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Review

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ABSTRACT

Estimating the consequences of environmental changes, specifically in a global change context, is essential for conservation issues. In the case of pollutants, the interest in using an evolutionary approach to investigate their consequences has been emphasized since the 2000s, but these studies remain rare compared to the characterization of direct effects on individual features. We focused on the study case of anthropogenic ionizing radiation because, despite its potential strong impact on evolution, the scarcity of evolutionary approaches to study the biological consequences of this stressor is particularly true. In this study, by investigating some particular features of the biological effects of this stressor, and by reviewing existing studies on evolution under ionizing radiation, we suggest that evolutionary approach may help provide an integrative view on the biological consequences of ionizing radiation. We focused on three topics: (i) the mutagenic properties of ionizing radiation and its disruption of evolutionary processes, (ii) exposures at different time scales, leading to an interaction between past and contemporary evolution, and (iii) the special features of contaminated areas called exclusion zones and how evolution could match field and laboratory observed effects. This approach can contribute to answering several key issues in radioecology: to explain species differences in the sensitivity to ionizing radiation, to improve our estimation of the impacts of ionizing radiation on populations, and to help identify the environmental features impacting organisms (e.g., interaction with other pollution, migration of populations, anthropogenic environmental changes). Evolutionary approach would benefit from being integrated to the ecological risk assessment process.

1. Introduction

The relative recent development of nuclear energy and the diversification in radionuclide usage, led to several cases of exposure of the environment to ionizing radiation from anthropogenic sources (power-plant accidents, atomic weapon tests, and so on) (Rhodes et al., 2020). The most obvious and dramatic examples are nuclear disasters, such as the Kyshtym (September 29, 1957), Chernobyl (April 26, 1986), or Fukushima accident (March 11, 2011). In the disaster areas, contaminated by radionuclides and usually evacuated by humans ("exclusion zones"), remaining wild organisms can be exposed to relatively high dose rates of ionizing radiation (e.g., $\sim 110 \text{ mGy h}^{-1}$ within a month after the Chernobyl nuclear accident, in the 600 ha most contaminated (Geras'kin et al., 2008)) and for several decades. Some rare and

charismatic species are observed in these human-excluded areas (Der-yabina et al., 2015), which might suggest that positive effect of human activity loss could outweigh the potential negative effects of radiation. But several studies still display adverse effects of ionizing radiation on some organisms in these places, leading to a scientific debate on the generalization of ionizing radiation effects to the all biotic community after a nuclear disaster (Beresford et al., 2020b). These questions also involve the issue of the linearity of the dose-response relationship for a range of doses observed in anthropogenic contaminated areas and the existence of a threshold under which no effect is expected (Tubiana et al., 2006). There are thus still major scientific, but also societal challenges related to the study of the effects of ionizing radiation on the environment (Centemeri et al., 2021).

As some other pollution like lead or benzo(a)pyrene (Binelli et al.,

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2008; Ferraro et al., 2004), ionizing radiation is known to induce mutations (Breimer, 1988). Anthropogenic ionizing radiation is also very persistent: an environment contaminated with long-lived radionuclides can be exposed for a very long time to ionizing radiation and undergo its effects (e.g., the two current major radionuclides in the Chernobyl exclusion zone, e.g., zone where populations were evacuated and access was restricted, are ^{90}Sr and ^{137}Cs , with a half-life of respectively 28.91 and 30.08 years). Finally, ionizing radiation are known to induce potential fitness impairments, notably due to a disturbance on oxidative status (Einor et al., 2016). All these specific features of the biological consequences of ionizing radiation can lead to changes in the transmitted variations across generations, which is the fundamental basis of biological evolution. Nevertheless, despite the interest of radioecology for evolutionary concepts, studies investigating evolution and its processes remain relatively scarce (see Box 1 for bibliometric analysis applied to the case of field studies of ionizing radiation effects).

The under-representation of evolution in radioecology is in line with ecotoxicology in general, in which the awareness of evolutionary biology is quite secondary, with still few studies investigating changes in the intensity of evolutionary processes faced with pollutants compared to mechanistic studies investigating effects at the individual scale (Coutellec and Barata, 2013; Straub et al., 2020). In addition to physiological or biochemical measurements, efforts since the 2000s have focused on the development of new molecular biological biomarkers, in particular using "omics" tools (Forbes et al., 2006; Zhang et al., 2018). The interest for molecular biology has allowed for example to explain genetically the sensitivity of organisms to pollutants (Jo et al., 2009) or to study their mode of action (Larras et al., 2020; Peng et al., 2016). Concurrently, the integration of an evolutionary approach to investigate the effects of pollutants on the environment has been developed with the emergence of studies in "evolutionary ecotoxicology" (see for example Bickham et al., 2000). This approach allowed to make assumptions about the intensity of evolutionary processes, notably supported by the development of molecular biology (Belfiore and Anderson, 1998).

In this review, we followed concurrently two directions, by investigating currently existing studies on the evolutionary consequences of ionizing radiation, and by examining the specific biological consequences of ionizing radiation and how they could involve changes in the intensity of evolutionary processes of exposed organisms. We thus show that evolutionary questioning is indispensable to shed new light on scientific debates in radioecology. Indeed, ionizing radiation can disrupt evolution by their effect on genetic or non-genetic inheritance and populations (Section 2), and consequently have an impact on organisms at ecological and geological time scales (Section 3). In addition, evolution is necessary to apprehend the particular features of exclusion zones, and make the link between laboratory and field studies (Section 4).

2. Ionizing radiation induces the apparition of new genotypic and phenotypic changes, and can modify evolutionary processes

2.1. Impact on genetic and non-genetic inheritance

Ionizing radiation is mutagen and induces genetic alteration (Breimer, 1988) through direct effects on the DNA or through indirect oxidative damages (Einor et al., 2016). This alteration occurs at the chromosomes level, with chromosomal aberrations (Bender et al., 1974; Sudprasert et al., 2006), and at the DNA molecule scale, with single or several base lesions (e.g., single or double strand breaks, base oxidation: Frankenberg-Schwager, 1990; Sage and Shikazono, 2017). It results in mutations such as substitutions, deletions/insertions, copy-number variants (Adewoye et al., 2015; Han and Yu, 2010). Ionizing radiation has a significant impact on spermatozoa, related to a negative regulation of DNA repair and to the loss of apoptotic capacities during spermatogenesis (Lewis and Aitken, 2005). Because of an important cellular activity (replication for example), reproduction and the first steps of development can be highly vulnerable to mutations. Specifically,

deleterious mutations could lead to gamete loss or embryo death.

Increased germline mutation rate can increase the diversity of alleles transmitted to the offspring. For example, germline mutation rate has increased in humans following nuclear disasters (twofold increase in contaminated places from Belarus after the Chernobyl accident (Dubrova et al., 1996)) or nuclear weapon tests (twofold increase in the places contaminated in Semipalatinsk region (Dubrova et al., 2002), and threefold increase after irradiation from the Goiânia accident (Costa et al., 2018)). A comparable increase mutation rate occurred in the Chernobyl exclusion zone in barn swallows (*Hirundo rustica*) (two to tenfold increase; Ellegren et al., 1997) and in plants: eight to sixty-fold increase in Scots pine (*Pinus sylvestris*) and no increase in wheat (*Triticum aestivum*), but very specific type of mutations (Geras'kin and Volkova, 2014; Kovalchuk et al., 2003).

Not all mutations are conserved at the population scale, because the majority of *de novo* mutations could be deleterious (i.e. underwent a negative selection) or neutral for fitness (i.e. underwent the genetic drift) (Eyre-Walker and Keightley, 2007). In rare cases, mutations may confer a higher individual fitness and increase in frequency in the population, as discussed for *Drosophila* exposed to X-rays (Nöthel, 1983). However, the cut-off between these three categories is not obvious, for example all deleterious mutations are not leading to direct major impacts on fitness. Nevertheless, the accumulation of slightly deleterious mutations could have harmful long-term population effects (with an interaction between genes called "synergistic epistasis" for example: Domínguez-García et al., 2019) especially in small populations, which could experience a "mutational meltdown", leading to extinction (Loria et al., 2019; Lynch et al., 1995). In particular, non or slightly recombinant genomes as haploid genomes, are particularly sensitive to deleterious mutations as they can accumulate in an irreversible way (i.e., 'Muller's ratchet', Felsenstein, 1974).

Mutations constitute an important source of evolutionary novelties, a "potential reservoir" for evolution, generating diversity, but may represent a genetic load for small populations (Lynch and Gabriel, 1990). Nevertheless, while adaptive evolution has often been interpreted as solely driven by selection, mutations can also be seen for themselves as conditioning the adaptive response (Yampolsky and Stoltzfus, 2001). In particular, specific types of mutation (e.g., adaptive substitutions) involved in the adaptive response can be mediated by the entire mutation spectrum (Cano Alejandro V. et al., 2022). For example, in the case of environmental stressors, some results indicate that the types of mutation generated are stressor-specific and can lead to different evolutionary responses (Agashe, 2017). Mutations generated after an exposure to ionizing radiation can be specific to oxidative stress, as observed on crustaceans exposed to a relatively high background radiation which showed a higher proportion of C:G→A:T mutation type in more radioactive areas (Saclier et al., 2020). Ionizing radiation could thus be an interesting case study to test the potential consequences of such mutational signature on evolutionary processes.

Another transmitted variation increasingly studied in radioecology is the non-genetic transmission of information through generations (see Box 2). This idea of non-genetic transmission can be related to the concept of "non-targeted effects", defined as the effects that do not require direct exposure by irradiation (Desouky et al., 2015). While non-targeted effects describe effects on cells, tissues or organs non-directly exposed to ionizing radiation, they also describe effects on individuals non-exposed to ionizing radiation but from which parents were exposed, and not mediated by DNA directly exposed to ionizing radiation, which refers to a non-genetic transmission of information. For example, an increased tendency for mutation rate (i.e., genetic instability: "Enhanced tendency for the genome to acquire mutations; ranging from changes to the nucleotide sequence to chromosomal gain, rearrangements or loss" (Langie et al., 2015)) can be transmitted after an exposure to ionizing radiation. Until today, genetic instability has been an important subject of investigations in radioecology (Dubrova, 2003; Yeager et al., 2021). These studies suggest that a part this increased

Box 1

How central is evolution in radioecology field studies?

To analyze the consideration and treatment of evolution in radioecology, we conducted a systematic Web of Science survey in the subset of field radioecology studies. Details about the query and the 117 analyzed studies is available in the Supplementary Information section (Table S1). To represent these studies and their treatment of evolution, a Principal Component Analysis was performed on nine evolution-related characteristics extracted from these studies (Fig. 3).

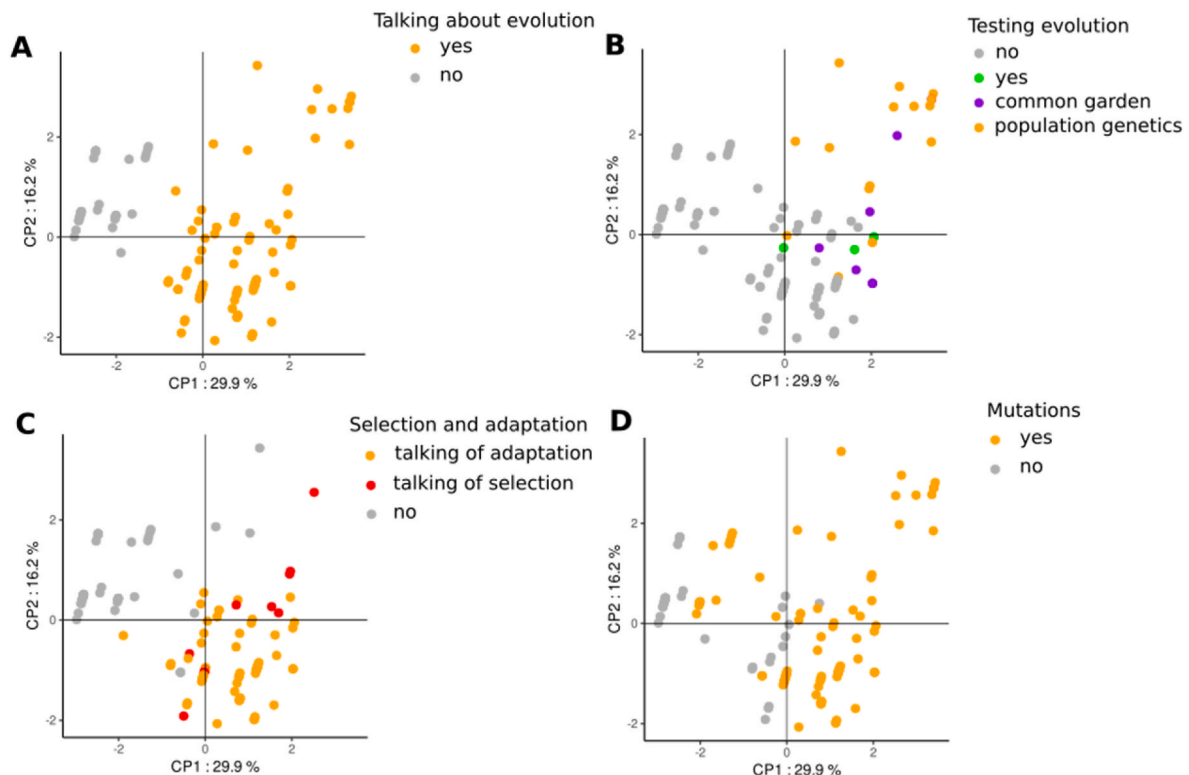


Fig. 3. Representation of a subsample of radioecology field studies from a PCA conducted on nine evolution-related characteristics. Four of these characteristics are represented because of their particularly interesting distribution: (A) evolution talk, (B) evolution study, (C) adaptation talk and (D) mutation talk.

For all these studies, a vast majority talk about evolution (83), indicating the current and past interest on these topics. A low number of papers (25) study evolution compared to papers talking about evolution (83, about 30%, Fig. 3A and B). As observed in a large number of papers, evolution is often only mentioned as context or hypothesis for perspective, but evolution is still poorly studied for itself, thus hypothesis (often adaptation, see Møller and Mousseau, 2016) remain to be tested. Many studies talk about adaptation and/or selection (77) and mutations (81), two major evolutionary processes. But contrary to the use of adaptation and/or selection which is linked to the fact of talking about evolution (only seven differences, chisq: $p = 2.2 \times 10^{-16}$, Fig. 3C), there are more studies talking about mutations which do not talk about evolution (9) and studies talking about evolution which do not talk about mutations (13, total chisq: $p = 4.7 \times 10^{-6}$, Fig. 3D), as for migrations not linked to talking about evolution (chisq: $p = 0.6$). Thus, mutations and migrations are sometimes taken as an individual effect, impacting only the individual exposed, and not as an evolutionary process, creating genetic diversity for example. Few other studies deal with evolution, or studies testing evolution over years (Wilcox: $p = 0.07$), but more studies talking about non-genetic transgenerational modifications (Wilcox: $p = 0.028$, Fig. 4B), also linked to the fact of talking about evolution (Wilcox: $p = 0.001$, Fig. 4A). This can indicate a shift in the view of evolution applied to

ionizing radiation, closer to the ideas of an inclusive evolutionary synthesis (Danchin et al., 2019a; Laland et al., 2015).

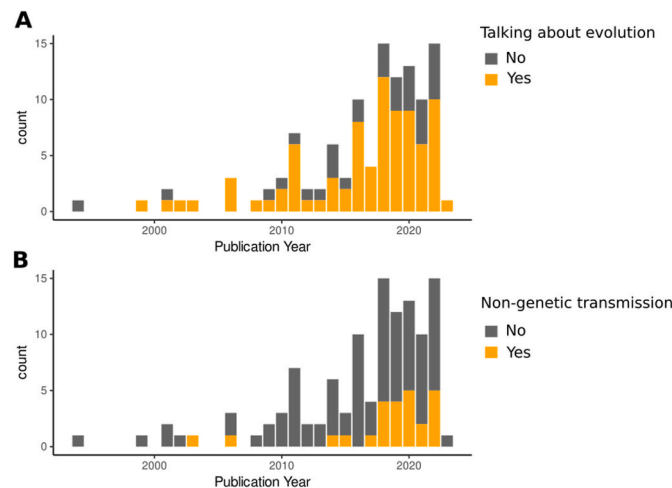


Fig. 4. Temporal changes of the topics covered by a subsample of radioecology field studies. A. the fact of talking about evolution. B. the fact of talking about a transmission over generations not only from genetic material.

mutation rate in offspring is probably linked to epigenetic mechanisms (Dubrova, 2006). Because of the epigenetic nature (in a conservative sense, see Heard and Martienssen, 2014) of genomic instability, it can be seen as a non-genetic transmission of information.

The transmission of non-genetic information, like epigenetic information such as proposed for genetic instability are difficult to demonstrate in a dose-response relationship study, as they induced delayed impact over generations (Morgan and Sowa, 2009). Epigenetic transmitted variations can also be studied, like genetic variation, as part of variation impacting evolution (Muyle et al., 2021). As proposed by

supporters of an "inclusive evolutionary synthesis" (Danchin et al., 2011; Laland et al., 2015), this non-genetic inheritance could be compared to the genetic inheritance with some particularities, including different timescales of inheritance and reversibility (Danchin et al., 2019a). Several laboratory studies observed radiation-induced transgenerational modifications leading notably to an impaired viability or fertility (parental effects, epigenetic modification or genetic instability, Dubrova and Sarapultseva, 2020), for example in *Daphnia magna* (Parisot et al., 2015; Sarapultseva and Dubrova, 2016; Trijau et al., 2018), *Danio rerio* (Guirandy et al., 2022), *Oncorhynchus mykiss* (Smith et al., 2016),

Box 2

Semantical point

From 'radio-adaptation' to 'adaptation'

In radioecology, the word 'radio-adaptation' is defined as an individual response after a first exposure to ionizing radiation (Rodgers and Holmes, 2008; Rodgers et al., 2001; Wickliffe et al., 2003). For example, Rodgers and Holmes (2008) highlighted a reduction of micronuclei - a biomarker of DNA double strand breaks - for mice exposed to an acute dose of 1.5 Gy when mice were exposed first to 10 cGy priming doses. Thus, in radioecology, 'adaptation' word is far from its classical meaning in evolutionary biology. That is why, even if these studies use 'adaptation' word, they focused on a plastic, individual response and did not studied 'adaptation' as an evolutionary process.

Hormesis, the incomplete interpretation

In (eco)toxicology, "hormetic" effect of a stressor, like ionizing radiation is defined as a biphasic dose-response relationship, usually considered 'positive' for the organism at low doses and harmful at high doses (Mattson, 2008). This concept appears difficult to involve in an evolutionary point of view. Indeed, in evolutionary biology, it is difficult to describe an effect as 'positive' *per se*, because a response is part of a trade-off. Because resources are limited, a positive effect on a trait may be costly and may be antagonist of another trait (Reznick et al., 2000). In the case of ionizing radiation, evolutionary trade-offs (*i.e.*, the trade-off on how some traits are selected at the expense of other traits) were tested in Chernobyl on life-history traits in wild carrots (*Daucus carota*) (Boratyński et al., 2016), between sperm length and integrity on barn swallows (Hermosell et al., 2013) or between developmental rate and resistance to DNA damage in grasshoppers (*Chorthippus albomarginatus*) (Bonisoli-Alquati et al., 2017).

Exclusion zones as "natural laboratories"

Human exclusion zones are frequently compared to "natural laboratories", and are considered as ideal places to study the long-term effects of ionizing radiation on wildlife (see for example Goodman et al., 2019; Jernfors et al., 2021; Mousseau and Møller, 2020; Orizaola, 2020). This term appears confusing because it refers to the idea of a controlled experiment in natural environment. This type of controlled experiment is what Diamond (1983) defined by the term 'field experiment' in which only the parameter of interest (here "ionizing radiation") is modified and other variables controlled. But all studies in exclusion zones are closer to 'natural experiment' as they do not control the ionizing radiation dose, but only compare the effect of different doses by the site selection. In our opinion, the use of "natural laboratories" and "field experiments" is more consistent with the study of Amiro and Sheppard (1994) or that of Woodwell (1962) in which an irradiator has been set in natural area to observe the potential ionizing radiation effects.

Caenorhabditis elegans (Buisset-Goussen et al., 2014; Guédon et al., 2021) or *Eisenia fetida* (Hertel-Aas et al., 2007). Although some results suggested the same kind of transgenerational modification in Chernobyl or Fukushima (embryonic loss, morphological abnormalities, genomic instability), on butterflies (*Zizeeria maha*), rodents (*Myodes glareolus*), plants (*Arabidopsis thaliana*), birds (*Hirundo rustica*) or humans (*Homo sapiens*) (see for example: Aghajanyan et al., 2011; Hancock et al., 2019, 2020; Omar-Nazir et al., 2018; Shuryak and Brenner, 2021), the proximate mechanism remains to be fully investigated. Nevertheless, the existence of several epigenetic changes may indicate that the same kind of phenomenon should appear in the field. For example, a modification of genome-wide DNA methylation has been observed at Chernobyl for *Brassicaceae* (Horemans et al., 2018), and Scots pine trees (Volkova et al., 2018), and at Fukushima on tree frogs (Gombeau et al., 2020). These changes are observed at a single time, but recent results suggest a possible transmission over generations (Horemans et al., 2019; Laanen et al., 2021). Non-genetic inheritance could be a particularly important mechanism to generate novelty and shaping the evolution of populations, particularly following a major event such as a nuclear disaster for example (Kuijper and Hoyle, 2015; Lind and Spagopoulou, 2018).

2.2. Other consequences at the population level

Ionizing radiation is not solely a factor of genetic novelty due to its mutagenic effect. Oxidative stress caused by ionizing radiation can cause

a large spectrum of stress to individuals (oxidative damage to DNA, lipids, proteins, and many metabolites: Bonisoli-Alquati et al., 2010; Dauer et al., 2010; Einor et al., 2016; Galván et al., 2014) that can modify individual fitness without necessarily generating transmitted novelties. After reviewing the mutation process in the section 2.2, we focus on other evolutionary processes whose intensity can be modified in an environment contaminated by radionuclides.

Evolutionary processes are all the processes by which the relative frequency of inherited variations is modified in a population (inducing its evolution). By studying these evolutionary processes - especially through genetic variation - we can estimate the long-term consequences of individual ionizing radiation effects. This approach was conducted in evolutionary ecotoxicology by Bickham (2011) who proposed the four cornerstones of genetic response of populations to a contaminant exposure corresponding to the classic evolutionary processes: (1) genetic variability caused by increased mutation rates; (2) neutral modifications of genetic diversity; (3) genetic variability caused by gene flow induced by dispersal; and (4) selection through the survival of the fittest. These processes can be distinguished but they also interact. For example, neutral genetic drift can interact with mutations by favoring the fixation of new genetic variation. Mutations can also generate new variation on which selection can act (Fig. 1). In this section we described these evolutionary processes in the context of radioecology, with the exception of selection developed in section 3.1.

Genetic drift, which is the neutral fixation of genetic variations, is an

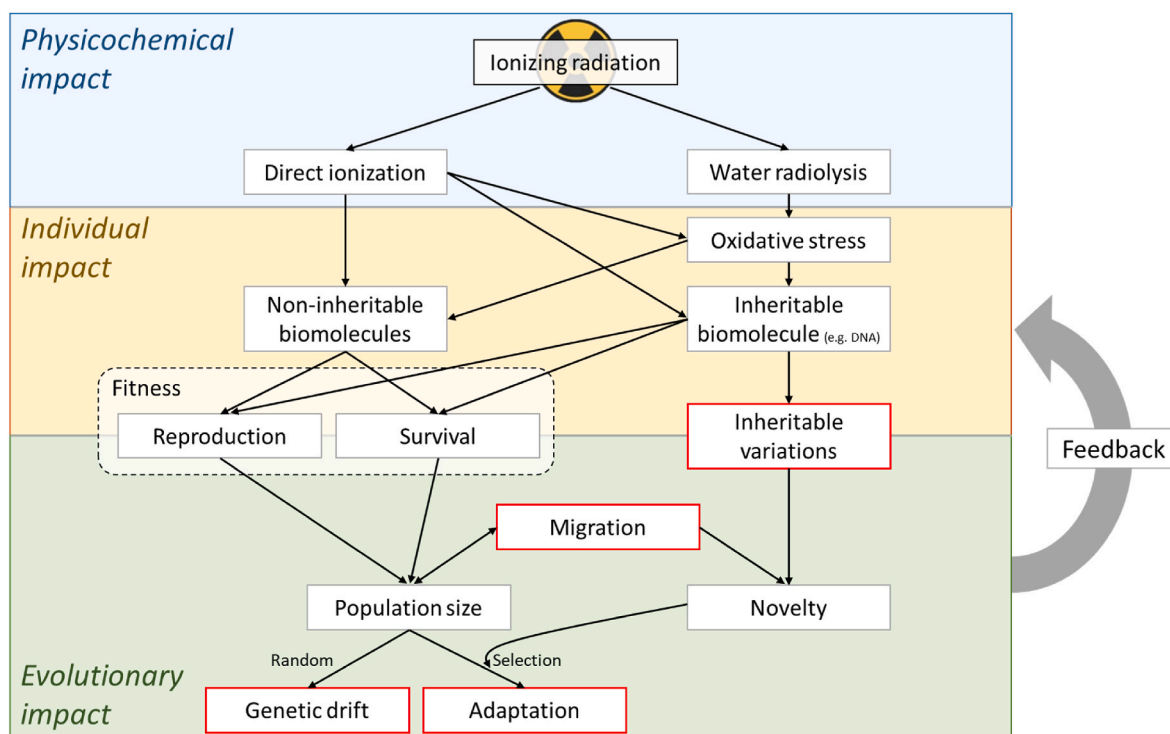


Fig. 1. Conceptual schema which presents the impact of ionizing radiation on the evolutionary processes (framed in red). Effects of ionizing radiation starts from physicochemical impacts (area in blue), which operates in two ways: it is generally considered that ionizing radiation affects living organisms by direct ionization of biomolecules (proteins, lipids, carbohydrates and nucleic acids) or indirectly by water radiolysis. Physicochemical impacts lead to (I) individual changes (area in yellow). Direct or indirect ionization can be at the origin of an oxidative stress, which impacts biomolecules, whether they are transmitted between generations (e.g., DNA) or not. The modification of biomolecules can lead to an alteration of individual traits, and consequently challenges the differential reproduction and survival of organisms (i.e., evolutionary fitness). Jointly, ionizing radiation can cause new inheritable variations (e.g., mutations). Introducing new variations and altering the fitness of organisms have an (II) evolutionary impact at the population level (area in green). Fitness change and migrations of individuals (i.e., emigration and immigration) alter population characteristics (size, dynamics, etc.). Depending on the effective population size, genetic drift resulting from the random fixation of variations can be modulated. But the fixation of variations can also be the result of a selective process, which can lead to adaptation. Adaptation may be enhanced by the contribution of novel variations emerging from immigration and radiation-induced heritable variations. It is important to note that evolutionary impacts can modulate individual effects (Feedback - grey arrow): for example, population adaptation to ionizing radiation may modify the impact of this stressor (sensitivity), improving evolutionary fitness, which can then impact the intensity of evolutionary processes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

evolutionary process dependent on population sizes. In a population with a small effective population size (i.e., the individuals involved in reproduction: Crow and Kimura, 1970; Nei and Tajima, 1981), stochastic effects can decrease of genetic diversity. In evolutionary ecotoxicology, because of a potential effect of pollutants on demography and population sizes, this phenomenon has been called “genetic erosion” (van Straalen and Timmermans, 2002) and may lead to a decreased evolutionary potential (Frankham et al., 1999). For example, a reduced genetic diversity attributed to genetic drift was observed on marsh frogs living in a contaminated industrial place of Azerbaijan (Matson Cole W. et al., 2006). Conversely, in the case of ionizing radiation, a study of tree frogs living in the Chernobyl region showed an increased mitochondrial diversity in the most contaminated area (Car et al., 2021). This diversity is attributed to mutations (as also confirmed in Car et al., 2023 for nuclear DNA), but genetic drift (due to bottleneck effect induced by deleterious mutations) is necessary to explain the fixation of these mutations over generations (Kimura, 1983; Nei and Tajima, 1981; Whitlock and Bürger, 2004). Other studies of populations subject to radioactive contamination did not highlight any increase in genetic drift (e.g., earthworms and aquatic crustaceans in Chernobyl: Fuller et al., 2019; Newbold et al., 2019); *Trifolium pratense* in Komi Republic (Rybak et al., 2018). Du Boulay (1977) proposed that genetic drift could purge chromosomal aberrations induced by irradiation. Anecdotal mechanisms can probably allow the emergence of advantageous variations (reverse or back mutation and compensatory mutations) in a context of genetic drift (Whitlock and Bürger, 2004).

When population size is reduced in a contaminated place, migration processes/rate can buffer the impact of genetic drift by providing new variations in the area. With low population size in a “poor-quality” habitat (sink), the competition for resources may be less important by a decrease in reproduction or survival, making that habitat more attractive and promote the migration of individuals from good quality habitats with a demographic surplus (source). This phenomenon is called “source-sink” dynamics and may affect the viability of sink populations (Dias, 1996; Pulliam, 1988). Reduced population size observed for some organisms in the most polluted places (Horiguchi et al., 2016; Mappes et al., 2019; Möller and Mousseau, 2007; 2013) makes them particularly favourable to such dynamics. Frequent migrations toward the Chernobyl most contaminated area has been tested with stable isotopes for barn swallows (*Hirundo rustica*), suggesting a demographic sink (Möller et al., 2006). A population genetic approach also emphasizes the existence of a population sink on kangaroo rats (*Dipodomys merriami*) in the Nevada test Site, where nuclear weapons were tested between 1951 and 1963 (Theodorakis et al., 2001). Migration processes can thus modify the genetic diversity of organisms and, besides source-sink dynamics, be important evolutionary processes. According to Baker et al. (2017) a higher mutation rate explained the higher mitochondrial diversity of bank voles (*Myodes glareolus*) in the most contaminated area of the Chernobyl region. But migration can also generate this diversity (Kesäniemi et al., 2018; Matson et al., 2000), and explain bank vole population dynamics (Vives i Batlle et al., 2020). While migrations can have beneficial effects by increasing the diversity and thus the evolutionary potential of contaminated populations, deleterious effect can emerge from outbreeding depression and lead to the extinction of the population independently of the low-quality of the habitat (Vuillaume et al., 2015). Outbreeding depression is still poorly studied in ecotoxicological context, or mainly in the laboratory for the selection of strains for effective chemical testing (Brown et al., 2009), but it is a serious consideration in conservation biology management (Edmands, 2007).

Places contaminated by radionuclides like the Chernobyl or Fukushima regions are thus of interest to study the fundamental question: how can wild populations cope with a sudden environmental change in their environment? Currently, there is still too few studies to provide definitive conclusions. Specifically, compared to mutations or selection (see section 2.2), genetic drift and gene flow have been relatively understudied in the case of ionizing radiations (see Box 1). While a

lot of research is centred on the selection/adaptation process, many studies fail to evaluate adaptation process by not using suitable methodology (i.e., common garden, reciprocal transplant, genetic approaches) as suggested by Möller and Mousseau (2016).

3. Multiple temporalities in the exposure to ionizing radiation

3.1. From plastic responses to selective process

Organisms may be able to cope with rapid environmental change by plastically changing hormone concentrations, development, etc. (Taborsky et al., 2021). But if this change persists, organisms displaying better ability to survive and reproduce will have more descendants, i.e., a better fitness. And if this ability is heritable, it can be selected over generations, and increase in frequency in population. While character states selected, called adaptations, are phenotypically comparable to plastic responses, these adaptations are transmitted over generations via genotype of the individuals. Acquired individual plastic modifications may also sometimes be transmitted across generations (see the idea of non-genetic transmission discussed section 3.1), but they are generally less persistent than selected modifications (Danchin et al., 2019a). Another link existing between plastic changes and transmitted variations is “genetic assimilation”. A phenotypic change initially resulting from plastic response may be secondarily fixed in the genome (favored by plastic response) (Waddington, 1953). Several mechanisms are suggested to explain this genetic assimilation, as a facilitation by epigenetic mechanisms that may modify mutation rate in specific parts of the genome (Danchin et al., 2019b), or an incremental accumulation of numerous minor genetic mutations (Nishikawa and Kinjo, 2018). Identifying the mechanisms at the origin of responses to ionizing radiation may help to understand the potential long-term consequences of these modifications (inertia, genetic erosion, genetic load, loss of evolutionary potential) (Chevin et al., 2010).

There are several ways to identify, or demonstrate, case of selection or even adaptation (see Lambert et al., 2021). First, as mentioned in section 2.2, genetic diversity may help to identify populations or even loci submitted to selection (Bickham, 2011), and with next-generation sequencing, gene-environment and gene-phenotype association approaches can also be conducted to identify loci displaying signatures of selection (Oziolor et al., 2017, 2019). Classically, the use of indices of genetic differentiation like the *F*_{st} between populations may help the identification of candidate genomic regions (and genes) being subjected to selection according to environmental conditions. For example, this method was applied on dogs from the Chernobyl exclusion zone and 52 candidate genes potentially being subjected to selection were identified (Dillon et al., 2023). These inductions based on field data remain correlational, field or laboratory experiments being necessary to confirm or infirm the selection process on candidate genes. For example, directed evolution experiments in the laboratory with *Escherichia coli* have generated strains that are ultra-resistant to ionizing radiation. With next-generation sequencing, the authors demonstrated that resistance is mainly linked to only three variants involved in DNA repair (Byrne et al., 2014). Second, by testing the persistence of a phenotypic modification, it may be possible to identify cases of selection and adaptation (Kawecki and Ebert, 2004). ‘Common garden experiments’ consist in rearing in the same conditions and during several generations organisms from differentially contaminated places, to test whether the phenotypic differences between these populations are caused by phenotypic plasticity or genetic differentiation. There are several examples at Chernobyl for grasshoppers (*Chorthippus albomarginatus*) (Bonisoli-Alquati et al., 2017) or plants (Boratyński et al., 2016; Pernis et al., 2020) or on the laboratory for bacteria exposed to ⁶⁰Co irradiation for hundreds of generations (Harris et al., 2009). Third, the gold standard is “reciprocal transplant”. In these experiments, there is not just one rearing place, but organisms from contaminated and non-contaminated are both reared for ideally at least four generations in contaminated and non-contaminated places, to

ensure that the differences between populations reflected genetic differentiation (Badyaev and Uller, 2009; Kawecki et al., 2012; Dutilleul et al., 2014). Local adaptation occurs if the selected traits improve fitness in the contaminated environment. For the Chernobyl region, two studies conducted reciprocal transplant experiments to test for the adaptation to ionizing radiation of organisms exposed to ionizing radiation for several generations: Ruiz-González et al. (2016) identified bacterial communities from intermediate-exposed site in Chernobyl which survived and reproduced better under exposure to ionizing radiation, even than higher contaminated places in Chernobyl. In contrast Arnaise et al. (2020) showed no evidence of adaptive response to selection to ionizing radiation for anther-smut fungus (*Microbotryum lychnidis-dioicae*). Laboratory studies on nematodes (*Caenorhabditis elegans*) have also characterized selection processes under exposure to radionuclides with reciprocal transplant experiments (Dutilleul et al., 2017; Quevarec et al., 2022, 2023).

3.2. Different kinetics of exposure to ionizing radiation and its impact on selection process

Background ionizing radiation is consistent over time at an ecological time scale, even in the highest naturally radioactive places like Ramsar (Iran) (Ghiassi-nejad et al., 2002) or Kerala (India) (Derin et al., 2012). On the contrary, after anthropogenic radioactive contamination, the exposure of organisms to ionizing radiation may be acute before a fast decrease and a decreasing plateau at a lower dose rate (see Caplin and Willey, 2018 for an example of the evolution of activity after the Chernobyl accident). These temporal radioactive dynamics may modulate the response of organisms, depending on their past exposure and the exposure of their ancestors, and thus complicate the study of the dose-effect relationship. The difficulty in interpreting the observed evolutionary changes could be amplified by another aspect of radiation, ionizing radiation could accelerate the rate of adaptation (see the hypothesis made by Grodzinsky, 2016). For example, are trait differences between organisms exposed to current low dose rates and "control populations" caused by radiation they are currently experiencing or the consequence of past modifications, transmitted since the first high doses? At Chernobyl for example, some authors argued that current doses (for example: from 0.7 to 1753 $\mu\text{Gy h}^{-1}$ absorbed dose rates by soil organisms (Beresford et al., 2022), from 0.04 to 32.4 $\mu\text{Gy h}^{-1}$ ambient dose rates (Car et al., 2021; Car et al., 2023)) are too low to induce observed damages (Smith et al., 2012), and oxidative stress (Baker and Chessier, 2000; Deryabina et al., 2015).

To study the temporality of modifications, some studies compare doses and effects at different times, to determine if the effects are caused by current or historical/ancient doses. For example, Omar-Nazir et al. (2018) studied the link between mutation rate estimated on birds more than 20 years after the Chernobyl accident to a reconstruction of dose absorbed by birds the first six months after the accident. Authors suggested that the acute dose initially received by the birds (individual external dose absorbed from 0.2 to 500 mGy at sampling sites for the first six months) still had effects on mutation rate several generations later (between 9 and 11 generations). The first doses after the Chernobyl accident were also estimated on *Drosophila* and bank voles and associated with the effects observed during the first ten years (respectively from 41.9 to 558 mGy for the year 1986 for *Drosophila* and from 3.80 mGy to 10,28 Gy over the 2-year lifespan of *Myodes* starting in 1986). These studies suggested transgenerational effects related to the first doses received following the Chernobyl accident (Hancock et al., 2019, 2020). At the Fukushima prefecture, the same kind of approach was undertaken on pale blue grass butterfly (Hancock et al., 2019). The authors indicate the existence of genetic instability induced by radiation (the first generation exposed to an external dose from 0.1 to 200 mGy), but they do not question the evolutionary component of changes.

3.3. Long-term past evolution, resistance and exaptation

Natural radioactivity has existed on Earth since its formation 4.6 Ga ago, and may have contributed to the emergence and development of life, as B.G. Ershov argues (Ershov, 2022). However, from the origin of life, background radiation exposure significantly decreased (Caplin and Willey, 2018). For example, radiation dose rate from internal Potassium 40 has decreased by a factor eight since 4 Ga ago (Karam and Leslie, 1999). And while other radionuclides responsible for background radiation at that time had longer half-lives (e.g., ^{238}U , ^{232}Th) and therefore a smaller decrease, total radiation exposure still fell significantly. Thus, Todd (1994) has proposed that selection for radiation resistance occurred early in the evolution of life, and played a role in the establishment of DNA repair mechanisms. According to this hypothesis, Wassmann et al. (2010) showed the possibility to select resistance to radiation in conditions of UV exposure mimicking the Archaean period, when the earth did not have a significant ozone layer. They studied the evolution of *Bacillus subtilis* during 700 generations and showed that the populations developed resistance to UV and ionizing radiation by adaptive mechanisms. This resistance also seemed to extend to hydrogen peroxide, increased salinity and desiccation (Wassmann et al., 2010). Similarly, the extreme resistance and radiotropism of certain species of melanized fungi (Dadachova and Casadevall, 2008; Robertson et al., 2012) would go back to the beginning of the Cretaceous. Indeed, a large quantity of highly melanized fungal spores may have been found in deposits from the early Cretaceous, while this period is characterized by the extinction of many animal and plant species. The authors explain that this period coincides with Earth's crossing the 'magnetic zero', resulting in the loss of its 'shield' against cosmic radiation (Dadachova and Casadevall, 2008). Because the intensity of exposure to cosmic radiation has largely decreased since then, this raises the question if this stressor is still sufficient to maintain a selective pressure on resistance mechanisms, and especially repair systems.

Other theories have proposed explanations for the emergence of resistance mechanisms to ionizing radiation. Resistance to radiation may arise from an exaptation (Gould and Vrba, 1982). Exaptation must be understood as an adaptive trait for a function, for which they had not been initially selected. Theoretically, this process may provide resistance to ionizing radiation without the resistance trait being specifically selected for that stressor. For Shuryak (2020) resistance to ionizing radiation may result from selection for resistance to stressors, such as oxidative stress, desiccation, or salinity. For example, non-extremophile species can tolerate radioactive contamination (Shuryak, 2020). Resistance of rotifers to ionizing radiation seems to come from an adaptation to desiccation (Gladyshev and Meselson, 2008). Radiation-resistant biofilm communities at Chernobyl are adapted to UV and desiccation (Ragon et al., 2011). Resistance to ionizing radiation in the amoeba, *D. discoideum*, may come from its resistance to genotoxic effects from the organisms it feeds on (Todd, 1994). More broadly, every preexisting trait can influence sensitivity to ionizing radiation. For example, in plant taxa, reproduction strategy, root system, or life-span modulate the exposure to radionuclides and determine the fitness in contaminated areas (Shuryak, 2020).

Resistance traits to ionizing radiation seem to have appeared in different forms and at multiple times, and is therefore not specific to some phylogenetic groups (Shuryak, 2020). But, the lack of radioecological knowledge of the majority of living species (Sazykina, 2018) dramatically limits the characterization of these traits through the tree of life. However, it is known that some taxonomic groups are resistant to ionizing radiation, indicating a probable appearance of this trait upstream of the group. In a context of acute radiation, Harrison and Anderson (1996) underlines the existence of a great disparity of radiosensitivity between taxonomic groups. For example, Gymnosperms are radiosensitive species, whereas fungi, bryophytes or pteridophytes seem more resistant to ionizing radiation (Real et al., 2004). The genus *Betula* (belonging to Angiosperms) is known to have a greater tolerance to

Box 3

Using evolution to assess ecological radiological risk

Evolutionary tools and concepts are not solely interesting for scientific purposes in radioecology, but also to enrich the ecological risk assessment, which is the practice seeking describing, predicting, and controlling risks to ecosystems from human activities (Suter II, 2016). The implementation of evolution in ecological risk assessment is still scarce in the case of pollutants like pesticides (Straub et al., 2020; Topping et al., 2020), metals (Hoeks et al., 2020), and more broadly chemicals (Rodríguez-Romero et al., 2021; Saaristo et al., 2018). In the case of ionizing radiation, evolution is also poorly considered, and from the topics described in this review we identified four points on which evolution can inform ecological radiological risk assessment.

(i) Considering the evolutionary pattern: phylogenetically-based species sensitivity

Differences in species sensitivity to ionizing radiation is a central element to predict risks associated with ionizing radiation. As detailed in Box 3, the specific differences in ionizing radiation sensitivity can be studied through the lens of evolutionary history, and this may help to improve the integration of specific sensitivity in risk assessment. Current kinship relationships (phylogeny) may reflect the sensitivity of organisms to different environmental stressors, and phylogeny can be used to predict sensitivity and risks associated. The idea behind this “phylogenetically-based species sensitivity”, is that more species are related, more chance they have homologous characters states, from which depend on their sensitivity to ionizing radiation. To our knowledge, this approach has never been conducted for ionizing radiation – there is still a lot of uncertainties on species sensitivity to ionizing radiation (Bréchnignac et al., 2016) – but some models tried to predict sensitivity of species to chemical pollutants (see for example Guénard et al., 2011; Malaj et al., 2016) or tested the influence of relationship among species on several pollutants (Brady et al., 2017; Mikryukov et al., 2020; Raimondo et al., 2010), and show that without testing the sensitivity of each species, phylogeny may help its prediction.

(ii) Considering the evolutionary processes

a Exposure: the complexity to estimate representative dose at the population level

The international actors of radiation protection which provide the basis for criteria and guidance of ecological radiological risk assessment advocate assessing risks at the ecosystem and population levels (IAEA, 2014; ICRP, 2007). But the doses on which risks are assessed are mostly individual dose rates at a certain time point (see for example the ERICA tool which is mostly used to estimate an individual dose rate (Brown et al., 2008)), and are not reflecting the multiplicity of exposures at ecosystem and population levels. Some authors argued the necessity to integrate “historical doses”, from which ancestors of current individuals were exposed (notably in the first times after nuclear accidents) when dose rates were more elevated (Mothersill et al., 2018) (see Box 3). In this debate including evolutionary processes bring us to consider doses in the first times after accidents, doses cumulated through the life of individuals (as discussed in Stark et al., 2017) and the accumulation of doses since the beginning of the exposure, over generations. Indeed, changes in exposed populations can accumulate over generations. For example, if mutations are induced by ionizing radiation, these mutations can accumulate over generations and lead to profound changes which cannot be only associated with late doses (see this point discussed in Car et al., 2021). These novel issues specific to an assessment of the exposure at different time points, is compounded by other challenges for a realistic wildlife dose assessment which should also be taken into account. As the unconservative estimations of dose rate produced by measuring only ambient dose rate (Beresford et al., 2020a), recent studies demonstrate the interest of having a better picture of individual movements to not underestimate external dose exposure (e.g., GPS-dosimetry study, Hinton et al., 2019).

b Effects

i Evolution in action: the fitness endpoint

By investigating the evolutionary processes occurring in populations exposed to ionizing radiation, it is possible to assess the ability of current and future populations to persist in the environment, and assess their evolutionary potential. In particular, the concept of fitness, still little used in radioecology, could be interesting to avoid measures centred on mortality, and neglecting sublethal effects (Straub et al., 2020). The definition of fitness would also benefit from clarification. Indeed, in studies interested on the effects of ionizing radiation, fitness is sometimes used to qualify mortality (Nohara et al., 2014), reproduction (as in Beresford et al., 2020b about Fuller et al., 2018; Lerebours et al., 2018), or individual health status (notably in medicine: Piscione et al., 2017; Putora et al., 2019, and agronomy: Cai et al., 2018; Yang et al., 2017). To better determine the consequences at population level, because of a possible trade-off between mortality and reproduction, it is essential to define fitness as a product of survival and reproduction measures. In evolutionary biology, the concept of fitness led to major debates in its precise definition (in Dawkins, 1982, chapter “An agony in five fits”; in Grene, 1986, chapter “Adaptation”) but this practical definition (a combination of survival and reproduction) can be implemented in ecological radiological risk assessment. In the 80s, (Auerbach, 1984) already preconized the use of fitness to study the effect of ionizing radiation on populations. Its use is still scarce, but some studies showed the interest of this estimate, for example on nematodes *Caenorhabditis elegans* (Dutilleul et al., 2017) showed with fitness (computed as the product of fertility by survival rate or fertility multiplied by survival frequency) the existence of costs of adaptation to ionizing radiation, which may affect the persistence of populations. Goodman et al. (2019) calculated also fitness, as the rate of population increase, including measures of the proportion of surviving females and the number of offspring produced, and showed no relation of fitness with exposure to ionizing radiation.

ii What are the past and current evolutionary processes? Intra and interspecific variation endpoint

Another way to monitor past and current evolutionary processes, and predict evolutionary potential, is to be attentive to intraspecific variations (Des Roches et al., 2021). Several tools like measures of genetic diversity can report how different populations from the same species evolve depending on environmental changes. These approaches are increasingly studied, for example in the Chernobyl exclusion zone (Baker et al., 2017; Car et al., 2021; Fuller et al., 2019), and may be integrated into risk assessment in the future. The study of interspecific diversity indices like phylogenetic diversity, defined as “the sum of the branch lengths of the minimum spanning path joining a set of taxa on a tree” (Véron et al., 2019), seems also particularly interesting for estimating *a posteriori* effects of contamination on communities.

ionizing radiation than gymnosperms (Shuryak, 2020). Within metazoans, homeothermic species, and notably mammals, are more sensitive to this stress than invertebrates such as rotifers, Porifera and Hydrozoa (Harrison and Anderson, 1996; Gladyshev and Meselson, 2008; Sazykina, 2018). Among microorganisms, the bacteria and the paraphyletic group of protozoa, can show very high resistance to ionizing radiation (Harrison and Anderson, 1996). Rely on phylogeny to study species sensitivity to ionizing radiation should thus be better developed to improve predictions (Box 3).

4. From exclusion zones to experimental evolution

Following major nuclear accidents, humans have established exclusion zones to reduce their activities in the most contaminated places (Alexis-Martin and Davies, 2017; Hamada et al., 2012; Smith and Beresford, 2005). The effect of ionizing radiation on wildlife in these places is subjected to an active debate (Beaugelin-Seiller and Garnier-Laplace, 2020; Beaugelin-Seiller et al., 2020; Smith, 2020), with important societal consequences (Fassert and Hasegawa, 2019; Oughton, 2011; Stawkowski, 2016) and high visibility in the media (Beresford et al., 2020b). This debate poses the question of the status of wildlife in contaminated areas and their capability to persist and adapt under ionizing radiation. In practice, this debate concerns for example the dose threshold at which no effect on organisms is expected or the difference between effects on the field and on laboratory conditions. In this section, we would like to introduce the idea that this current debate is mostly based on snapshots of the situation, neglecting eco-evolutionary dynamics. As human activities modify the environment and have evolutionary consequences on populations, radioecology may benefit by better considering them in exclusion zones. Taking an evolutionary perspective, a better dialogue may also take place between researchers who conduct field or laboratory experiments.

4.1. Debate on wildlife status in exclusion zones

Human exclusion from the most contaminated places is frequent after major nuclear accidents, for sanitary reasons (Bondarkov et al., 2011). After the Kyshtym disaster in 1957, the Eastern Ural State Radioactive Reserve was created restricting the access by humans (Barescut et al., 2009; Pozolotina and V, K.N., 1991). The Chernobyl Exclusion Zone was set up in 1986 in Polesia, around the powerplant. A "difficult to return zone" has been defined in the most contaminated places around the Fukushima Daiichi power plant (Harada et al., 2014).

Exclusion zones are directly characterized by an increase in ionizing radiation (with a complex cocktail of different radionuclides and radiation types, see Steinhauser et al., 2014), and indirectly by the drastic decrease of human activities during several years or decades. Human activities cause effects on wildlife, which can counteract or exacerbate the effects of ionizing radiation, and it is thus necessary to consider the interaction between these two stressors. For example, human activities were included in a study of the abundance of several vertebrate species in the Fukushima prefecture (Lyons et al., 2020). We can describe exclusion zones as a biogeographical island (MacArthur and Wilson, 1963; Wilson and MacArthur, 1967), in discontinuity with surrounding areas and with two specific characteristics: nuclear pollution and wilderness. These two characteristics have each a specific dynamic. Both are expected to disappear in the future (radioactive decay and human resettlement) but in the first years the radioactive decay is far faster than the increase of human activities. By studying the relative level of these two characteristics, their temporal dynamics, and the modifications they induce on organisms, it could be possible to characterize the specific effect of ionizing radiation, considering in the same time the consequences of human activities (Fig. 2). We may get inspired from the study of the interaction between two other kinds of abiotic (urban) island (heat and pollution, see Li et al., 2018; Ulpiani, 2021).

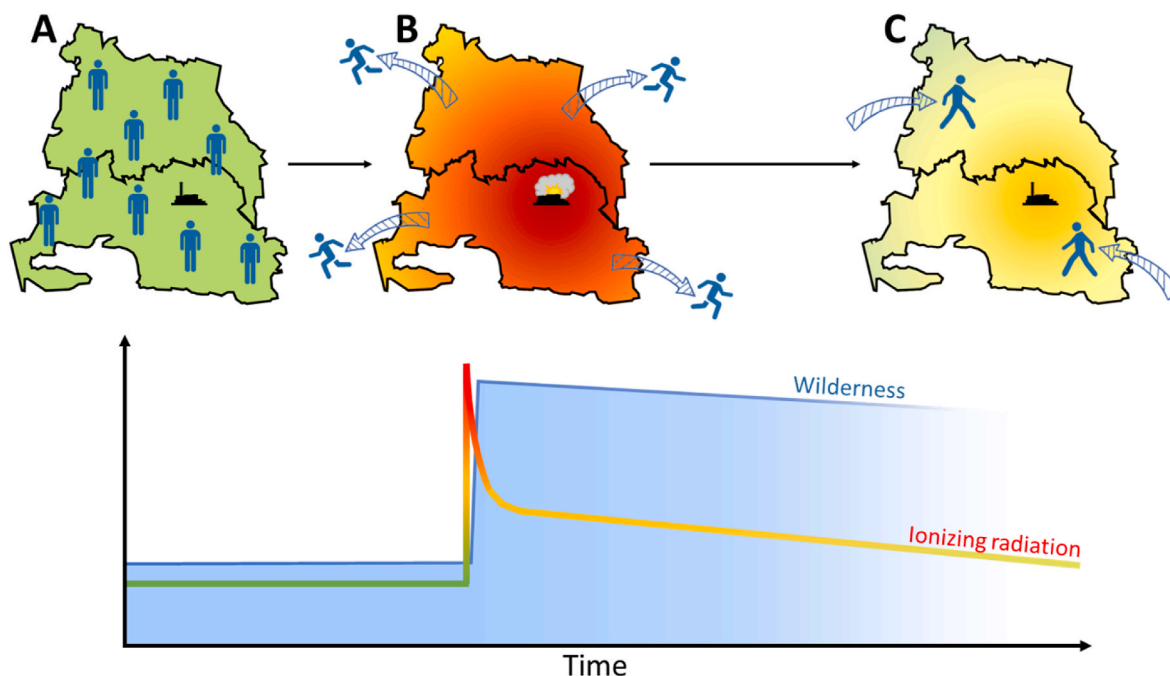


Fig. 2. Temporal change in nuclear pollution (Ionizing radiation emitted by radionuclides remaining in the environment), and human activity (wilderness generated by the exclusion zone) in a theoretical area (based on the CEZ) following a nuclear accident. (A) Before the accident, human activity is high (wilderness low) and there is no significant ionizing radiation level. (B) The nuclear accident occurs, quickly causing a gradient in ionizing radiation culminating near the nuclear power plant (orange to red area). This event induces a rapid and massive evacuation of the area by humans and the implementation of legislation to drastically restrict access to this area, causing a quick increase in wilderness. (C) After several months or years depending on the contamination, the radioactive decay causes a fast decrease in ionizing radiation up to an almost constant level (i.e., exponential decay), but still relatively important (orange to yellow area) and human activities are slowly recovering in the area (slow decrease of wilderness). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

These two characteristics are differently perceived by organisms: ionizing radiation is imperceptible for the overwhelming majority of organisms (with a very few known exceptions, such as mushrooms which move towards ionizing radiation sources; Steinhauser, 2015; Dadachova et al., 2007; Zhdanova et al., 2004), contrary to the decrease in human activities. Land cover changes, and particularly a soil greening were monitored in the Chernobyl region (Gemitz, 2020) and the Fukushima prefecture (Sekizawa et al., 2015). These environmental modifications induced by the decrease of anthropogenic pressure attract some species like mammals (Lyons et al., 2020; Webster et al., 2016). As discussed before (section 4.1), radioactive environment may induce a source-sink dynamic, which could be reinforced by low human activities. Thus, exclusion zone can be perceived as attractive for some species due to release of ecological niches (cues), although being of poor-quality due to ionizing radiation (outcomes), and thus represent an "ecological trap" (Battin, 2004). However, if the benefits of the human departure are higher than the ionizing radiation costs, stay in exclusion zone is beneficial for organisms and thus this area can become 'source' habitat. In order to display this potential trap in exclusion zones, it is necessary to make longitudinal studies of populations (i.e., evolution) by considering fitness measures, genetic diversity, landscape genetics, etc. (Robertson and Blumstein, 2019). Beyond the specific case of source-sink dynamic, the characteristics of exclusion zones may influence otherwise population dynamic. For example, as it is already well described in urban ecology, the modification of interaction with humans may influence more broadly gene flow between wildlife populations (for example Miles et al., 2019; Zuñiga-Palacios et al., 2021). This is the case, even if this modification is a decrease of human activities as observed in exclusion zones. For example, Matsushima et al. (2021) showed in the Fukushima prefecture a reduced suitable habitat for a frog species dependant on rice paddies since human departure and agricultural decrease.

In addition to the focus on wildlife in exclusion zones, study surrounding populations could help us to clarify the potential effects of ionizing radiation. Indeed, populations in exclusion zones share a common evolutionary history with surrounding populations which is at the origin of inter-individual variations at different levels (e.g., phenotypic, genotypic, demographic, etc.). Clarify these 'natural' geographic variations can help to decipher the changes caused by ionizing radiation. This biogeographical perspective has been conducted on bank voles in Ukraine compared to CEZ populations (Meeks et al., 2009) and tree frogs in Europe compared to CEZ populations (Car et al., 2021). Currently, studies on the long-term effects of ionizing radiation in exclusion zones rarely include the evolutionary history of populations. Studies mentioned describing the debate only focus on a snapshot of abundance or interspecific diversity (e.g. Deryabina et al., 2015; Möller and Mousseau, 2013), but they do not provide any information on their long-term dynamic (i.e. origin and maintenance of genetic diversity). Thus, they only give partial information on organisms, notably on individual health status, survival, reproduction and migration.

4.2. Field vs laboratory debate: an evolutionary contribution?

The part of the debate on wildlife in exclusion zones, which rely on the differences of effects of ionizing radiation between field and laboratory studies can be clarified in the light of evolution. Meta-analysis highlighted that organisms are more sensitive to ionizing radiation in the field than in controlled laboratory experiments (Garnier-Laplace et al., 2013; Beaugelin-Seiller et al., 2020). Although Smith (2020) identified methodological issues, such as the non-consideration of studies showing no effect and a flawed analysis of metadata, these differences of sensibility remain plausible hypothesis even if not yet properly tested (Beresford et al., 2016). Garnier-Laplace et al. (2013) suggested that these differences can be explained by ecological mechanisms (as a different access to resources in the field, or the presence of predators, which could interact with ionizing radiation exposure, to

induce stronger effect) or a different exposure to ionizing radiation. More broadly, other meta-analysis in ecotoxicology have also identified differences in organism sensitivity between laboratory and field studies, due to the organism variability, their ecology and the tools used for their study (tests and data analysis) (Schmitt-Jansen et al., 2008). Here, we put forward an evolutionary approach to contribute to clarifying the causes of these differences of sensibility between field and laboratory studies.

In the field, populations exposed to a given dose rate have generally been exposed during several generations to this stressor. This chronic exposure impacted the evolutionary trajectory of populations, which may have modified the response to ionizing radiation compared with ancestral population 'naïve' to ionizing radiation. An effect displayed at a given dose rate and time can thus be the result of several generations irradiated. In laboratory conditions, organisms are usually not exposed to irradiation until experiments. Thus, at the same dose rate than in the field, responses are expected to be different due to an evolutionary trajectory not impacted by ionizing radiation. However, it is possible to simulate the exposure of several generation through experimental evolution (Lampe et al., 2017).

In addition to the difference in past exposure between laboratory and field populations, the organisms used in the experiments will largely influence their sensitivity to ionizing radiation, especially considering their past evolutionary history. For example, the evolvability (i.e., the capability to adapt, by providing variation, shaping the effect of variation, and shaping the process of selection (Riederer et al., 2022)) of a diverse population will potentially be much better than a population with little diversity (Watson, 2021). The choice of a laboratory model and how to breed this model could also drastically modify the evolutionary response to a stressor (Cutter et al., 2019). For example, the *Caenorhabditis elegans* N2 strain reference, probably the most widely used strain of *C. elegans* (Zhao et al., 2018), is rather unrepresentative of *C. elegans* as a whole. For example, males of the N2 strain are particularly inefficient for reproduction, influencing largely sex-ratio of the population (Anderson et al., 2010). Yet, by using another strain with higher male frequency and genetic diversity, Quevarec et al. (2022) showed that ionizing radiation alter the reproductive strategy of a population, by outcrossing selection in a few generations. This result would probably have been more difficult to observe with the N2 strain and without multigenerational experiments.

Although evolution may explain a part of the apparent differences of organism sensitivity between laboratory and field conditions, these two ways of experiment are not supposed to give the same type of information, and this initial debate could be artificial and based on a mutual incomprehension of both approaches. Field studies show the real consequences of exposure to ionizing radiation, and hypothesis has to be done for example on past evolutionary processes. The processes inferred can then help to design laboratory studies, in which mechanisms can be demonstrated. Experimental evolution can thus fulfill the role of dialogue between field and laboratory experiments on the question of evolution. Some of laboratory studies have already investigated the effect of ionizing radiation on evolutionary mechanisms in bacteria (Harris et al., 2009; Lampe et al., 2019) or *Caenorhabditis elegans* (Quevarec et al., 2022).

5. Conclusion

Human activity has largely contributed to the increase of ionizing radiation in the environment, leading in several places to a chronic exposure (e.g., up to several decades) of organisms never experienced since several million years. It appeared essential to consider the long-term impact of ionizing radiation on these organisms, to preserve the integrity of ecosystems. In this review, we showed that an evolutionary context may help to give an integrative view on the biological responses to ionizing radiation. This "top-down" approach opens notably the gate to including spatial and temporal dimensions. Considering the temporal

dimension, the evolutionary history helps to better characterize the sensitivity of different organisms to this environmental stress. Additionally, the study of the current evolution of a population contributes to estimate the impact of environmental stressors on the following generations and their fate. Study of evolution is also interesting to be better anchored in the spatial dimension (e.g., landscape genomics), by helping to consider other environmental characteristics (e.g., interaction with other pollution, potential “cocktail effect”, migration of populations, or more broadly the whole set of anthropic environmental changes).

In this review, we emphasize that ionizing radiation is intimately linked to evolutionary change, whether from a biological/process (i.e., the induction of inheritable biological changes and by its potential impact on fitness) or historical/pattern point of view (i.e., the current situation of exclusion zones or the history of irradiation on earth). Radioecology is therefore an invaluable study case for applying the concepts and methods of evolutionary biology in the study of a pollution (as it has been and is done marginally). But the interest of an evolutionary perspective is much broader than radioecology, and the points highlighted in this review are relevant for research on pollutants and are already used depending on the field. Finally, this approach is relevant to identify endpoints measurement for ecological risk assessment (Straub et al., 2020).

CRediT authorship contribution statement

Clément Car: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Loïc Quevarec:** Writing – review & editing, Writing – original draft, Visualization, Conceptualization. **André Gilles:** Writing – review & editing, Validation. **Denis Réale:** Writing – review & editing, Validation. **Jean-Marc Bonzom:** Writing – review & editing, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

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