Soil Microbes in Chernobyl and Fukushima

Subjects: Environmental Sciences
Contributor: Ko Sakauchi , Joji M. Otaki

Compositional changes in soil microbes associated with decreases in abundance and species diversity were reported, especially in heavily contaminated areas of both Chernobyl and Fukushima, which may accompany explosions of radioresistant species. In Chernobyl, the population size of soil microbes remained low for at least 20 years after the accident, and the abundance of plant-associated microbes, which are related to the growth and defense systems of plants, possibly decreased. These reported changes in microbes likely affect soil conditions and alter plant physiology. These microbe-mediated effects may then indirectly affect insect herbivores through food-mass-mediated, pollen-mediated, and metabolite-mediated interactions. Metabolite-mediated interactions may be a major pathway for ecological impacts at low pollution levels and could explain the decreases in insect herbivores in Fukushima.

radioactive pollution | nuclear power plant accident | Chernobyl | Fukushima | soil microbes | plant-associated microbes

1. Introduction

The famous and influential "Atoms for Peace" speech was delivered by the U.S. President Eisenhower in 1953 to promote research and practical applications on nuclear energy and ionizing radiation for benefits to humankind beyond military uses [1]. This speech was delivered 8 years after the speech by the U.S. President Truman to announce the atomic bomb attacks at Hiroshima and Nakagaki, Japan, in 1945 [1], and 58 years after the first discovery of ionizing radiation, X-rays, by Röntgen in 1895 [2][3]. Practical applications of ionizing radiation have indeed flourished in medical technologies (e.g., X-ray examination, computerized tomography scan, and cancer treatment) [4][5][6] and agricultural technologies (e.g., breeding, sterilization of food, and sterilization of insect pests) [7][8]. Basic biological sciences have also advanced [9]. Simultaneously, nuclear fission technologies have culminated in nuclear power plants in addition to ever-powerful nuclear weapons.

The massive impacts of radioactive pollution on environments from the beneficial uses were brought about in the Chernobyl nuclear accident in 1986 and the Fukushima nuclear accident in 2011. In both cases, multiple species of radionuclides were dispersed into the surrounding environment [10][11], among which the major pollutant remaining heterogeneously today is radioactive cesium-137 (^{137}Cs) due to its relatively long half-life of 30 years [12][13]. In the Fukushima nuclear accident, approximately 300 years are estimated to be required for the current environmental radiation levels to return to pre-accident levels [14]. As such, numerous studies on Chernobyl and Fukushima have investigated the levels of absorbed radiation in humans and other organisms [10][11][12][13][15][16][17]. Although such dosimetric studies are important, they evaluate environmental effects based on estimated doses in reference to laboratory-based irradiation studies alone. Such laboratory studies often use high-level irradiation protocols (e.g., more than 1 Gy in a relatively short time) on the implicit assumption that radiation-induced genetic damage to DNA is the major (and often sole) mechanism of adverse radiation effects.

Without question, these studies provide invaluable information on the biological impacts of the nuclear accidents. However, as these studies accumulate, serious discrepancies in the sensitivity levels of organisms between field data (based on field surveys in contaminated areas or based on field-based experiments) and laboratory data (based on exposure experiments under controlled laboratory conditions) have become evident [18][19][20][21][22].

The field–laboratory paradox appears to be resolved, at least partially, when one considers different mechanisms of biological effects between fields and laboratories [20]. In other words, there is biotic and abiotic complexity in the field and simplicity in the laboratory [20]. Although this point has been emphasized in radioecology since the 1960s [23][24][25][26][27][28], it is still challenging for not only radioactive pollution but also other pollutions, such as those generated by pesticides and heavy metals [29][30]. In the field, there are numerous biotic and abiotic interactions with organisms of interest, which may significantly modify the radiation sensitivity of the organisms to direct exposure. In other words, the synergistic effects of environmental stress and direct irradiation may enlarge the field–laboratory gap. Moreover, organisms in the field may be damaged by other "indirect" mechanisms, which are not necessarily detected in controlled laboratory experiments. For example, changes in plant secondary metabolites may influence plant-eating insects [21]. The bystander effect in fish may also be a good example [31].

Furthermore, one should admit that there are many unknown indirect pathways for deleterious effects in the field. In that case, these effects cannot be reproduced in dosimetric laboratory experiments simply because they are unknown. These unknown indirect cases were originally emphasized as field effects [20].

Many types of field effects at the individual level likely occur in an ecological context and are often called ecological field effects [20]. It is undoubtedly necessary to position each species-based study in the ecological network. The importance of ecological producers (i.e., photosynthetic plants) cannot be overemphasized to understand an ecological network in a contaminated environment. Herbivorous animals are completely dependent on food supplies from plants as ecological consumers.

2. Multiple Pathways for Biological Effects

First, one should recognize that there are multiple pathways for biological effects of a nuclear accident. Here, one should be careful about the terminology. At the molecular level, "direct" damage occurs when ionizing radiation directly breaks the covalent bonds of biological molecules (especially those of DNA), and "indirect" damage occurs via reactive oxygen species (ROS) produced by water radiolysis [20]. At the individual (organismal) level, both direct and indirect molecular mechanisms for ionization are considered "direct" effects on a given organism. As a secondary effect of these "direct" effects, several "indirect" effects may occur. For example, the sole host plant of the pale grass blue butterfly may synthesize insect toxins in response to irradiation, and butterfly larvae die due to ingested toxins (**Figure 1**). Changes in metabolites in the host plant may be considered direct or primary effects, and if so, larval death is the secondary effect. However, the primary and secondary effects may not always be fixed. Plant metabolite changes may be caused by soil microbes and plant-associated microbes, and if so, these microbial changes are the primary effects; plant metabolite changes should be considered secondary effects, and larval death should be considered to occur through tertiary effects. In reality, soil microbes, plant-associated microbes, plants, and insects are exposed to radiation simultaneously. That is, these direct effects and indirect field effects work simultaneously in the field.

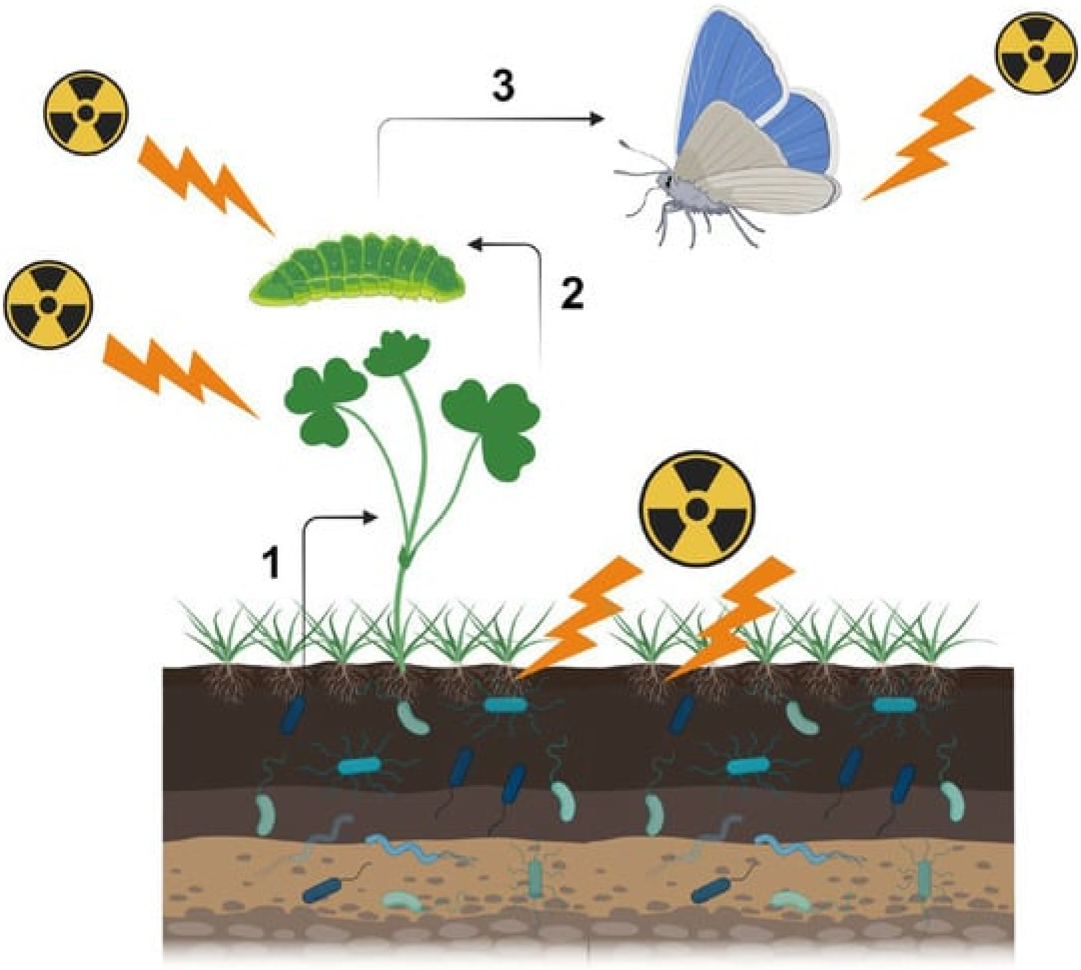

Figure 1. Direct and indirect effects of a nuclear accident on insect herbivores in the context of the ecosystem. Here, the butterfly system is depicted as an example. All entities (soil microbes, plant-associated microbes, plants, larvae, and adult butterflies) are irradiated in radioactively contaminated areas simultaneously, but because radioactive materials accumulate in soil, microbes may be affected the most in terms of exposure levels. Changes in microbes will affect plants (microbe-mediated effect indicated as “1”), and changes in plants will affect plant-feeding larvae (metabolite-mediated effect indicated as “2”). Adult butterflies are then affected at the population level (indicated as “3”). In this figure, plant-associated microbes are not shown. This figure was created with BioRender.com and Adobe Photoshop Elements.In addition to the direct and indirect effects discussed above, these effects may result in population-level changes in the numbers of animal species in the field. When a key species in a food web is highly sensitive to radioactive pollution, the balance of the food web may be disrupted, and

other species may be affected "indirectly" due to a lack (or surplus) of food. This type of population-level indirect effect is theoretically straightforward and does not always lead to a paradoxical interpretation against laboratory-based results, especially at high doses that directly eradicate a given species. The population sizes and ^{137}Cs concentrations of many organisms (including spiders [32][33], cicadas [32], dragonflies [32][33], butterflies [32][33], grasshoppers [32][33], bark beetles [16][33], bumblebees [32][33][34], booklice [16], springtails [16], soil invertebrates [35][36], reptiles [34], birds [32][37], and mammals [34]) have been reported in field surveys in Chernobyl.

The distinction between direct and indirect effects and the distinction among primary, secondary, and tertiary effects require careful and laborious laboratory experiments that consider field conditions. However, researchers should consider these potential effects carefully to interpret field data. It is important to note that the same biological result (e.g., the death of butterfly larvae) may be caused by very different mechanisms (**Figure 2**).

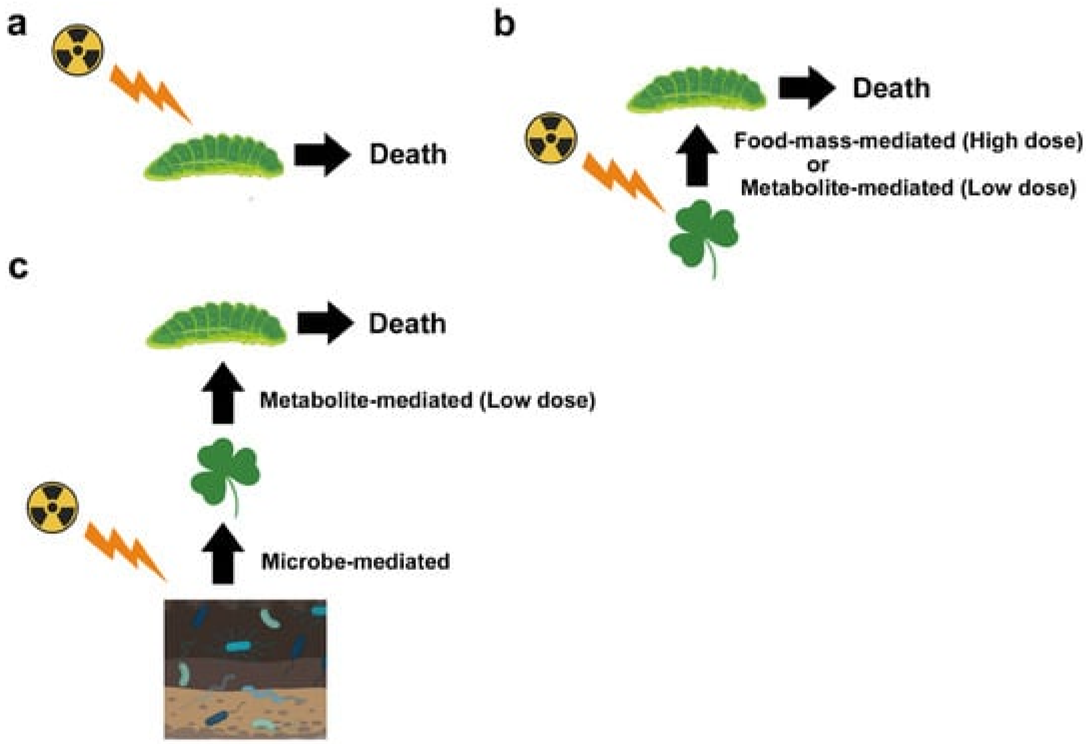

Figure 2. Different pathways that could lead to the death of insect herbivores (butterfly larvae as an example) in radioactively contaminated fields. (**a**) Direct effect only. Most dosimetric studies take this standpoint. If larvae are affected directly by high-dose exposure, this type of study may be consistent with a decrease in butterfly (adult) populations. (**b**) Larvae receiving the secondary effect from their host plant leaves. After high-dose exposure, plants may die, resulting in larval death due to a lack of food (food-mass-mediated effect). After low-dose exposure, plants may synthesize secondary metabolites that are toxic to larvae, resulting in larval death due to the toxins (metabolite-mediated effect). (**c**) Larvae receiving tertiary effects from their host plant leaves (metabolite-mediated effect) that receive secondary effects from soil microbes and plant-associated microbes (microbe-mediated effect). Depending on the exposure level, microbes, and other soil conditions, the effects on plants may vary and be nonlinear. In the field, synergistic effects from other stressors may also occur, but they are not indicated in this figure. This figure was created with BioRender.com and Adobe Photoshop Elements.

3. Soil Microbes and Soil Invertebrates

3.1. Chernobyl Studies

Field-based surveys of soil microbes began shortly after the Chernobyl accident in April 1986 to observe microbial abundance, species diversity, and composition. One of the earliest studies, from 1986 to 1989, within the 30 km zone of the Chernobyl nuclear power plant (NPP), called the exclusion zone, found radioresistant mycobiota and discovered an increase in melanized mycelia [38][39], whose function has been extensively investigated since the 2000s [40][41][42]. During this time period (1986–1989), rainfall transferred radionuclides from the plant surface to the soil [12], and most radiation doses were due to β-rays [16], which had a large impact on soil microbes. In the 1990s, several papers reported the reduced abundance and species diversity of soil microbes [39]. The number of heterotrophic bacteria and the total bacterial species in the surface layer (0–20 mm depth) of the 10 km zone of the NPP were less than those in the control site, indicating that an altered population size had not yet recovered by 1993 [39][43]. Aerobic chemoorganotrophic bacteria were cultured from the soil of the 10 km zone on nutrient agar, and the abundance of cellulose-fermenting, nitrifying, sulfate-reducing, and nitrogen-fixing bacteria, as well as heterotrophic ion-oxidizing bacteria, decreased by up to two orders of magnitude in number [39][44].

Similar declines in abundance and species diversity are known for soil invertebrates [45]. These changes in numbers are understandable considering their food web interactions. Lecomte-Pradines et al. (2014) [36] noted that radiation might have indirectly affected the abundance of nematode assemblages collected within 30 km of the Chernobyl NPP in 2011 by modifying their food resources, i.e., soil bacteria (see also Section 5.1). Moreover, 11 mGy/h (23 Gy in total) of chronic irradiation with ^{60}Co, which is approximately 1/30 of the $LD_{50/30}$ (half lethal dose for 30 days), or 650 Gy for acute irradiation with ^{137}Cs induced severe adverse effects on the reproduction of adult earthworms [46][47]. Thus, the reduced population of soil invertebrates (nematodes and earthworms) could be caused by both direct irradiation and an indirect lack of food. According to the International Atomic Energy Agency (IAEA) (2006) [12], within two months of the accident, the number of invertebrates in the litter layer of forests became 1/30 (3–7 km from the Chernobyl NPP), and the estimated cumulative exposure amount at that time was 30 Gy.

3.2. Fukushima Studies

The Fukushima nuclear accident occurred in March 2011, 25 years after the Chernobyl nuclear accident. Although advanced research methods and techniques have become more accessible, only a handful of studies on soil microbes have been documented in Fukushima. Ihara et al. (2021) [48] explored the soil bacterial community at the base of mugwort via high-throughput sequencing. They approached 1 km to the NPP at the closest location, where the ^{137}Cs concentration in the soil sample was 563 kBq/kg (dry) in 2014. Notably, for comparison, soil samples were collected from four geographically remote sites with the same vegetation and land use. The authors demonstrated the following three points in terms of bacterial communities: at the most contaminated site, (i) the species diversity was lower, (ii) the composition was different, and (iii) the radioresistant bacterium *Geodermatophilus bullaregiensis* was more abundant. Similarly, Higo et al. (2019) [49] examined the community dynamics of the arbuscular mycorrhizal fungus colonizing the roots of napiergrass *Pennisetum purpureum* under different land uses (paddy field and grassland) before an accident within 30 km of the Fukushima NPP in 2013 and 2014. The deposition density of ^{137}Cs was 3404 kBq/m^2 in paddy fields and 3322 kBq/m^2 in grasslands at the time of 2013. Illumina MiSeq sequencing data revealed that species diversity was lower in 2014 for both land-use types and that the species composition differed between sampling years and between land-use types. The most abundant family, Glomeraceae, may be tolerant of complex environments [50][51].

3.3. Commonalities between Chernobyl and Fukushima

Declines in the abundance and species diversity and compositional differences in soil microbes have been reported both in Chernobyl and Fukushima, and some microbes with radioresistance or accumulation of ^{137}Cs have been reported in both studies; however, in highly contaminated areas in Chernobyl, composition and species diversity may not follow these rules. Furthermore, the ^{137}Cs concentration in leaf litter increased during the decomposition process in Chernobyl and Fukushima, and the movement of ^{137}Cs in soil was potentially mediated by microbes to organisms in the soil and on the ground through trophic connections. As ^{137}Cs is cycled and maintained in the environment over time, the ecological half-life becomes much longer than initially estimated.

Species diversity is understood to decrease due to the simultaneous elimination of more radiosensitive species and also due to the increase in radioresistant species and immigrants [16]. In other words, radioresistance is a key trait for the abundance, species diversity, and composition of overall microbial communities in soil. Additionally, in general, radioresistant bacteria are resistant to ultraviolet rays [52][53] and dryness [54], suggesting that soil microbes adapt flexibly to various environmental stressors. Therefore, the abundance, species diversity, and composition of radioresistant microbes in the field seem to fluctuate on a large scale in response to stressor types.

4. Plant-Associated Microbes

4.1. Chernobyl Studies

Studies on herbaceous plants were initiated as early as 1986 (see also Section 5). Geras'kin et al. (2002) [55] collected seeds of winter rye within 30 km of the Chernobyl NPP approximately 4 months after the accident, and after germination, the plants were subjected to cytogenetic tests. In a different study, germination of wild carrot seeds from maternal plants exposed to radiation in Chernobyl showed the lower gemination rate and other abnormal life-history traits [56]. However, plant-associated microbes have rarely been explored. Mousseau et al. (2014) [57] suggested that the reduced rate of litter mass loss and thicker forest floor (poor levels of decomposition in other words) in the 30 km zone of Chernobyl could have an effect on growth conditions for plants because free-living microbes strongly regulate plant productivity through mineralization during the decomposition process, which makes nutrients such as nitrogen and phosphorus available to plants [58].

Several papers have noted that the effect of radiation exposure on plants is a weakened defense system when radiation levels are relatively high. A decrease in the disease resistance of wheat, rye, and maize was observed within 10 km of the NPP, and in fact, brown rust and true mildew infection increased in winter wheat, corresponding to radioactive contamination [10]. Simultaneously, the emergence of a new causal agent of stem rust, *Puccinia graminis*, with a high frequency of more virulent clones was detected within 10 km [10][59]. Thus, the prevalence of plant diseases in Chernobyl could be caused by both reduced disease resistance and enhanced toxicity.

4.2. Fukushima Studies

Within the context of even fewer studies on plant-associated microbes in Fukushima, Sakauchi et al. (2022) [60] subjected the field-picked creeping wood sorrel *Oxalis corniculata* to LC–MS analysis to quantify secondary metabolites. The radiation level ranged from nondetectable to 718 Bq/kg for the ^{137}Cs radioactivity concentration in the leaves and from 0.04 μGy/h to 4.55 μGy/h for the ground dose rate at which the leaves grew. This study demonstrated that *Oxalis* leaves, which were field-picked in Fukushima and looked completely healthy to the naked eye, upregulated and downregulated secondary metabolites in response to low-dose radiation exposure [60].

In addition to these findings, Zhu et al. (2021) [61] studied contaminated soil samples containing three different ^{137}Cs concentrations (low: 20–40 Bq/kg, medium: 40–60 Bq/kg, and high: >60 Bq/kg) from a historic nuclear test site in China and found that the richness of the endophytic bacteria in the roots of *Kalidium schrenkianum* was significantly greater only in low-radiation soil than in the control soil. Thus, endophytes could sensitively change their abundance in response to low-radiation exposure.

4.3. Commonalities between Chernobyl and Fukushima

In Chernobyl, various adverse effects have been observed on plants, including morphological changes, disturbances in growth, suppressed reproductive ability, death, disease, and pest infections [12]. A few of these events have also been observed in Fukushima [62][63][64][65]. It is highly likely that plant-associated microbes are involved in these observations, although no causal relationship has been demonstrated thus far. No reports of poor growth, disease, or pest infections were available in Fukushima, despite the large number of crop fields and fruit trees in the contaminated area.

Partially considering Mousseau et al. (2014) [57] and Zhu et al. (2021) [61], plant-associated microbes may become less common in relatively severely contaminated areas in Chernobyl and Fukushima, possibly leading to growth failure and low immunity in plants. For example, arbuscular mycorrhizal fungi (AMF) that colonize plant roots and form symbiotic associations with 80% of terrestrial plant species are generally accepted to contribute to plant growth by facilitating the production of growth hormones and phosphorus uptake. The antibacterial endophytic fungus *Streptomyces galbus* improved resistance to Pestalotia disease, root rot, and anthracnose and was inoculated for practical use on flowering plants such as *Rhododendron* [66]. On the other hand, based on the LC–MS analysis of *Oxalis* leaves in Fukushima, the abundance of *Streptomyces* sp., which produces antibiotics, did not always decrease [60].

5. Plants and Insect Herbivores

5.1. Food-Mass-Mediated Indirect Effects

Early studies, mostly conducted in 1986 at the time of the Chernobyl accident, reported reproductive degradation in various herbaceous plants [10]: a reduced number of seeds or a lower germination rate in winter wheat, cocksfoot *Dactylis glomerata*, and ribwort plantain *Plantago lanceolata*, and sterility in winter wheat, winter ryes, and wild vetch *Vicia cracca*. Taskaev et al. (1992) [67] observed no effect on the seeds of 15 species within 30 km of the Chernobyl NPP. Boratyński et al. (2016) [56] conducted a germination experiment using seeds of the wild carrot *Daucus carota,* collected from an abandoned field within 10 km from the Chernobyl NPP in 2012, and showed that the more radiation the maternal plants were exposed to, the longer the time that the seeds took to germinate and produce leaves and the lower the germination rate. Therefore, it is reasonable to speculate that the overall mass of phytocoenoses decreased around the Chernobyl NPP in heavily contaminated areas.

The perturbation of phytocoenoses causes severe impacts on insect herbivores, which have no other option but to eat plants. Generalist herbivores may converge on surviving radioresistant plants. As a result, interspecies competition necessarily becomes more intense. In the case of specialist herbivores, survival will be difficult if their host plants are sensitive to radiation. This indirect effect through food loss, which many be called the food-mass-mediated effect, was mentioned in the early 1970s based on irradiation experiments [35]. The United Nations Scientific Committee on Effects of Atomic Radiation (UNSCEAR) 1996 report provided the example of a booklice, *Psocoptera* [16]. In this respect, the smaller population sizes of not only insect herbivores but also other various terrestrial organisms in Chernobyl could suggest insufficient amounts of food available for the following organisms, although direct effects on these organisms cannot be excluded: spiders [32][33], cicadas [32], dragonflies [32][33], butterflies [32][33], grasshoppers [32][33], bark beetles [16][33], bumblebees [32][33][34], booklice [16], springtails [16], soil invertebrates [35][36], reptiles [34], birds [32][37], and mammals [34].

5.2. Pollen-Mediated Indirect Effects

A version of the food mass-mediated effect is the pollen-mediated effect, in which the reproductive and pollination systems of plants are specifically affected via direct irradiation. Pollens are foods for some insects, but the relationships between plants and pollinating insects (i.e., bees, butterflies, and others) are more complex than the simple predator-prey relationship. A decrease in the plant population may occur slowly through low pollen viability, resulting in a decrease in pollinating and other related insects.

5.3. Metabolite-Mediated Indirect Effect

In Fukushima, the pollution level was relatively low compared to that in Chernobyl. One of the main radionuclides detected when measured was ^{137}Cs in both Chernobyl and Fukushima, and its released amount in Fukushima was estimated to be, at most, 40% of that in Chernobyl [68]. This is probably why plants in Fukushima seem to be healthy, at least to the naked eye; no deleterious effects on plants have been reported, although there are a few reports on morphological abnormalities [64][65][69]. In this sense, food mass-mediated indirect effects (**Figure 3**) may not occur in Fukushima between plants and insect herbivores. Pollination also does not seem to be affected much in Fukushima [70]. However, lower abundances of insects such as butterflies [32][71] and cicadas [32] have been reported along with an increasing radiation dose. They are insect herbivores.

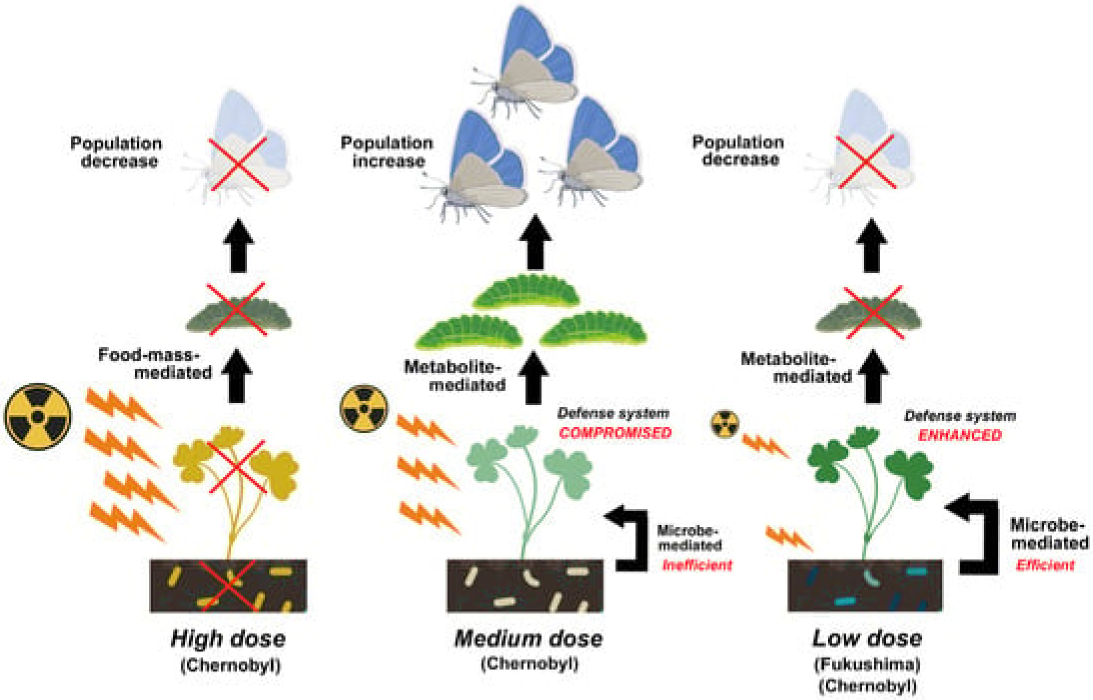

Figure 3. Comparison of possible mechanisms of population changes in insect herbivores among high-dose exposure (Chernobyl), medium-dose exposure (Chernobyl), and low-dose exposure (Fukushima and Chernobyl). In this example, both high-dose and low-dose pathways potentially cause a decrease in the population of adult butterflies in the field, but the medium-dose pathway causes the opposite result. This figure was created with BioRender.com and Adobe Photoshop Elements.

6. Conclusions

It is said that 10–100 billion bacteria and a large number of fungi and other microbes inhabit one gram of soil [58] and interact with each other in the soil ecosystem, responding sensitively to multiple stressors in the field. Plant-associated microbes also appear to respond to radiation exposure. These changes certainly affect plant physiology, which seem to be inevitable, even at relatively low levels of radioactive pollution, because the sensitivity of microbes to radioactive pollution varies greatly depending on the species and environmental conditions. Importantly, such changes seem to persist for many years after a pollution event. Plants respond to these changes actively or passively, depending on the radiation level. The defense system of plants is likely enhanced at the low-level exposure, which may cause the eradication of insect herbivores in the field. The defense system of plants is compromised at the medium-level exposure, which may cause an increase in insect herbivores in the field. In any case, plant responses likely affect insect herbivores through food-mass-mediated, pollen-mediated, and metabolite-mediated interactions.

Although precisely distinguishing between direct and indirect effects requires many types of field surveys and laboratory experiments, because both effects work simultaneously in the field, indirect field effects are much less studied than direct effects but likely play a major role in the health of ecosystems in contaminated environments involving long-term low-dose radiation exposure. Population decreases in insect herbivores in Fukushima may be considered field-based evidence for metabolite-mediated indirect effects at relatively low contamination levels. it speculates that at the low exposure, the impacts of metabolite-mediated effects may be much greater than one might think, covering wide geographical areas and various species of insect herbivores in Fukushima. In this sense, the long-term impacts of microbe-plant interactions and metabolite-mediated interactions between plants and insect herbivores in the field cannot be overemphasized. These effects will then cause the adaptation of organisms to contaminated environments over time [72][73]. Epigenetic modifications, represented by DNA methylation, may occur as a mechanism of transgenerational effects [74][75][76][77][78][79]. Genetic changes at the population level may also be expected due to “natural” selection for more surviving individuals.

References

1. Wagner, H.N., Jr. Atoms for peace (and health). J. Nucl. Med. 2004, 45, 24N.
2. Babic, R.R.; Babic, G.S.; Babic, S.R.; Babic, N.R. 120 years since the discovery of x-rays. Med. Pregl. 2016, 69, 323–330.
3. Nüsslin, F. Wilhelm Conrad Röntgen: The scientist and his discovery. Phys. Med. 2020, 79, 65–68.
4. Brodsky, A.; Kathren, R.L.; Willis, C.A. History of the medical uses of radiation: Regulatory and voluntary standards of protection. Health Phys. 1995, 69, 783–823.
5. Reed, A.B. History of radiation use in medicine. J. Vasc. Surg. 2011, 53 (Suppl. S1), 3S–5S.
6. Scatliff, J.H.; Morris, P.J. From Röntgen to magnetic resonance imaging: The history of medical imaging. N. C. Med. J. 2014, 75, 111–113.
7. Ma, L.; Kong, F.; Sun, K.; Wang, T.; Guo, T. From classical radiation to modern radiation: Past, present, and future of radiation mutation breeding. Front. Public Health 2021, 9, 768071.
8. Riviello-Flores, M.d.l.L.; Cadena-Iñiguez, J.; Ruiz-Posadas, L.d.M.; Arévalo-Galarza, M.d.L.; Castillo-Juárez, I.; Hernández, M.S.; Castillo-Martínez, C.R. Use of gamma radiation for the genetic improvement of underutilized plant varieties. Plants 2022, 11, 1161.
9. Whitmore, G.F. One hundred years of X rays in biological research. Radiat. Res. 1995, 144, 148–159.
10. Geras’kin, S.A.; Fesenko, S.V.; Alexakhin, R.M. Effects of non-human species irradiation after the Chernobyl NPP accident. Environ. Int. 2008, 34, 880–897.

11. Yoshida, N.; Kanda, J. Geochemistry. Tracking the Fukushima radionuclides. Science 2012, 336, 1115–1116.
12. International Atomic Energy Agency (IAEA). Environmental Consequences of the Chernobyl Accident and their Remediation: Twenty Years of Experience; Radiological Assessment Reports Series No. 8; IAEA: Vienna, Austria, 2006.
13. Aliyu, A.S.; Evangeliou, N.; Mousseau, T.A.; Wu, J.; Ramli, A.T. An overview of current knowledge concerning the health and environmental consequences of the Fukushima Daiichi Nuclear Power Plant (FDNPP) accident. Environ. Int. 2015, 85, 213–228.
14. Ministry of the Environment (Government of Japan). Chapter 4. Concept of radiological protection. In BOOKLET to Provide Basic Information Regarding Health Effects of Radiation, 3rd ed.; Ministry of the Environment (Government of Japan): Tokyo, Japan, 2016; Available online: https://www.env.go.jp/en/chemi/rhm/basic-info/1st/04.html (accessed on 13 January 2024).
15. International Atomic Energy Agency (IAEA). Effects of Ionizing Radiation on Plants and Animals at Levels Implied by Current Radiation Protection Standards; Technical Reports Series No. 332; IAEA: Vienna, Austria, 1992.
16. United Nations Scientific Committee on the Effects of Atomic Radiation (UNSCEAR). Sources and Effects of Ionizing Radiation UNSCEAR 1996 Report to the General Assembly, with Scientific Annex; United Nations: New York, NY, USA, 1996.
17. European Commission. Protection of the Environment; European Union: Luxembourg, 2014; Available online: https://energy.ec.europa.eu/system/files/2014-11/177_0.pdf (accessed on 13 January 2024).
18. Hiyama, A.; Nohara, C.; Taira, W.; Kinjo, S.; Iwata, M.; Otaki, J.M. The Fukushima nuclear accident and the pale grass blue butterfly: Evaluating biological effects of long-term low-dose exposures. BMC Evol. Biol. 2013, 13, 168.
19. Garnier-Laplace, J.; Geras'kin, S.; Della-Vedova, C.; Beaugelin-Seiller, K.; Hinton, T.G.; Real, A.; Oudalova, A. Are radiosensitivity data derived from natural field conditions consistent with data from controlled exposures? A case study of Chernobyl wildlife chronically exposed to low dose rates. J. Environ. Radioact. 2013, 121, 12–21.
20. Otaki, J.M. Understanding low-dose exposure and field effects to resolve the field-laboratory paradox: Multifaceted biological effects from the Fukushima nuclear accident. In New Trends in Nuclear Science; Awwad, N.S., AlFaify, S.A., Eds.; InTechOpen: London, UK, 2018; pp. 49–71.
21. Otaki, J.M.; Sakauchi, K.; Taira, W. The second decade of the blue butterfly in Fukushima: Untangling the ecological field effects after the Fukushima nuclear accident. Integr. Environ. Assess. Manag. 2022, 18, 1539–1550.

22. Beaugelin-Seiller, K.; Della-Vedova, C.; Garnier-Laplace, J. Is non-human species radiosensitivity in the lab a good indicator of that in the field? Making the comparison more robust. J. Environ. Radioact. 2020, 211, 105870.
23. Woodwell, G.M.; Sparrow, A.H. Predicted and observed effects of chronic gamma radiation on a near-climax forest ecosystem. Radiat. Botany 1963, 3, 231–237.
24. Caffrey, E.; Leonard, M.; Napier, J.; Neville, D.; Higley, K. Radioecology: Why Bother? J. Environ. Prot. 2014, 5, 181–192.
25. Bradshaw, C.; Kapustka, L.; Barnthouse, L.; Brown, J.; Ciffroy, P.; Forbes, V.; Geras'kin, S.; Kautsky, U.; Bréchignac., F. Using an Ecosystem Approach to complement protection schemes based on organism-level endpoints. J. Environ. Radioact. 2014, 136, 98–104.
26. Brèchignac, F.; Doi, M. Challenging the current strategy of radiological protection of the environment: Arguments for an ecosystem approach. J. Environ. Radioact. 2009, 100, 1125–1134.
27. Woodwell, G.M. Ecological Effects of Nuclear War; Brookhaven National Laboratory: Upton, NY, USA, 1963.
28. Bréchignac, F.; Alexakhin, R.; Godoy, J.M.; Oughton, D.; Sheppard, S.; Strand, P. Integrating environment protection, a new challenge: Strategy of the International Union of Radioecology. Radioprotection 2008, 43, 339–356.
29. Dalkvist, T.; Topping, C.J.; Forbes, V.E. Population-level impacts of pesticide-induced chronic effects on individuals depend more on ecology than toxicology. Ecotoxicol. Environ. Saf. 2009, 72, 1663–1672.
30. Clements, W.H.; Rohr, J.R. Community responses to contaminants: Using basic ecological principles to predict ecotoxicological effects. Environ. Toxicol. Chem. 2009, 28, 1789–1800.
31. Mothersill, C.; Seymour, C. Communication of ionising radiation signals—A tale of two fish. Int. J. Radiat. Biol. 2009, 85, 909–919.
32. Møller, A.P.; Nishiumi, I.; Suzuki, H.; Ueda, K.; Mousseau, T.A. Differences in effects of radiation on abundance of animals in Fukushima and Chernobyl. Ecol. Indic. 2013, 24, 75–81.
33. Møller, A.P.; Mousseau, T.A. Reduced abundance of insects and spiders linked to radiation at Chernobyl 20 years after the accident. Biol. Lett. 2009, 5, 356–359.
34. Møller, A.P.; Mousseau, T.A. Efficiency of bio-indicators for low-level radiation under field conditions. Ecol. Indic. 2011, 11, 424–430.
35. Turner, F.B. Effects of continuous irradiation on animal populations. Adv. Radiat. Biol. 1975, 5, 83–144.

36. Lecomte-Pradines, C.; Bonzom, J.M.; Della-Vedova, C.; Beaugelin-Seiller, K.; Villenave, C.; Gaschak, S.; Coppin, F.; Dubourg, N.; Maksimenko, A.; Adam-Guillermin, C.; et al. Soil nematode assemblages as bioindicators of radiation impact in the Chernobyl Exclusion Zone. Sci. Total Environ. 2014, 490, 161–170.

37. Møller, A.P.; Mousseau, T.A. Species richness and abundance of forest birds in relation to radiation at Chernobyl. Biol. Lett. 2007, 3, 483–486.

38. Zhdanova, N.N.; Vasilevskaia, A.I.; Artyshkova, L.V.; Gavriliuk, V.I.; Lashko, T.N.; Sadovnikov, I.S. Kompleksy pochvennykh mikrokitsetov v zone vliianiia Chernobyl'skoĭ AES . Mikrobiol. Zh. 1991, 53, 3–9. (In Russian)

39. Yablokov, A.V.; Nesterenko, V.B.; Nesterenko, A.V. Consequences of the Chernobyl catastrophe for public health and the environment 23 years later. Ann. N. Y. Acad. Sci. 2009, 1181, 318–326.

40. Cordero, R.J.; Casadevall, A. Functions of fungal melanin beyond virulence. Fungal Biol. Rev. 2017, 31, 99–112.

41. Dadachova, E.; Bryan, R.A.; Huang, X.; Moadel, T.; Schweitzer, A.D.; Aisen, P.; Nosanchuk, J.D.; Casadevall, A. Ionizing radiation changes the electronic properties of melanin and enhances the growth of melanized fungi. PLoS ONE 2007, 2, e457.

42. Dadachova, E.; Casadevall, A. Ionizing radiation: How fungi cope, adapt, and exploit with the help of melanin. Curr. Opin. Microbiol. 2008, 11, 525–531.

43. Romanovskaia, V.A.; Stoliar, S.M.; Malashenko, I.R.; Shatokhina, E.S. Vliianie radiatsii dlitel'nogo deĭstviia na raznoobrazie geterotrofnykh bakteriĭ v pochvakh 10-kilometrovoĭ zony Chernobyl'skoĭ atomnoĭ élektrostantsii . Mikrobiol. Z. 1996, 58, 3–12. (In Russian)

44. Romanovskaia, V.A.; Sokolov, I.G.; Rokitko, P.V.; Chernaia, N.A. Ekologicheskie posledstviia radioaktivnogo zagriazneniia dlia pochvennykh bakteriĭ v 10-km zone ChAES . Mikrobiologiia 1998, 67, 274–280. (In Russian)

45. Krivolutzkii, D.A.; Pokarzhevskii, A.D. Effects of radioactive fallout on soil animal populations in the 30 km zone of the Chernobyl atomic power station. Sci. Total Environ. 1992, 112, 69–77.

46. Suzuki, J.; Egami, N. Mortality of the earthworms, Eisenia foetida, after γ-irradiation at different stages of their life history. J. Radiat. Res. 1983, 24, 209–220.

47. Hertel-Aas, T.; Oughton, D.H.; Jaworska, A.; Bjerke, H.; Salbu, B.; Brunborg, G. Effects of chronic gamma irradiation on reproduction in the earthworm Eisenia fetida (Oligochaeta). Radiat. Res. 2007, 168, 515–526.

48. Ihara, H.; Kumagai, A.; Hori, T.; Nanba, K.; Aoyagi, T.; Takasaki, M.; Katayama, Y. Direct comparison of bacterial communities in soils contaminated with different levels of radioactive

cesium from the first Fukushima nuclear power plant accident. Sci. Total Environ. 2021, 756, 143844.

49. Higo, M.; Kang, D.J.; Isobe, K. First report of community dynamics of arbuscular mycorrhizal fungi in radiocesium degradation lands after the Fukushima-Daiichi Nuclear disaster in Japan. Sci. Rep. 2019, 9, 8240.
50. Bever, J.D.; Richardson, S.C.; Lawrence, B.M.; Holmes, J.; Watson, M. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. Ecol. Lett. 2009, 12, 13–21.
51. Barto, E.K.; Hilker, M.; Müller, F.; Mohney, B.K.; Weidenhamer, J.D.; Rillig, M.C. The fungal fast lane: Common mycorrhizal networks extend bioactive zones of allelochemicals in soils. PLoS ONE 2011, 6, e27195.
52. Arrange, A.A.; Phelps, T.J.; Benoit, R.E.; Palumbo, A.V.; White, D.C. Bacterial sensitivity to UV light as a model for ionizing radiation resistance. J. Microbiol. Methods 1993, 18, 127–136.
53. Kawaguchi, Y.; Shibuya, M.; Kinoshita, I.; Yatabe, J.; Narumi, I.; Shibata, H.; Hayashi, R.; Fujiwara, D.; Murano, Y.; Hashimoto, H.; et al. DNA damage and survival time course of deinococcal cell pellets during 3 years of exposure to outer space. Front. Microbiol. 2020, 11, 2050.
54. Musilova, M.; Wright, G.; Ward, J.M.; Dartnell, L.R. Isolation of radiation-resistant bacteria from Mars analog Antarctic Dry Valleys by preselection, and the correlation between radiation and desiccation resistance. Astrobiology 2015, 15, 1076–1090.
55. Geras'kin, S.A.; Dikarev, V.G.; Zyablitskaya, Y.Y.; Oudalova, A.A.; Spirin, Y.V. Cytogenetic effects of radiation on agricultural plants observed in the Chernobyl region during the first years after the accident. KURRI-KR 2002, 79, 287–296.
56. Boratyński, Z.; Arias, J.; Garcia, C.; Mappes, T.; Mousseau, T.A.; Møller, A.P.; Pajares, A.J.M.; Piwczyński, M.; Tukalenko, E. Ionizing radiation from Chernobyl affects development of wild carrot plants. Sci. Rep. 2016, 6, 39282.
57. Mousseau, T.A.; Milinevsky, G.; Kenney-Hunt, J.; Møller, A.P. Highly reduced mass loss rates and increased litter layer in radioactively contaminated areas. Oecologia 2014, 175, 429–437.
58. van der Heijden, M.G.; Bardgett, R.D.; van Straalen, N.M. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 2008, 11, 296–310.
59. Dmitriev, A.; Guscha, N.; Dyachenko, A. Effects of low dose radiation on plant-pathogen interactions in Chernobyl Zone. Radioprotection 2008, 43, 148.
60. Sakauchi, K.; Taira, W.; Otaki, J.M. Metabolomic profiles of the creeping wood sorrel Oxalis corniculata in radioactively contaminated fields in Fukushima: Dose-dependent changes in key

metabolites. Life 2022, 12, 115.

61. Zhu, J.; Sun, X.; Zhang, Z.D.; Tang, Q.Y.; Gu, M.Y.; Zhang, L.J.; Hou, M.; Sharon, A.; Yuan, H.L. Effect of ionizing radiation on the bacterial and fungal endophytes of the halophytic plant Kalidium schrenkianum. Microorganisms 2021, 9, 1050.
62. Hayashi, G.; Shibato, J.; Imanaka, T.; Cho, K.; Kubo, A.; Kikuchi, S.; Satoh, K.; Kimura, S.; Ozawa, S.; Fukutani, S.; et al. Unraveling low-level gamma radiation-responsive changes in expression of early and late genes in leaves of rice seedlings at Iitate Village, Fukushima. J. Hered. 2014, 105, 723–738.
63. Rakwal, R.; Hayashi, G.; Shibato, J.; Deepak, S.A.; Gundimeda, S.; Simha, U.; Padmanaban, A.; Gupta, R.; Han, S.I.; Kim, S.T.; et al. Progress toward rice seed OMICS in low-level gamma radiation environment in Iitate Village, Fukushima. J. Hered. 2018, 109, 206–211.
64. Watanabe, Y.; Ichikawa, S.; Kubota, M.; Hoshino, J.; Kubota, Y.; Maruyama, K.; Fuma, S.; Kawaguchi, I.; Yoschenko, V.I.; Yoshida, S. Morphological defects in native Japanese fir trees around the Fukushima Daiichi Nuclear Power Plant. Sci. Rep. 2015, 5, 13232.
65. Yoschenko, V.; Nanba, K.; Yoshida, S.; Watanabe, Y.; Takase, T.; Sato, N.; Keitoku, K. Morphological abnormalities in Japanese red pine (Pinus densiflora) at the territories contaminated as a result of the accident at Fukushima Dai-Ichi Nuclear Power Plant. J. Environ. Radioact. 2016, 165, 60–67.
66. Shimizu, M. Endophytic actinomycetes: Biocontrol agents and growth promoters. In Bacteria in Agrobiology: Pant Growth Responses; Maheshwari, D.K., Ed.; Springer: Berlin/Heidelberg, Germany, 2011; pp. 201–220.
67. Taskaev, A.I.; Frolova, N.P.; Popova, O.N.; Shevchenko, V.A. The monitoring of herbaceous seeds in the 30-km zone of the Chernobyl nuclear accident. Sci. Total Environ. 1992, 112, 57–67.
68. Imanaka, T. Chernobyl and Fukushima: Comparison of accident process and radioactive contamination. Kagaku 2016, 86, 0252–0257. (In Japanese)
69. Ludovici, G.M.; Chierici, A.; de Souza, S.O.; d’Errico, F.; Iannotti, A.; Malizia, A. Effects of ionizing radiation on flora ten years after the Fukushima Dai-ichi disaster. Plants 2022, 11, 222.
70. Yoshioka, A.; Mishima, Y.; Fukasawa, K. Pollinators and other flying insects inside and outside the Fukushima evacuation zone. PLoS ONE 2015, 10, e0140957.
71. Hiyama, A.; Taira, W.; Nohara, C.; Iwasaki, M.; Kinjo, S.; Iwata, M.; Otaki, J.M. Spatiotemporal abnormality dynamics of the pale grass blue butterfly: Three years of monitoring (2011–2013) after the Fukushima nuclear accident. BMC Evol. Biol. 2015, 15, 15.
72. Cannon, G.; Kiang, J.G. A review of the impact on the ecosystem after ionizing irradiation: Wildlife population. Int. J. Radiat. Biol. 2022, 98, 1054–1062.

73. Nohara, C.; Hiyama, A.; Taira, W.; Otaki, J.M. Robustness and radiation resistance of the pale grass blue butterfly from radioactively contaminated areas: A possible case of adaptive evolution. J. Hered. 2018, 109, 188–198.
74. Hancock, S.; Vo, N.T.K.; Omar-Nazir, L.; Batlle, J.V.I.; Otaki, J.M.; Hiyama, A.; Byun, S.H.; Seymour, C.B.; Mothersill, C. Transgenerational effects of historic radiation dose in pale grass blue butterflies around Fukushima following the Fukushima Dai-ichi Nuclear Power Plant meltdown accident. Environ. Res. 2019, 168, 230–240.
75. Hinton, T.G.; Alexakhin, R.; Balonov, M.; Gentner, N.; Hendry, J.; Prister, B.; Strand, P.; Woodhead, D. Radiation-induced effects on plants and animals: Findings of the United Nations Chernobyl Forum. Health Phys. 2007, 93, 427–440.
76. Adam-Guillermin, C.; Hertal-Aas, T.; Oughton, D.; Blanchard, L.; Alonzo, F.; Armant, O.; Horemans, N. Radiosensitivity and transgenerational effects in non-human species. Ann. ICRP 2018, 47, 327–341.
77. Horemans, N.; Spurgeon, D.J.; Lecomte-Pradines, C.; Saenen, E.; Bradshaw, C.; Oughton, D.; Rasnaca, I.; Kamstra, J.H.; Adam-Guillermin, C. Current evidence for a role of epigenetic mechanisms in response to ionizing radiation in an ecotoxicological context. Environ. Pollut. 2019, 251, 469–483.
78. Gombeau, K.; Bonzom, J.M.; Cavalié, I.; Camilleri, V.; Orjollet, D.; Dubourg, N.; Beaugelin-Seiller, K.; Bourdineaud, J.P.; Lengagne, T.; Armant, O.; et al. Dose-dependent genomic DNA hypermethylation and mitochondrial DNA damage in Japanese tree frogs sampled in the Fukushima Daiichi area. J. Environ. Radioact. 2020, 225, 106429.
79. Hancock, S.; Vo, N.T.K.; Goncharova, R.I.; Seymour, C.B.; Byun, S.H.; Mothersill, C.E. One-Decade-Spanning transgenerational effects of historic radiation dose in wild populations of bank voles exposed to radioactive contamination following the chernobyl nuclear disaster. Environ. Res. 2020, 80, 108816.