradiation, whereas field experiments at base stations found harmful effects usually after several weeks or months (cf. “Discussion” section). However, some recent human epidemiological studies and field studies in insects, birds and pine trees around cellular towers point to chronic detrimental effects even at current power levels [104–109].

Toxicity estimates derived by meta-analysis number at a ratio of means of about 1.5 for the HF-EMF devices (Supplementary Figures S8, S9, S10, Supplementary Table 1). This estimate includes all types of observed bioeffects that could be unequivocally classified as detrimental or beneficial (Figure 6), and might be interpreted as a 50 % increase in DNA damage or a 33 % reduced reproductive capacity, in the worst case scenario. The toxicity estimate for base stations is about 1.49 (Supplementary Figure S6). This estimate also includes findings that observed avoidance of, or reduced abundance of insects around base stations, and further research is needed to clarify the actual impact of insects

avoiding base stations, but behavioral effects should not be underestimated [110]. An estimate based only on direct markers of toxicity (like reduced brood, egg laying etc.) yielded a much lower toxicity of 1.09, corresponding to an 8 % reduction in reproductive capacity (Supplementary Figure S7). The toxicity estimates are statistically highly significant for DECT, mobile phones and the RF signal generators, barely significant for coil systems and nonsignificant for base stations. Forest plots show considerable heterogeneity among studies (I^2 typically >90 %), and wide prediction intervals describing the range of observed effect sizes. This may be due to large differences in measured parameters as well as EMF exposure strength, type and duration. Heterogeneity could also indicate a lacking understanding of underlying mechanisms of action, leading to inadequate experimental designs (with notable exceptions), leading to strong variation among experimental findings.

The results of the meta-analysis for all experiments finding reproductive toxicity in *Drosophila* at over 7 V/m E-field strength (Supplementary Figure S3) are close to those for the cohort of experiments at between 2 and 7 V/m (Supplementary Figure S4): Random effects estimate: 1.40 or 1.44, corresponding to 29–31 % reduced reproductive capacity

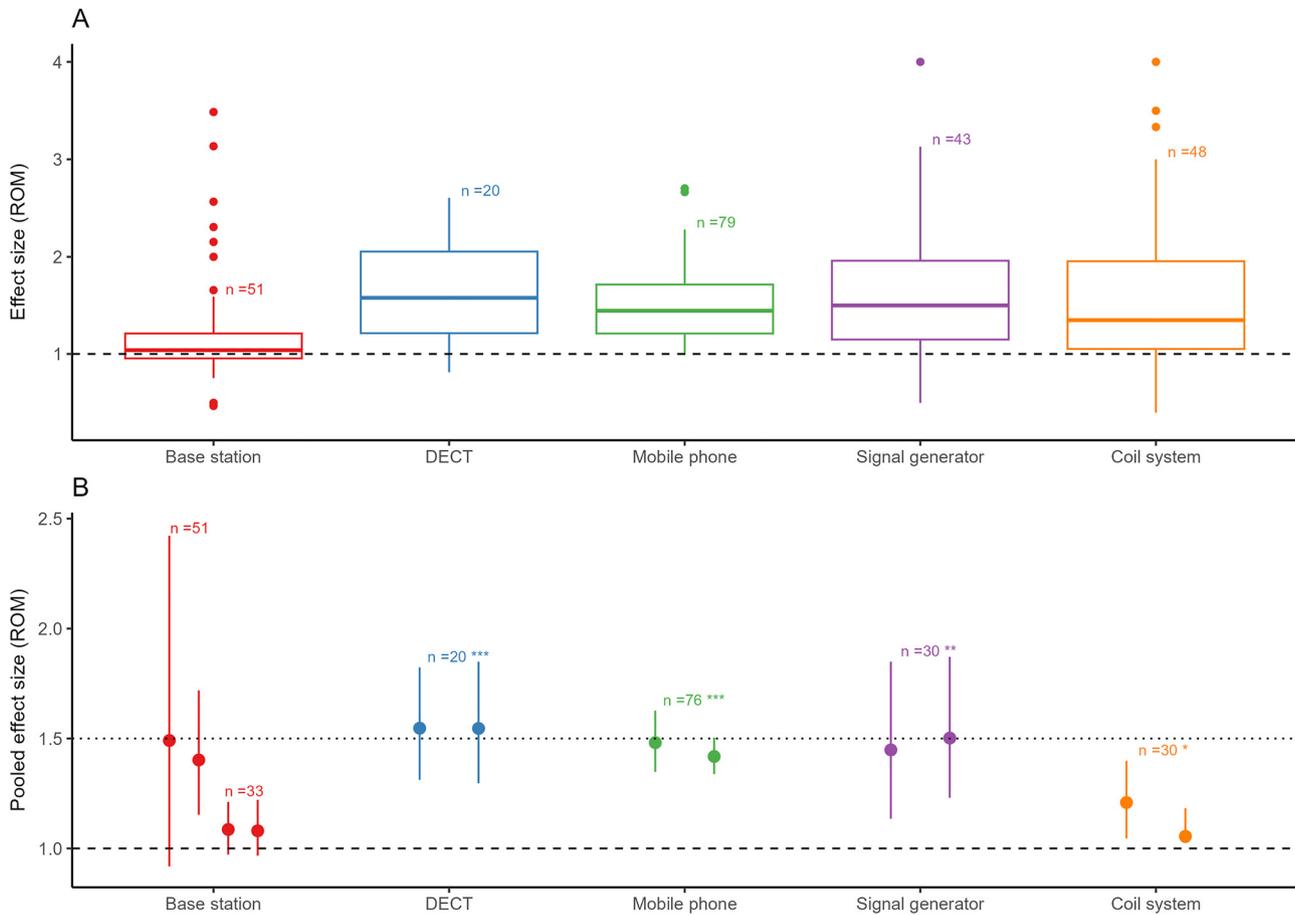


Figure 5: (A) Boxplots (median and quartiles) of effect size found in experiments by EMF type, given as normalized ratio of means (ROM), with indication of the number n of experiments. ROM>1 indicative of detrimental effects. (B) Toxicity estimate derived from meta-analysis, with effect size given as ratio of means with 95 % confidence interval (* p <0.05, ** p <0.01 & *** p <0.001). Estimate from “clustered” three-level analysis (R package “meta”) besides Bayesian estimate (R package “bayesmeta”), with indication of the number n of experiments the estimate is derived from. For base stations, estimates including all findings of reduced abundance or altered behavior (left) besides estimates based on toxicological findings only (right).

($p=0.01$). The meta-analysis for all experiments finding reproductive toxicity at less than 2 V/m (Supplementary Figure S5) indicate a lesser toxicity, with an effects estimate of 1.22, corresponding to a reduction of 18 % in reproductive capacity ($p=0.03$). Supplementary Tables 1 and 2 list all estimates derived by clustered, three-level meta-analysis and Bayesian meta-analysis respectively.

Summary of study findings

A number of studies on the effect of power lines on honey bees were conducted in the 1970s and 1980s [111–115]. Most later studies used Helmholtz coils or other coil systems in the laboratory, which allows more easily controlling the experimental parameters. Coils produce much stronger magnetic fields, but weaker (induced) electric fields, when compared with HF-EMF sources [116–118].

The frequencies used in HF experiments were distributed as follows: 55 % of the HF experiments used frequencies near 900 MHz, corresponding to the GSM (2G) and LTE (4G) mobile phone standard. 8 % used 1900 MHz (DECT), 7.6 % used 1800 MHz, which corresponds to DCS (2G), and 3.6 % used 3,500 MHz, like low-band 5G.

The biological effects of LF- and HF EMF observed in experiments clearly differed (Figures 5, 6 and 7), which could indicate differing biological targets for LF-EMF coil systems compared to HF-EMFs, and may be due to the fact that coils usually were operated with alternate-current sine-wave, whereas HF-EMF devices used pulsed carrier signals; RF signal generators used a pulsed signal in 21 % of experiments, a 50 kHz frequency-modulated signal in 17 %, and a continuous sine-wave signal in 61 % of experiments. For the HF-EMF, observed effects were mostly detrimental as to their impact (57 %). About one quarter were classified as uncertain effect (such as increased or reduced locomotion).

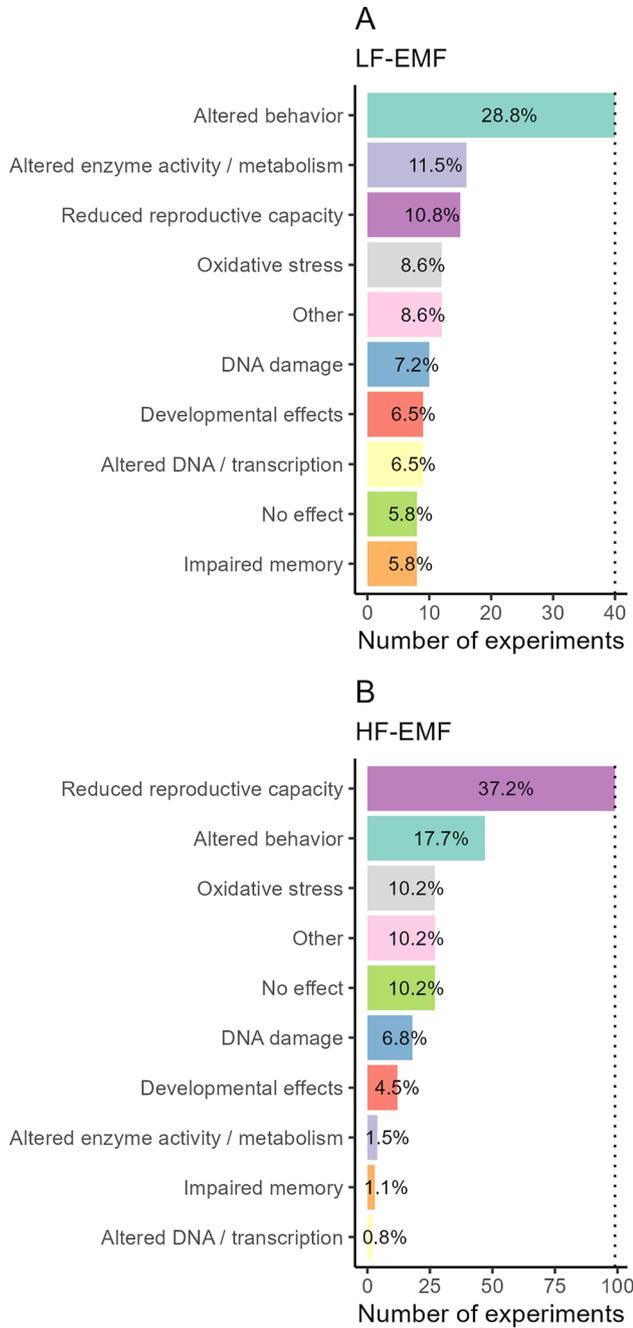


Figure 6: Number and percentage of experiments classified according to bioeffect categories, (A) low-frequency EMF, (B) high-frequency EMF.

For the LF-EMFs (133 experiments), a behavioral effect was observed in 29 % of experiments, in 12 % of experiments, the effect concerned metabolism, and in 11 %, reproductive ability was impaired. For HF-EMFs (238 experiments), the following trends were observed: decreased reproductive capacity in 37 % of experiments, altered behavior (18 %), oxidative stress (10 %), DNA damage (7 %) and impaired development (5 %). In 10 % of experiments, no effect could be

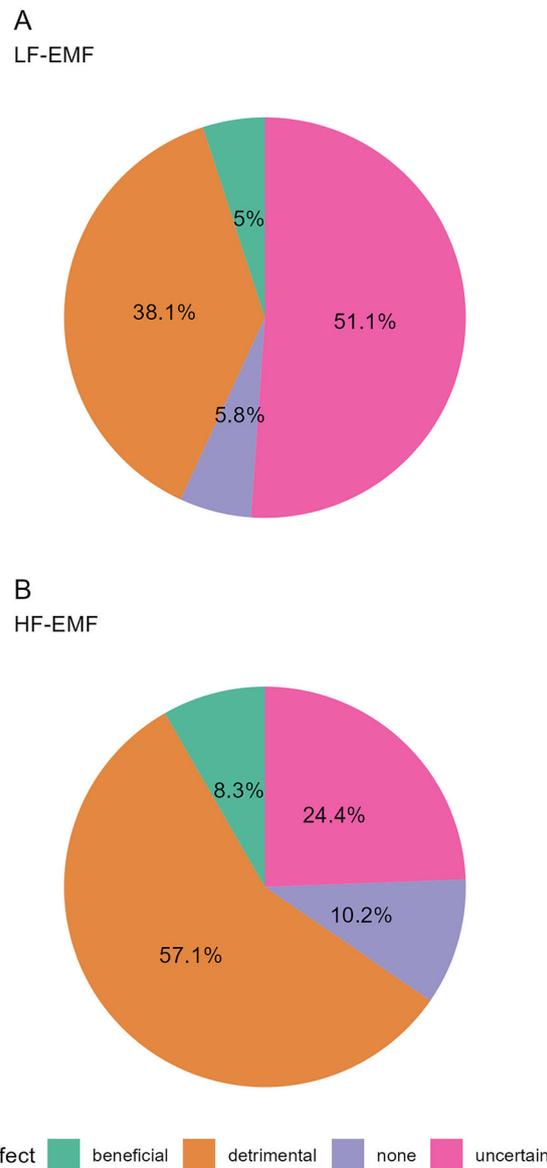


Figure 7: Percentage of experiments finding biological effects of EMF on insects by direction of effect, (A) low-frequency EMF, (B) high-frequency EMF.

found; this higher number than for LF-EMF (6 %) is probably due to the fact that several HF studies were field studies with base stations, at low field strengths, and that it is easier to find significant results in laboratory studies.

Discussion

The vast majority of studies found effects, generally harmful ones. These findings are unlikely to be the result of chance. Sceptics might object that most studies were not randomized controlled trials (but see here [103]). Despite these

shortcomings, the existence of consistent results from numerous studies conducted by various research groups using various protocols make an irrefutable case for adverse effects of low-power LF- and HF-EMF on insects [86, 119]. This is further corroborated by a recent report commissioned by the Swiss federal office for the environment (BAFU) [120]. HF-EMF seem to produce stronger and more harmful effects in insects, compared to LF-EMF. It is highly probable that the effects shown in the laboratory also occur under real conditions [110]. A summary and chronicle of individual studies in insects is available in the supplemental materials, and in other reviews [86, 105, 121]. EMF bioeffects have also been shown in plants and all studied animals, as well as in humans [86, 122, 123, 124]. Insects are expected to be affected the most however, since they are already under pressure of multiple threats, less resilient to stressors and pollutants than larger animals, and due to their small size, more vulnerable to increasingly high frequencies used by the mobile phone infrastructure (5G and 6G in the future) [12, 100, 125].

Comparison between the problem of artificial light at night (ALAN) and other electromagnetic fields

Some environmental and biodiversity threats have been gaining interest recently among researchers and policy-makers, e.g. anthropogenic noise and artificial light at night [126, 127]. The same has not yet happened concerning electromagnetic pollution, even though its increase in recent years has been exponential [15, 86, 128]. Here, we compare the effects of artificial light at night (ALAN) with those of wireless communications high-frequency electromagnetic fields (HF-EMF). Light has driven the development and organization of biological systems from the molecular level to ecosystem cycles [127]. Also, life evolved in a matrix of relatively weak, natural electromagnetic and geomagnetic fields. ALAN is entirely unprecedented and has been introduced in places, times and at intensities at which it does not naturally occur and with a different spectrum from that of sunlight [127]. Likewise, man-made HF-EMF also have been rapidly introduced worldwide, at intensities far above those occurring naturally. Anthropogenic EMF are polarized, pulsed, modulated and include extremely low frequencies in their pulse-rate, while natural EMF lack these characteristics [128]. Light pollution has been on the rise during the past 100 years, whereas the development of mobile communications started just a few decades ago. HF-EMF

have been introduced very quickly worldwide, and levels of exposure have increased by a factor of about 10^{18} compared to natural ambient levels [15]. The physiological and behavioural effects of ALAN and HF-EMF are widely documented, but the extent to which this translates into impacts on populations and ecosystems remains poorly understood [86, 127, 129].

General considerations

Considerable evidence suggests many medical applications of EMF waiting to be developed [130–133]. Although an earlier review cautioned against medical PEMF (“pulsed electromagnetic field”), PEMF devices are now being used with success, although their mechanism of action has only partly been elucidated [134–136]. Nevertheless, this should be secondary in a medical context: if an agent or device is effective for some medical condition, e.g. cancer or viral infection, and if no serious side effects occur, the agent should be used. Conversely, agents or technologies that produce serious adverse effects should not be used. Even if current wireless technologies are generally toxic in a dose-dependent manner, it should be possible to significantly improve their biocompatibility, similarly to what has already been achieved for e.g. computer and TV screens, for example by eliminating “biomimetic” low-frequency pulsing [132, 137, 138, 139]. An experiment on cockroaches suggests that the simultaneous presence of static magnetic fields or LF-EMF together with HF-EMF is more harmful than each separately, as had been shown earlier for birds and theoretically postulated [140–142]. It is so far unclear if EMF are synergistically toxic with pesticides, with some studies indicating synergistic toxicity, but others not [143, 144].

Most studies included in this review that were amenable to meta-analysis come from one very prolific group of scientists from Athens University. A recent study from Italy does however confirm the basic mechanisms for toxicity described and posited by Panagopoulos et al., which is that HF-EMF cause first oxidative stress, leading to defective transposon silencing, causing chromosomal aberrations and DNA damage, which finally causes reduced reproductive capacity [139, 145].

At which field strengths are toxic effects expected to occur in insects?

Looking back at the history of science, it seems that adverse effects have frequently been reported early on, but mostly been ignored – e.g. in the cases of asbestos, lead and

cigarettes. It has typically taken decades to understand the mechanisms of toxicity and for the official position to shift. The European Environment Agency EEA has produced several reports on this topic under the title “Late lessons from early warnings” [146, 147].

Thirty-six of the fifty-five HF-EMF studies reported in this review used field strengths lower than 6 V/m ($\sim 100 \text{ mW/m}^2$), and 31 of these 36 studies (86 %) nevertheless found statistically significant adverse effects, starting at about 2 V/m and peaking around 6 V/m. This is below the regulatory thresholds established by the International Commission on Non-Ionizing Radiation Protection (ICNIRP) (41 V/m, or 61 V/m above 2 GHz), and even below the particularly stringent installation limits only found in a handful of countries [94]. (The installation limit is measured where people can stay for long periods of time, i.e. homes, schools, working places and playgrounds for kids.)

Panagopoulos et al. detected a bioactive window at a distance of 20–30 cm from GSM mobile phones, where the power density equaled 100 mW/m^2 ($\sim 6 \text{ V/m}$), and where toxic effects in *Drosophila* are already observed after a 1-min exposure. These results have been replicated several times [148–150]. If this is generally true for insects, the limit for toxic effects would be 100 times below the current ICNIRP limit (10 W/m^2 or 61 V/m), which protects only against thermal effects (in humans), and possibly 1,000 times lower than current limits for chronic exposure, i.e. 10 mW/m^2 or 2 V/m (all comparisons based on power densities, i.e. energy per surface area units) [94]. A recent study found significant effects on gene transcription and chromosomal abnormalities using a WiFi signal at 4.8 mW/m^2 or 1.35 V/m in *Drosophila* exposed for 9 days [145]. These findings of biological effects in insects starting at around 2 V/m imply that existing standards would have to be revised and made more stringent, to include nature protection/wild-life concerns.

Current ambient power densities are generally still below 10 or 100 mW/m^2 (i.e. 2 or 6 V/m). A recent study measured values of 0.17–0.53 V/m in the field ($0.1\text{--}0.8 \text{ mW/m}^2$) [101]. Values mainly in the range of 0.5–1 V/m were found around schools in Crete [151]. Nationwide measurements of the National Observatory of electromagnetic fields (NOEF) in Greece found average values higher than 1 V/m in 55 % of sites, and values greater than 2 V/m in 20 % of measurement sites [152]. A recent review lists power densities ranging from 0.23 V/m in Swiss residential areas to 1.85 V/m in an Australian university neighborhood [86]. In urban hot spots (UK), a maximum of 150 mW/m^2 (7.5 V/m) and an average of 25 mW/m^2 (3.3 V/m) were measured (including WiFi) [153]. The French “Agence nationale des fréquences” (ANFR) found

an average of 1.17 V/m at 1,300 5G base stations, and the authors expect a 20 % increase in the next years [154]. In Belgium, Italy, Switzerland, Russia and China, the installation limit is 6 V/m (100 mW/m^2) for mobile telephony base stations, whereas Germany, the UK, the USA and many other countries adhere to the much higher ICNIRP limits [94, 155]. The ICNIRP limits have recently been questioned, since they are based on findings from more than 20 years ago, and their assumptions have been proven false [156]. Furthermore, the ICNIRP limits are designed to protect humans and have not been tested as to their adequacy in protecting wildlife and insects [157].

In the future

The mechanisms of biological effects, apart from the magnetosensitive cryptochrome and HF effects on reproduction, are not yet well understood [65, 139, 145]. The following questions need to be clarified:

- to what extent biological processes triggered by HF- and LF-EMF are comparable;
- to what extent interference effects or synergies take place between Earth’s static magnetic field, man-made LF-EMF and HF-EMF;
- to what extent findings with HF-EMF in the laboratory are transferable to cellular towers, and emerging EMF sources like high-band 5G;
- what are power densities in the natural environment (detailed EMF maps).

Compared to most animals, humans are quite resilient in terms of how much stress or toxins they can withstand before developing clinical symptoms [158]. On the other hand, many pesticides initially considered harmless to humans have subsequently proven harmful, such as DDT, organophosphates, and pyrethroids [159]. Insects are more sensitive to pollutants, including EMFs, than humans [86, 120]. Healthy ecosystems and sustainable agriculture require insects. Although ecological practices and organic agriculture are on the rise in Europe, important measures to protect insect populations, such as banning neonicotinoids and reducing monocultures, are being implemented too slowly [125, 160].

According to Thielens, De Borre et al., the EMF power absorbed by insect bodies (for the same emitted power of 1 V/m) increases by up to a hundredfold for a change in frequency from $\sim 1 \text{ GHz}$ (e.g. 4G and low-band 5G) to 10 GHz and higher, e.g. high-band 5G at 26 GHz, hence an increase in

negative effects on insects is to be expected, since low-level (non-thermal) effects are still dependent on absorbed power [100–102]. As power losses become greater due to scattering, reflection, and the lower penetration force of higher frequencies, the radiated power of base stations will also have to increase to ensure comfortable wireless connections in homes and vehicles. The 5G expansion is leading to a significant increase in EMF emissions, as suggested by recent measurements [152, 154, 161]. Based on an assessment of the overall study situation on insects, we must warn against a careless deployment of further mobile telephony infrastructure, as harmful effects on insect populations would be likely, especially if interactions with other noxious agents are taken into account (including high-voltage power lines and artificial lighting). This might lead to further declines of already dwindling populations of pollinators, and would thereby entail costs for humanity. It is also possible, and would need further clarification (which could be reached by a few well-planned field studies), that some insect populations are already negatively impacted by the present infrastructure.

The ongoing 5G-deployment should be closely monitored, and toxicological testing for the evaluation of adverse effects should begin immediately, so that protective guidelines can be enacted. Experimental findings should be reported transparently, and granted the political presence necessary to lead to timely response, as there is a tendency for scientific discussion to become polarized into extreme positions, which rarely reflects the truth and causes substantial waste of resources [160]. Toxic effects on insects may occur at radiation levels that are considered safe for humans, particularly in the higher frequency bands. We refer to the so-called precautionary principle, detailed in article 191 of the Treaty on the Functioning of the European Union. Pollinator conservation requires a stronger and broader application of the precautionary principle as currently practiced [125]. Also, the EU precautionary principle implies that legislative action should already be taken if there is a founded suspicion of negative effects.

Research ethics: Not applicable.

Informed consent: Not applicable.

Author contributions: The authors have accepted responsibility for the entire content of this manuscript and approved its submission.

Competing interests: The authors state no conflict of interest.

Research funding: The lead author was financed by the environmental and consumer protection NGO Diagnose: Funk.

Data availability: The raw data can be obtained on request from the corresponding author.

Appendix

Calculations

The SI unit for expressing the strength of an electromagnetic field is volts per meter [V/m], and this is also the common unit of measurement for electric fields. It can be used for calculating the average (RMS) power density or radiation intensity in watts per square meter [W/m^2] in the case of electromagnetic fields, which is also used in solar cell technology. For all radiofrequency studies here included, all given values of field strength were converted into V/m if they were described in a different unit. The following formulas were used [18, 162]:

$$S = \frac{E^2}{Z_0} \text{ or also: } E = \sqrt{S \cdot Z_0}$$

where E is the electric field strength [V/m], S the power density [W/m^2], Z_0 the wave impedance [377 Ω].

For electromagnetic waves, electric field strength is linked to magnetic field strength, according to: $B=E/c$ with B the magnetic field in Tesla, E the electric field in volts per meter and c the speed of light (3×10^8 m/s) (derived from the Ampère-Faraday law, or directly from the Poynting vector [162]).

In the near-field, i.e. below one wavelength (e.g. <30 cm for GSM900), the electric and magnetic fields are present as a vortex field. Averaged over many measurements, however, the proportionality of electric and magnetic field strength is maintained here as well.

The SAR value (abbreviation for “Specific Absorption Rate”) expresses how much energy is actually absorbed by irradiated tissue, and therefore depends on the tissue type (or generally on the material), and was estimated here according to [100–102].

References

1. Ollerton J, Winfree R, Tarrant S. How many flowering plants are pollinated by animals? *Oikos* 2011;120:321–6.
2. Rodger JG, Bennett JM, Razanajatovo M, Knight TM, van Kleunen M, Ashman TL, et al. Widespread vulnerability of flowering plant seed production to pollinator declines. *Sci Adv* 2021;7:eabd3524.
3. Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, et al. Importance of pollinators in changing landscapes for world crops. *Proc Biol Sci* 2006;274:303–13.

4. Schowalter TD, Noriega JA, Tschartnke T. Insect effects on ecosystem services – introduction. *Basic Appl Ecol* 2018;26:1–7.
5. van der Sluijs JP. Insect decline, an emerging global environmental risk. *Curr Opin Sust* 2020;46:39–42.
6. Kehoe R, Frago E, Sanders D. Cascading extinctions as a hidden driver of insect decline. *Ecol Entomol* 2020;46:743–56.
7. Smith MR, Singh GM, Mozaffarian D, Myers SS. Effects of decreases of animal pollinators on human nutrition and global health: a modelling analysis. *Lancet* 2015;386:1964–72.
8. Smith MR, Mueller ND, Springmann M, Sulser TB, Garibaldi LA, Gerber J, et al. Pollinator deficits, food consumption, and consequences for human health: a modeling study. *Environ Health Perspect* 2022;130:127003.
9. Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, et al. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* 2017;12:0185809.
10. Sánchez-Bayo F, Wyckhuys KAG. Worldwide decline of the entomofauna: a review of its drivers. *Biol Conserv* 2019;232:8–27.
11. Sánchez-Bayo F. Indirect effect of pesticides on insects and other arthropods. *Toxics* 2021;9:177.
12. Cardoso P, Barton PS, Birkhofer K, Chichorro F, Deacon C, Fartmann T, et al. Scientists' warning to humanity on insect extinctions. *Biol Conserv* 2020;242:108426.
13. Sharma A, Kaur M, Katnoria JK, Nagpal AK. Heavy metal pollution: a global pollutant of rising concern. In: *Toxicity and waste management using bioremediation*. Hershey, Pennsylvania, USA: IGI Global; 2016:1–26 pp. <https://doi.org/10.4018/978-1-4666-9734-8.ch001>.
14. Rhind SM. Anthropogenic pollutants: a threat to ecosystem sustainability? *Philos Trans Biol Sci* 2009;364:3391–401.
15. Bandara P, Carpenter DO. Planetary electromagnetic pollution: it is time to assess its impact. *Lancet Planet Health* 2018;2:e512–14.
16. Siviter H, Bailes EJ, Martin CD, Oliver TR, Koricheva J, Leadbeater E, et al. Agrochemicals interact synergistically to increase bee mortality. *Nature* 2021;596:389–92.
17. Page MJ, Moher D, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. PRISMA 2020 explanation and elaboration: updated guidance and exemplars for reporting systematic reviews. *BMJ* 2021;372. <https://doi.org/10.1136/bmj.n160>.
18. Feynman C, Leighton RB, Sands M, Gottlieb MA, Pfeiffer R. The Feynman lectures on physics; 1965, vol. II. Available from: https://www.feynmanlectures.caltech.edu/II_toc.html.
19. Panagopoulos DJ, Johansson O, Carlo GL. Polarization: a key difference between man-made and natural electromagnetic fields, in regard to biological activity. *Sci Rep* 2015;5:14914.
20. International Telecommunication Union. Nomenclature of the frequency and wavelength bands used in telecommunications. Recommendation ITU/RV 2015:431–8.
21. Chou CK, Guy AW, Galambos R. Auditory perception of radio-frequency electromagnetic fields. *J Acoust Soc Am* 1982;71:1321–34.
22. Belyaev I. Biophysical mechanisms for nonthermal microwave effects. In: Markov MS, editor. *Electromagnetic fields in biology and medicine*. Boca Raton: CRC Press; 2015.
23. Popov T, Szyszka P. Alpha oscillations govern interhemispheric spike timing coordination in the honey bee brain. *Proc Biol Sci* 2020;287:20200115.
24. Gupta N, Singh SS, Stopfer M. Oscillatory integration windows in neurons. *Nat Commun* 2016;7:13808.
25. van Swinderen B, Greenspan RJ. Salience modulates 20–30 Hz brain activity in *Drosophila*. *Nat Neurosci* 2003;6:579–86.
26. Hinrikus H, Bachmann M, Lass J, Tomson R, Tuulik V. Effect of 7, 14 and 21 Hz modulated 450 MHz microwave radiation on human electroencephalographic rhythms. *Int J Radiat Biol* 2008;84:69–79.
27. Mohammed HS, Fahmy HM, Radwan NM, Elsayed AA. Non-thermal continuous and modulated electromagnetic radiation fields effects on sleep EEG of rats. *J Adv Res* 2013;4:181–7.
28. Agnati LF, Marcoli M, Maura G, Woods A, Guidolin D. The brain as a “hypernetwork”: the key role of neural networks as main producers of the integrated brain actions especially via the “broadcasted” neuroconnectomics. *J Neural Transm* 2018;125:883–97.
29. Martinez-Banaclocha M. Astroglial isopotentiality and calcium-associated biomagnetic field effects on cortical neuronal coupling. *Cells* 2020;9:439.
30. Chiang CC, Shivacharan RS, Wei X, Gonzalez-Reyes LE, Durand DM. Slow periodic activity in the longitudinal hippocampal slice can self-propagate non-synaptically by a mechanism consistent with ephaptic coupling. *J Physiol* 2018;597:249–69.
31. Hales CG, Pockett S. The relationship between local field potentials (LFPs) and the electromagnetic fields that give rise to them. *Front Syst Neurosci* 2014;8:233.
32. Weinberg SH. Ephaptic coupling rescues conduction failure in weakly coupled cardiac tissue with voltage-gated gap junctions. *Chaos Interdiscipl J Nonlinear Sci* 2017;27:093908.
33. Han KS, Guo C, Chen CH, Witter L, Osorno T, Regehr WG. Ephaptic coupling promotes synchronous firing of cerebellar Purkinje cells. *Neuron* 2018;100:564–78.
34. Zhang Y, Tsang TK, Bushong EA, Chu LA, Chiang AS, Ellisman MH, et al. Asymmetric ephaptic inhibition between compartmentalized olfactory receptor neurons. *Nat Commun* 2019;10:1–16.
35. Bokil H, Laaris N, Blinder K, Ennis M, Keller A. Ephaptic interactions in the mammalian olfactory system. *J Neurosci* 2001;21:173–3.
36. Fogle KJ, Baik LS, Houl JH, Tran TT, Roberts L, Dahm NA, et al. Cryptochrome-mediated phototransduction by modulation of the potassium ion channel beta subunit redox sensor. *Proc Natl Acad Sci USA* 2015;112:2245–50.
37. Zheng Y, Xia P, Dong L, Tian L, Xiong C. Effects of modulation on sodium and potassium channel currents by extremely low frequency electromagnetic fields stimulation on hippocampal CA1 pyramidal cells. *Electromagn Biol Med* 2021;40:274–85.
38. Cecchetto C, Maschietto M, Boccaccio P, Vassanelli S. Electromagnetic field affects the voltage-dependent potassium channel kv1.3. *Electromagn Biol Med* 2020;39:316–22.
39. Sun Z, Ge J, Guo B, Guo J, Hao M, Wu Y, et al. Extremely low frequency electromagnetic fields facilitate vesicle endocytosis by increasing presynaptic calcium channel expression at a central synapse. *Sci Rep* 2016;6:21774.
40. Pilla AA. Electromagnetic fields instantaneously modulate nitric oxide signaling in challenged biological systems. *Biochem Biophys Res Commun* 2012;426:330–3.
41. Kim JH, Lee JK, Kim KB, Kim HR. Possible effects of radiofrequency electromagnetic field exposure on central nerve system. *Biomol Therapeut* 2019;27:265.
42. Atlas D. The voltage-gated calcium channel functions as the molecular switch of synaptic transmission. *Annu Rev Biochem* 2013;82:607–35.
43. Valko M, Leibfritz D, Moncol J, Cronin MTD, Mazur M, Telser J. Free radicals and antioxidants in normal physiological functions and human disease. *Int J Biochem Cell Biol* 2007;39:44–84.
44. Saliev T, Begimbetova D, Masoud AR, Matkarimov B. Biological effects of nonionizing electromagnetic fields: two sides of a coin. *Prog Biophys Mol Biol* 2019;141:25–36.

45. Krylov VV. Biological effects related to geomagnetic activity and possible mechanisms. *Bioelectromagnetics* 2017;38:497–510.
46. Tonelli BA, Youngflesh C, Tingley MW. Geomagnetic disturbance associated with increased vagrancy in migratory landbirds. *Sci Rep* 2023;13:414.
47. Ferrari TE, Tautz J. Severe honey bee (*Apis mellifera*) losses correlate with geomagnetic and proton disturbances in Earth's atmosphere. *J Astrobiol Outreach* 2015;03:1–6.
48. Price C. ELF electromagnetic waves from lightning: the Schumann resonances. *Atmosphere* 2016;7:116.
49. Price C, Williams E, Elhalel G, Sentman D. Natural ELF fields in the atmosphere and in living organisms. *Int J Biometeorol* 2020;65:85–92.
50. Cifra M, Apollonio F, Liberti M, García-Sánchez T, Mir LM. Possible molecular and cellular mechanisms at the basis of atmospheric electromagnetic field bioeffects. *Int J Biometeorol* 2020;65:59–67.
51. Elhalel G, Price C, Fixler D, Shainberg A. Cardioprotection from stress conditions by weak magnetic fields in the Schumann resonance band. *Sci Rep* 2019;9:1645.
52. Bertagna F, Lewis R, Silva SRP, McFadden J, Jeevaratnam K. Thapsigargin blocks electromagnetic field-elicited intracellular Ca^{2+} increase in HEK 293 cells. *Physiol Rep* 2022;10:e15189.
53. Panagopoulos DJ, Balmori A. On the biophysical mechanism of sensing atmospheric discharges by living organisms. *Sci Total Environ* 2017;599–600:2026–34.
54. Panagopoulos DJ, Balmori A, Chrousos GP. On the biophysical mechanism of sensing upcoming earthquakes by animals. *Sci Total Environ* 2020;717:136989.
55. Bertagna F, Lewis R, Silva SRP, McFadden J, Jeevaratnam K. Effects of electromagnetic fields on neuronal ion channels: a systematic review. *Ann N Y Acad Sci* 2021;1499:82–103.
56. Panagopoulos DJ, Messini N, Karabarbounis A, Philippidis AL, Margaritis LH. A mechanism for action of oscillating electric fields on cells. *Biochem Biophys Res Commun* 2000;272:634–40.
57. Guerra PA, Gegear RJ, Reppert SM. A magnetic compass aids monarch butterfly migration. *Nat Commun* 2014;5:1–8.
58. Gegear RJ, Casselman A, Waddell S, Reppert SM. Cryptochrome mediates light-dependent magnetosensitivity in *Drosophila*. *Nature* 2008;454:1014–8.
59. de Oliveira JF, Wajenberg E, de Souza Esquivel DM, Weinkauff S, Winkelhofer M, Hanzlik M. Antennae: are they sites for magnetoreception? *J R Soc Interface* 2010;7:143–52.
60. Lambinet V, Hayden ME, Reid C, Gries G. Honey bees possess a polarity-sensitive magnetoreceptor. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 2017;203:1029–36.
61. Vácha M, Půzová T, Kvičalová M. Radio frequency magnetic fields disrupt magnetoreception in American cockroach. *J Exp Biol* 2009;212:3473–7.
62. Clites BL, Pierce JT. Identifying cellular and molecular mechanisms for magnetosensation. *Annu Rev Neurosci* 2017;40:231–50.
63. Nordmann GC, Hochstoeger T, Keays DA. Unsolved mysteries: magnetoreception – a sense without a receptor. *PLoS Biol* 2017;15:e2003234.
64. Ishay JS, Pertsis V, Skutelsky E, Kalicharan D, van der Want H. Ontogenesis of peripheral electromagnetic receptors in hornets. *J Electron Microsc* 2004;53:281–91.
65. Kyriacou CP, Rosato E. Genetic analysis of cryptochrome in insect magnetosensitivity. *Front Physiol* 2022;13:928416.
66. Solov'yov I, Schulten K. Cryptochrome and magnetic sensing; 2014. Available from: <http://www.ks.uiuc.edu/Research/cryptochrome/>.
67. Fedele G, Edwards MD, Bhutani S, Hares JM, Murbach M, Green EW, et al. Genetic analysis of circadian responses to low frequency electromagnetic fields in *Drosophila melanogaster*. *PLoS Genet* 2014;10:e1004804.
68. Sherrard RM, Morellini N, Jourdan N, El-Eswai M, Arthaut LD, Niessner C, et al. Low-intensity electromagnetic fields induce human cryptochrome to modulate intracellular reactive oxygen species. *PLoS Biol* 2018;16:e2006229.
69. Netušil R, Tomanová K, Chodáková L, Chvalová D, Doležel D, Ritz T, et al. Cryptochrome-dependent magnetoreception in a heteropteran insect continues even after 24 h in darkness. *J Exp Biol* 2021;224:jeb243000.
70. Kelleher FC, Rao A, Maguire A. Circadian molecular clocks and cancer. *Cancer Lett* 2014;342:9–18.
71. Chun SK, Chung S, Kim HD, Lee JH, Jang J, Kim J, et al. A synthetic cryptochrome inhibitor induces anti-proliferative effects and increases chemosensitivity in human breast cancer cells. *Biochem Biophys Res Commun* 2015;467:441–6.
72. Olejárová S, Moravčík R, Herichová I. 2.4 GHz electromagnetic field influences the response of the circadian oscillator in the colorectal cancer cell line DLD1 to miR-34a-mediated regulation. *Int J Mol Sci* 2022;23:13210.
73. Liang CH, Chuang CL, Jiang JA, Yang EC. Magnetic sensing through the abdomen of the honey bee. *Sci Rep* 2016;6:23657.
74. Shaw J, Boyd A, House M, Woodward R, Mathes F, Cowin G, et al. Magnetic particle-mediated magnetoreception. *J R Soc Interface* 2015;12:20150499.
75. Hsu CY, Ko FY, Li CW, Fann K, Lue JT. Magnetoreception system in honeybees (*Apis mellifera*). *PLoS One* 2007;2:e395.
76. Gao Y, Wen P, Cardé RT, Xu H, Huang Q. In addition to cryptochrome 2, magnetic particles with olfactory co-receptor are important for magnetic orientation in termites. *Commun Biol* 2021;4:1121.
77. Kong LJ, Crepaz H, Górecka A, Urbanek A, Dumke R, Paterek T. In-vivo biomagnetic characterisation of the American cockroach. *Sci Rep* 2018;8:5140.
78. Bazalova O, Kvalcova M, Valkova T, Slaby P, Bartos P, Netušil R, et al. Cryptochrome 2 mediates directional magnetoreception in cockroaches. *PNAS* 2016;113:1660–5.
79. Vacha M, Puzova T, Drstkova D. Ablation of antennae does not disrupt magnetoreceptive behavioural reaction of the American cockroach to periodically rotated geomagnetic field. *Neurosci Lett* 2008;435:103–7.
80. Cucurachi S, Tamis WL, Vijver MG, Peijnenburg WJ, Bolte JF, de Snoo GR. A review of the ecological effects of radiofrequency electromagnetic fields (RF-EMF). *Environ Int* 2013;51:116–40.
81. Balmori A. Electromagnetic radiation as an emerging driver factor for the decline of insects. *Sci Total Environ* 2021;767:144913.
82. Carpenter R, Livstone E. Evidence for nonthermal effects of microwave radiation: abnormal development of irradiated insect Pupae. *IEEE Trans Microw Theor Tech* 1971;19:173–8.
83. Weisbrot D, Lin H, Ye L, Blank M, Goodman R. Effects of mobile phone radiation on reproduction and development in *Drosophila melanogaster*. *J Cell Biochem* 2003;89:48–55.
84. Panagopoulos DJ, Karabarbounis A, Margaritis LH. Effect of GSM 900 MHz mobile phone radiation on the reproductive capacity of *Drosophila melanogaster*. *Electromagn Biol Med* 2004;23:29–43.
85. Atli E, Unlü H. The effects of microwave frequency electromagnetic fields on the development of *Drosophila melanogaster*. *Int J Radiat Biol* 2006;82:435–41.
86. Levitt BB, Lai HC, Manville AM. Effects of non-ionizing electromagnetic fields on flora and fauna, Part 2 impacts: how species interact with natural and man-made EMF. *Rev Environ Health* 2022;37:327–406.

87. Malkemper EP, Tscheulin T, Vanbergen AJ, Vian A, Balian E, Goudeseune L. The impacts of artificial electromagnetic radiation on wildlife (flora and fauna). Current knowledge overview: a background document to the web conference. A report of the EKLIPSE project. Eklipse.eu; 2018. https://eklipse.eu/wp-content/uploads/2020/10/EMR-KnowledgeOverviewReport_FINAL_27042018-1.pdf.
88. Goudeseune L, Balian E, Ventocilla J. The impacts of artificial electromagnetic radiation on wildlife (flora and fauna). Report of the web conference. A report of the EKLIPSE project. Eklipse.eu; 2018. https://eklipse.eu/wp-content/uploads/2020/10/EMR-WebConferenceReport_FINAL_27042018-1.pdf.
89. Vanbergen AJ, Potts SG, Vian A, Malkemper EP, Young J, Tscheulin T. Risk to pollinators from anthropogenic electro-magnetic radiation (EMR): evidence and knowledge gaps. *Sci Total Environ* 2019;695:133833.
90. Wan GJ, Jiang SL, Zhao ZC, Xu JJ, Tao XR, Sword GA, et al. Bio-effects of near-zero magnetic fields on the growth, development and reproduction of small brown planthopper, *Laodelphax striatellus* and brown planthopper, *Nilaparvata lugens*. *J Insect Physiol* 2014;68:7–15.
91. Sutton GP, Clarke D, Morley EL, Robert D. Mechanosensory hairs in bumblebees (*Bombus terrestris*) detect weak electric fields. *PNAS* 2016;113:7261–5.
92. Bae JE, Bang S, Min S, Lee SH, Kwon SH, Lee Y, et al. Positive geotactic behaviors induced by geomagnetic field in *Drosophila*. *Mol Brain* 2016;9:55.
93. Driessen S. Information platform EMF-Portal of the RWTH Aachen University; 2022. Available from: <https://www.emf-portal.org/en>.
94. International Commission on Non-Ionizing Radiation Protection. Guidelines for limiting exposure to electromagnetic fields (100 kHz to 300 GHz). *Health Phys* 2020;118:483–524.
95. Bordage G, Caellegh AS, Steinecke A, Bland CJ, Crandall SJ, McGaghie WC, et al. Review criteria for research manuscripts. *Acad Med J Assoc Am Med Coll* 2001;76:897–978.
96. ORSAA. ORSAA database on electromagnetic bioeffects; 2022. Available from: <https://www.orsaa.org/orsaa-database.html>.
97. Friedrich JO, Adhikari NK, Beyene J. The ratio of means method as an alternative to mean differences for analyzing continuous outcome variables in meta-analysis: a simulation study. *BMC Med Res Methodol* 2008;8:1–15.
98. Schwarzer G, Carpenter JR, Rücker G. Meta-analysis with R. Cham: Springer International Publishing; 2015.
99. Röver C, Friede T. Using the bayesmeta R package for Bayesian random-effects metaregression. *Comput Methods Progr Biomed* 2023;229:107303.
100. Thielens A, Bell D, Mortimore DB, Greco MK, Martens L, Joseph W. Exposure of insects to radio-frequency electromagnetic fields from 2 to 120 GHz. *Sci Rep* 2018;8:3924.
101. Thielens A, Greco MK, Verloock L, Martens L, Joseph W. Radio-frequency electromagnetic field exposure of western honey bees. *Sci Rep* 2020;10:461.
102. De Borre E, Joseph W, Aminzadeh R, Müller P, Boone MN, Jospovic I, et al. Radio-frequency exposure of the yellow fever mosquito (*A. aegypti*) from 2 to 240 GHz. *PLoS Comput Biol* 2021;17:e1009460.
103. Anglemeyer A, Horvath HT, Bero L. Healthcare outcomes assessed with observational study designs compared with those assessed in randomized trials. *Cochrane Db Syst Rev* 2014;2014. <https://doi.org/10.1002/14651858.mr000034.pub2>.
104. Balmori A. Evidence for a health risk by RF on humans living around mobile phone base stations: from radiofrequency sickness to cancer. *Environ Res* 2022;214:113851.
105. Balmori A. Effects of man-made and especially wireless communication electromagnetic fields on wildlife. In: Panagopoulos DJ, editor. Electromagnetic fields of wireless communications: biological and health effects. Boca Raton: CRC Press; 2022:393–446 pp.
106. Lazaro A, Chroni A, Tscheulin T, Devalez J, Matsoukas C, Petanidou T. Electromagnetic radiation of mobile telecommunication antennas affects the abundance and composition of wild pollinators. *J Insect Conserv* 2016;20:315–24.
107. Adelaja OJ, Ande AT, Abdurraheem GD, Oluwakorode IA, Oladipo OA, Oluwajobi AO. Distribution, diversity and abundance of some insects around a telecommunication mast in Ilorin, Kwara State, Nigeria. *Bull Natl Res Cent* 2021;45:1–7.
108. Nyirenda VR, Namukonde N, Lungu EB, Mulwanda S, Kalezu K, Simwanda M, et al. Effects of phone mast-generated electromagnetic radiation gradient on the distribution of terrestrial birds and insects in a savanna protected area. *Biologia (Bratisl)* 2022;77:2237–49.
109. Ozel HB, Cetin M, Sevik H, Varol T, Isik B, Yaman B. The effects of base station as an electromagnetic radiation source on flower and cone yield and germination percentage in *Pinus brutia* ten. *Biologia Futura* 2021;72:359–65.
110. Ford AT, Ågerstrand M, Brooks BW, Allen J, Bertram MG, Brodin T, et al. The role of behavioral ecotoxicology in environmental protection. *Environ Sci Technol* 2021;55:5620–8.
111. Wellenstein G. [The influence of high-voltage power lines on honey bees] Der Einfluss von Hochspannungsleitungen auf Bienenvölker (*Apis mellifica* L.). *J Appl Entomol* 1973;74:86–94.
112. Greenberg B, Bindokas VP, Frazier MJ, Gauger JR. Response of honey bees, *Apis mellifera* L., to high-voltage transmission lines. *Environ Entomol* 1981;10:600–10.
113. Horn H. Bienen im elektrischen Feld. *Apidologie* 1982;13:79–82.
114. Bindokas V, Greenberg B. Biological effects of a 765-kV, 60-Hz transmission line on honey bees (*Apis mellifera* L.): hemolymph as a possible stress indicator. *Bioelectromagnetics* 1984;5:305–14.
115. Korall H, Leucht T, Martin H. Bursts of magnetic fields induce jumps of misdirection in bees by a mechanism of magnetic resonance. *J Comp Physiol* 1988;162:279–84.
116. Dufor T, Grehl S, Tang AD, Doulazmi M, Traoré M, Debray N, et al. Neural circuit repair by low-intensity magnetic stimulation requires cellular magnetoreceptors and specific stimulation patterns. *Sci Adv* 2019;5:eaav9847.
117. Lohof AM, Dufor T, Sherrard RM. Neural circuit repair by low-intensity rTMS. *The Cerebellum* 2022;21:750–4.
118. Panagopoulos DJ, Johansson O, Carlo GL. Evaluation of specific absorption rate as a dosimetric quantity for electromagnetic fields bioeffects. *PLoS One* 2013;8:e62663.
119. Barnes F, Greenebaum B. Setting guidelines for electromagnetic exposures and research needs. *Bioelectromagnetics* 2020;41:392–7.
120. Mulot M, Kroeber T, Gossner M, Fröhlich J. Wirkung von nichtionisierender Strahlung (NIS) auf Arthropoden. Bericht im Auftrag des Bundesamts für Umwelt (BAFU); 2022. Available from: <https://www.bafu.admin.ch/bafu/en/home/topics/electrosmog/publications-studies/studies.html>.
121. Thielens A, European Parliament, Directorate-General for Parliamentary Research Services. Environmental impact of 5G: a literature review of effects of radio-frequency electromagnetic field exposure of non-human vertebrates, invertebrates and plants.

- Brussels: European Parliament; 2021. <https://data.europa.eu/doi/10.2861/318352>.
122. Halgamuge MN. Review: weak radiofrequency radiation exposure from mobile phone radiation on plants. *Electromagn Biol Med* 2016; 36:213–35.
 123. Waldmann-Selsam C, Balmori-de Puente A, Breunig H, Balmori A. Radiofrequency radiation injures trees around mobile phone base stations. *Sci Total Environ* 2016;572:554–69.
 124. Miller AB, Sears ME, Morgan LL, Davis DL, Hardell L, Oremus M, et al. Risks to health and well-being from radio-frequency radiation emitted by cell phones and other wireless devices. *Front Public Health* 2019;7: 223.
 125. Drivdal L, van der Sluijs JP. Pollinator conservation requires a stronger and broader application of the precautionary principle. *Curr Opin Insect Sci* 2021;46:95–105.
 126. Francis CD, Barber JR. A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Front Ecol Environ* 2013;11: 305–13.
 127. Gaston KJ, Visser ME, Hölker F. The biological impacts of artificial light at night: the research challenge. *Philos Trans Biol Sci* 2015;370: 20140133.
 128. Kostoff RN, Heroux P, Aschner M, Tsatsakis A. Adverse health effects of 5G mobile networking technology under real-life conditions. *Toxicol Lett* 2020;323:35–40.
 129. Sutherland WJ, Butchart SHM, Connor B, Culshaw C, Dicks LV, Dinsdale J, et al. 2018 A horizon scan of emerging issues for global conservation and biological diversity. *Trends Ecol Evol* 2018;33: 47–58.
 130. Coronado LM, Stoute JA, Nadovich CT, Cheng J, Correa R, Chaw K, et al. Microwaves can kill malaria parasites non-thermally. *Front Cell Infect Microbiol* 2023;13:67.
 131. Markov MS. Expanding use of pulsed electromagnetic field therapies. *Electromagn Biol Med* 2007;26:257–74.
 132. Pilla AA. Nonthermal electromagnetic fields: from first messenger to therapeutic applications. *Electromagn Biol Med* 2013;32:123–36.
 133. Costantini E, Aielli L, Serra F, Dominici LD, Falasca K, Giovanni PD, et al. Evaluation of cell migration and cytokines expression changes under the radiofrequency electromagnetic field on wound healing in vitro model. *Int J Mol Sci* 2022;23:2205.
 134. Hug K, Röösl M. Therapeutic effects of whole-body devices applying pulsed electromagnetic fields (PEMF): a systematic literature review. *Bioelectromagnetics* 2011;33:95–105.
 135. Gaynor JS, Hagberg S, Gurfein BT. Veterinary applications of pulsed electromagnetic field therapy. *Res Vet Sci* 2018;119:1–8.
 136. Mattsson MO, Simkó M. Emerging medical applications based on non-ionizing electromagnetic fields from 0 hz to 10 thz. *Med Dev Evid Res* 2019;12:347–68.
 137. Mert T, Yaman S. Pro-inflammatory or anti-inflammatory effects of pulsed magnetic field treatments in rats with experimental acute inflammation. *Environ Sci Pollut Res* 2020;27:31543–54.
 138. Lai H. Interaction of microwaves and a temporally incoherent magnetic field on spatial learning in the rat. *Physiol Behav* 2004;82:785–9.
 139. Panagopoulos D, Karabarbounis A, Yakymenko I, Chrousos G. Human-made electromagnetic fields: ion forced-oscillation and voltage-gated ion channel dysfunction, oxidative stress and DNA damage (Review). *Int J Oncol* 2021;59:1–16.
 140. Bartos P, Netušil R, Slaby P, Dolezel D, Ritz T, Vacha M. Weak radiofrequency fields affect the insect circadian clock. *J R Soc Interface* 2019;16:20190285.
 141. Ritz T, Thalau P, Phillips JB, Wiltshchko R, Wiltshchko W. Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature* 2004;429:177.
 142. Warnke U. Die Auswirkungen elektromagnetischer Wellen auf Tiere. Saarbrücken: Internetpublikation der Kompetenzinitiative e V; 2009. <https://kompetenzinitiative.com/die-auswirkungen-elektromagnetischer-felder-auf-tiere/>.
 143. Lupi D, Mesiano MP, Adani A, Benocci R, Giacchini R, Parenti P, et al. Combined effects of pesticides and electromagnetic-fields on honeybees: multi-stress exposure. *Insects* 2021;12:716.
 144. Shepherd S, Jackson CW, Sharkh SM, Aonuma H, Oliveira EE, Newland PL. Extremely low-frequency electromagnetic fields entrain locust wing beats. *Bioelectromagnetics* 2021;42: 296–308.
 145. Cappucci U, Casale AM, Proietti M, Marinelli F, Giuliani L, Piacentini L. WiFi related radiofrequency electromagnetic fields promote transposable element dysregulation and genomic instability in *Drosophila melanogaster*. *Cells* 2022;11:4036.
 146. Gee D. Late lessons from early warnings: towards realism and precaution with EMF? *Pathophysiology* 2009;16:217–31.
 147. European Environment Agency. Late lessons from early warnings: science, precaution, innovation – summary. Luxembourg: Publications Office of the European Union; 2016. <https://data.europa.eu/doi/10.2800/70069>.
 148. Panagopoulos DJ, Margaritis LH. The identification of an intensity ‘window’ on the bioeffects of mobile telephony radiation. *Int J Radiat Biol* 2010;86:358–66.
 149. Margaritis LH, Manta AK, Kokkaliaris KD, Schiza D, Alimisis K, Barkas G, et al. *Drosophila* oogenesis as a bio-marker responding to EMF sources. *Electromagn Biol Med* 2013;33:165–89.
 150. Geronikou S, Zimeras S, Davos CH, Michalopoulos I, Tsitomeneas S. Diverse radiofrequency sensitivity and radiofrequency effects of mobile or cordless phone near fields exposure in *Drosophila melanogaster*. *PLoS One* 2014;9:e112139.
 151. Kapetanakis TN, Ioannidou MP, Baklezos AT, Nikolopoulos CD, Sergaki ES, Konstantaras AJ, et al. Assessment of radiofrequency exposure in the vicinity of school environments in Crete Island, South Greece. *Appl Sci* 2022;12:4701.
 152. Karastergios I, Gialofas A, Karabetsos E. National observatory of electromagnetic fields: national telemetric network for the measurement of high-frequency electromagnetic fields in Greece. *Radiat Protect Dosim* 2020;188:413–23.
 153. Ofcom. 5G exposure measurements; 2020. Available from: https://www.ofcom.org.uk/_data/assets/pdf_file/0015/190005/emf-test-summary.pdf.
 154. ANFR. 5G exposure measurements; 2021. Available from: <https://www.anfr.fr/fileadmin/mediatheque/documents/expacement/20211214-exposition-5G.pdf>.
 155. funkstrahlung.ch. Grenzwerte; 2017. Available from: <https://www.funkstrahlung.ch/index.php/politik/grenzwerte>.
 156. Belyaev I, Blackman C, Chamberlin K, DeSalles A, Dasdag S, Fernández C, et al, International Commission on the Biological Effects of Electromagnetic Fields (ICBE-EMF). Scientific evidence invalidates health assumptions underlying the FCC and ICNIRP exposure limit determinations for radiofrequency radiation: implications for 5G. *Environ Health* 2022;21:92.
 157. Levitt BB, Lai HC, Manville AM. Low-level EMF effects on wildlife and plants: what research tells us about an ecosystem approach. *Front Public Health* 2022;10:4654.

158. Scheffer M, Bolhuis JE, Borsboom D, Buchman TG, Gijzel SMW, Goulson D, et al. Quantifying resilience of humans and other animals. *Proc Natl Acad Sci USA* 2018;115:11883–90.
159. Mostafalou S, Abdollahi M. Pesticides: an update of human exposure and toxicity. *Arch Toxicol* 2016;91:549–99.
160. Chartres N, Sass JB, Gee D, Bălan SA, Birnbaum L, Coglianò VJ, et al. Conducting evaluations of evidence that are transparent, timely and can lead to health-protective actions. *Environ Health* 2022;21:123.
161. Chiaraviglio L, Cacciapuoti AS, Di Martino G, Fiore M, Montesano M, Trucchi D, et al. Planning 5G networks under emf constraints: state of the art and vision. *IEEE Access* 2018;6:51021–37.
162. tutorialspoint.com. Poynting-vector; 2021. Available from: https://www.tutorialspoint.com/antenna_theory/antenna_theory_poynting_vector.htm.

Supplementary Material: This article contains supplementary material (<https://doi.org/10.1515/reveh-2023-0072>).