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Research article

Ionizing radiation and taxonomic, functional and evolutionary diversity of bird communities

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ABSTRACT

Ionizing radiation from nuclear accidents at Chernobyl, Fukushima and elsewhere has reduced the abundance, species richness and diversity of ecosystems. Here we analyzed the taxonomic, functional and evolutionary diversity of bird communities in forested areas around Chernobyl. Species richness decreased with increasing radiation, mainly in 2007. Functional richness, but not functional evenness and divergence, decreased with increasing level of ionizing radiation. Evolutionary distinctiveness of bird communities was higher in areas with higher levels of ionizing radiation. Regression tree models revealed that species richness was higher in bird communities in areas with radiation levels lower than 0.7 μSv/h. In contrast, when radiation levels were higher than 16.67 μSv/h, bird species richness reached a minimum. Functional richness was affected by two variables: Forest cover and radiation level. Higher functional richness was found in bird communities in areas with forest cover lower than 50%. In the areas with forest cover higher than 50%, the functional richness was lower when radiation level was higher than 0.91 μSv/h. Finally, the average evolutionary distinctiveness of bird communities was higher in areas with forest cover exceeding 50%. These findings imply that level of ionizing radiation interacted with forest cover to affect species richness and its component parts, i.e. taxonomic, functional, and evolutionary diversity.

1. Introduction

The loss of biodiversity is of critical concern, and an increasing number of studies indicate that biodiversity plays a central role in long-term ecosystem functioning (Groombridge and Jenkins, 2002; Pereira et al., 2012). For this reason, research focused on the spatial distribution of biodiversity is necessary. Species richness is often used as an operational variable reflecting the state of biological diversity (Jiguet et al., 2005), constituting one of the most useful biodiversity metrics, especially for the evaluation of bird communities (Gotelli and Colwell, 2001; Morelli, 2013; Ricklefs, 2012; Young et al., 2013), providing simple univariate measures of the community (Magurran, 2004). However, the species richness approach is limited by its inability to account for the ecological role and the diverse contributions species make to ecological communities (Safi et al., 2013). For this reason, multi-level or multidimensional approaches are needed and were recently proposed in many studies considering functional and phylogenetic aspects of diversity (Clough et al., 2009; Luck et al., 2013; Morelli et al., 2016, 2017; Sol et al., 2017).

Nuclear power plant accidents such as those at Chernobyl, Fukushima, Mayak and many others have contaminated several hundred thousand square kilometres in Europe and Asia (Lelieveld et al., 2012). Even if research activities were relatively modest during the first decades after these accidents, recently the interest of such research is increasing, considering that studies of animals may have significant implications for humans (Møller et al., 2013b). Some studies described the effects of radiation after nuclear accidents, highlighting many negative effects for biodiversity as well as for ecosystem services (Geras'kin, 2016; Sazykina and Kryshev, 2006; Wagner, 1965; Wehrden et al., 2012). These research activities can broadly be divided into studies of mutations (Abend et al., 2014; Bonisoli-Alquati et al., 2015, 2010; Dubrova et al., 2006; Ellegren et al., 1997; Møller et al., 2015b, 2010) and abnormalities (Hiyama et al., 2012; Kubota et al., 2015; Møller et al., 2007, 2005). Ionizing radiation has also resulted in medical conditions such as cataracts (Lehmann et al., 2016; Mousseau and Møller, 2013), tumors (Møller et al., 2013a) and other diseases (Abend et al., 2015; Leuraud et al., 2015; Moseeva et al., 2014), reduced brain size (Hayama et al., 2017; Møller et al., 2011), reduced

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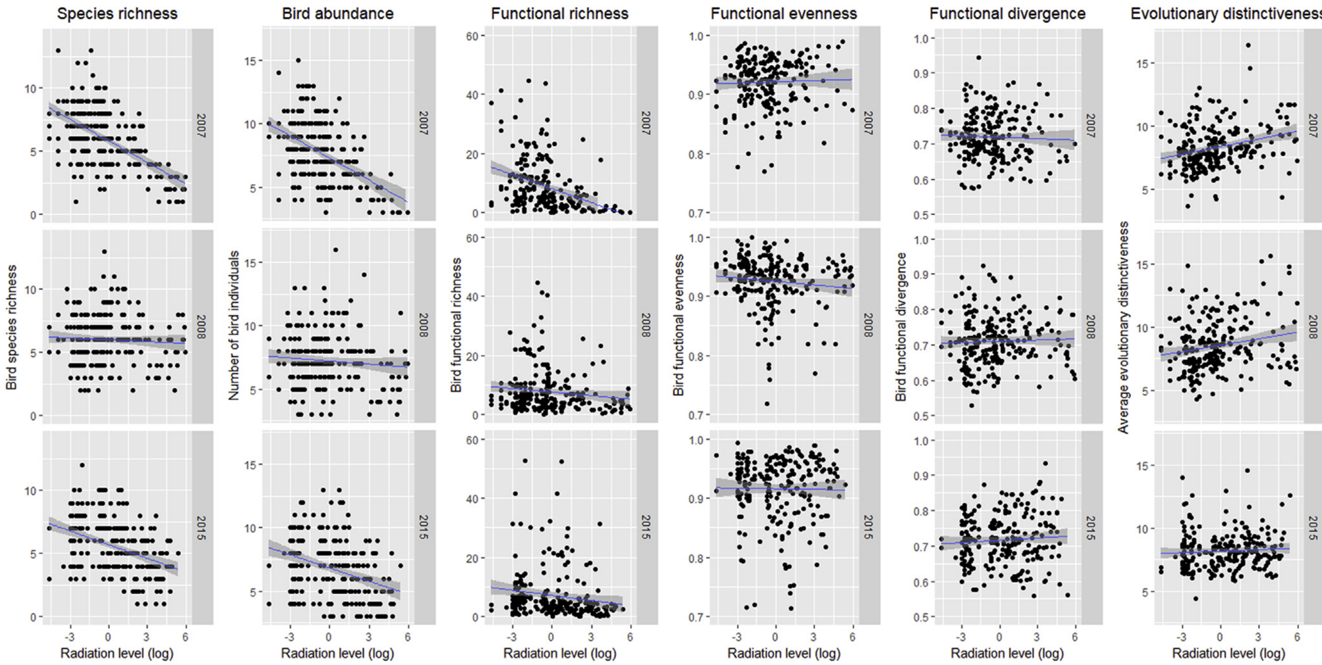

Fig. 1. Association between radiation level and each diversity and community metric estimated for bird communities in the Chernobyl region of Ukraine and Belarus. The plots show the linear regressions, split in the three different years of survey: 2007, 2008 and 2015. Envelopes around lines are 95% confidence intervals.

Table 1
Results of GLMM for best models relating species richness (a), bird abundance (b), functional richness (c) and community evolutionary distinctiveness (d) of bird communities in Chernobyl to background radiation level and environmental characteristics. The table shows estimates, 95% confidence intervals (CI), SE, *z* or *t* and p values.

Predictors	Estimate	CI	SE	*z/t*	*P*
a) Species richness					
Intercept	21.986	4.543/39.429	8.900	2.470	0.014
log Radiation	−0.003	−0.004/-0.002	0.000	−6.328	2.5e-10
Year	−0.010	−0.019/-0.002	0.004	−2.318	0.020
b) Bird abundance					
Intercept	24.526	8.172/40.880	8.344	2.939	0.003
log Radiation	−0.003	−0.004/-0.002	0.002	−6.848	7.5e-12
Year	−0.011	−0.019/-0.002	0.003	−2.756	0.006
c) Functional richness					
Intercept	60.359	18.064/102.654	21.579	2.797	0.005
log Radiation	−0.005	−0.007/-0.003	0.001	−4.897	9.7e-07
Year	−0.029	−0.050/-0.008	0.011	−2.742	0.006
d) Evolutionary distinctiveness					
Intercept	42.864	−30.898/116.627	37.635	1.139	0.255
log Radiation	0.004	0.002/0.007	0.001	3.368	0.001

sperm performance (Bonisoli-Alquati et al., 2010; Hermosell et al., 2013; Møller et al., 2014) and pollen viability (Møller et al., 2016). Impaired gamete function may reduce seed germination rates (Møller and Mousseau, 2017) and growth rates (Boratyński et al., 2016), but also biased sex ratios (Møller et al., 2012). An increased frequency of detrimental effects of ionizing radiation have resulted in an increased frequency of mortality (Møller et al., 2012, 2005) and a reduction in fecundity (Møller et al., 2005). In turn such effects have been shown to have population consequences for many species with dramatic decreases in the abundance and species richness of birds (Galván et al., 2011; Møller et al., 2013b; Møller and Mousseau, 2007), but also other organisms (Bezrukov et al., 2015; Møller et al., 2013b). These effects of nuclear accidents are not restricted to human activity. Indeed, naturally occurring ionizing radiation due to composition of the underlying rock has resulted in significant effects of radiation on wild organisms and their performance (Møller et al., 2013b). Thus, research on the effects of radiation on free living organisms may have implications beyond a few accidents at nuclear power plants (Møller et al., 2013b).

In this study, we assessed the association between the level of ambient ionizing radiation and land use composition on different components of bird diversity in Chernobyl, Ukraine, specifically, species richness, functional diversity and evolutionary uniqueness of bird communities. In addition, we investigated the environmental characteristics driving the change for each diversity metric and ecological score in these forested areas.

2. Methods

2.1. Study area and bird data collection

We studied birds in sites around Chernobyl on 25 May - 5 June, in three years between 2007 and 2015 (Møller et al., 2011, 2012). These sites are located within a distance of 60 km from Chernobyl and covered a wide range of radiation levels ranging from normal background radiation (0.02 μSv/h) to some of the most contaminated areas in the Chernobyl region. All sites were in early successional stages of primary forest with some parts having been covered by forest during the last 10 years.

Field data were collected using the point count survey method which provides reliable information on occurrence and abundance of bird species (Bibby et al., 2005; Blondel et al., 1970; Møller, 1983; Voříšek et al., 2010). The method is based on an observer recording all birds and other animals seen and heard for a period of 5 min at a given location. The breeding bird survey points were located at ca. 100-m intervals in forested areas within the Chernobyl Exclusion Zone or adjacent areas, or in areas in southern Belarus around Gomel during the breeding seasons 2007, 2008 and 2015 (898 census points) (Møller et al., 2015a). A.P.M. conducted all point counts. The fact that one person made all counts eliminates any variance in results due to inter-observer variability. There are no bird census data from before the Chernobyl accident, nor to the best of our knowledge have other scientists conducted bird censuses comparable to ours in the years following the accident (Møller et al., 2013b).

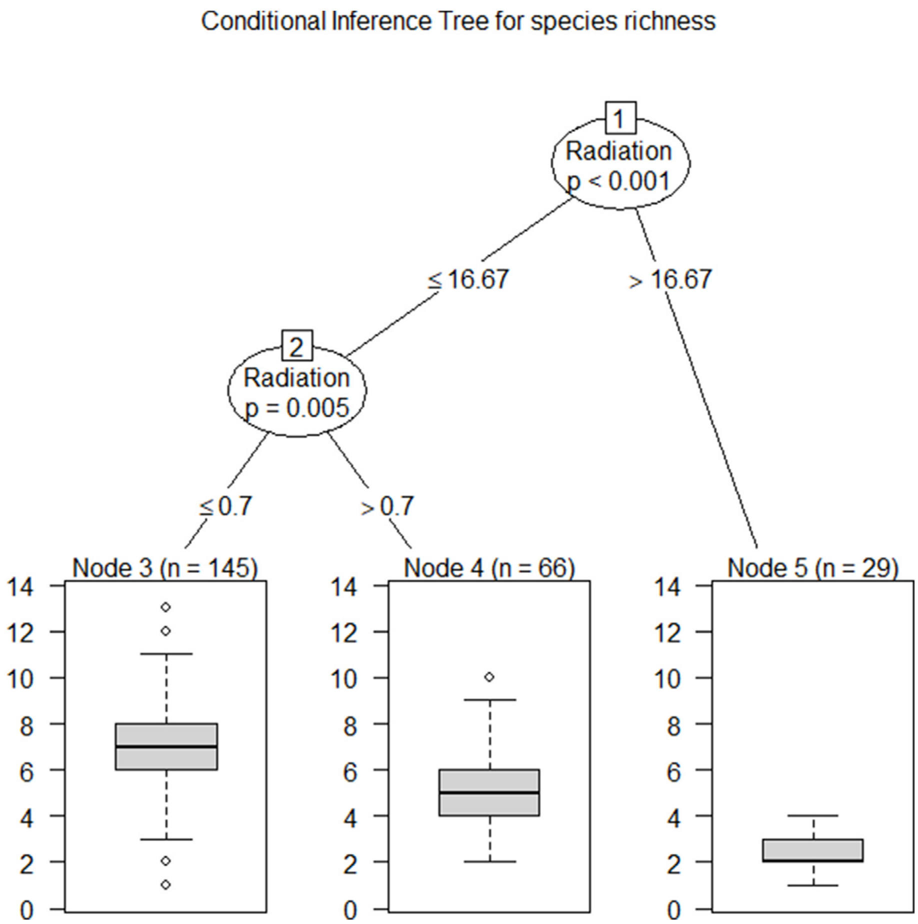

Fig. 2. Regression tree created with the environmental variables and the radiation level sampled in Chernobyl explaining the species richness in bird communities. Under each branch, in the nodes 'n' is the number of sampling sites in the leaf (group); the values shown in the boxplots are the species richness for the group. Leaves of the tree indicate average catch weight per two of each group given the conditions and thresholds stipulated by the splits. The first split is for radiation level (16.67 μSv/h), and the second for radiation level (0.7 μSv/h).

2.2. Radiation level, environmental variables and bird diversity

We measured radiation in the field at each census point, and we cross-validated these measurements with those reported by the Ukrainian Ministry of Emergencies. Once having finished the 5-min survey, we measured α, β, and γ radiation levels at ground level directly in the field at each censuss point using a hand-held dosimeter (Model: Inspector; SE International, Summertown, TN, USA). We measured levels two–three times at each site and averaged the results. We cross-validated our measurements in Ukraine against data published by Shestopalov (1996), estimated as the mid-point of the ranges published in the Chernobyl atlas. This analysis revealed a very strong positive relationship [linear regression on log–log transformed data: $F = 1546.49$, df = 1, 252, $r^2 = 0.86$, $P < 0.0001$, slope (SE) = 1.28 (0.10)], suggesting that our field estimates of radiation dose rates provided reliable measurements of levels of radioactive contamination among sites.

The general ecological environment was also recorded for 100 m around at each census point. Land use categories used to describe the environment were: farmland, forest (deciduous and coniferous) and soil quality.

Five different measures of biodiversity were used, calculated for each bird community (sampling site): a) one related to taxonomic diversity, b) three related to functional diversity, and c) one related to phylogenetic uniqueness.

Bird species richness, expressed as the number of recorded bird species at each sampling site, was used as a measure of taxonomic diversity (Magurran, 2004). In each community, we also calculated the bird abundance as the sum of all individuals recorded.

The biodiversity metrics based on species-trait approaches were focused on functional aspects of biodiversity, and constitute an additional tool to the traditional taxonomic approach (de Bello et al., 2010). In this study, three complementary and multidimensional functional diversity (FD) indices were calculated (Villéger et al., 2008), using avian niche traits based on foraging and breeding ecology for all recorded species. The traits table consists of 72 traits characterizing body mass, foraging ecology (e.g. diet, acquisition behaviour, foraging habitats and acquisition substrate), activity period and nesting habitats (Pearman et al., 2014). All variables, except body mass, were binomial (scored as either 0 or 1). The complete list of traits used for the estimation of functional diversity is provided in Table S1, ESM.

Functional Richness (FRic) represents the amount of functional space occupied by a species assemblage; Functional Evenness (FEve) indicates the regularity of the degree to which the biomass of the species assemblage is distributed in niche space to allow an effective use of the entire range of resources available, while Functional Divergence (FDiv) defines how far high species abundances are from the center of the functional space (Villéger et al., 2008). The functional diversity indices were calculated using the 'FD' package for R (Laliberté et al., 2015).

We used the evolutionary distinctiveness (ED) score as a measure of species uniqueness (Frishkoff et al., 2014; Isaac et al., 2007). We downloaded the ED score for each bird species included in the study, from the EDGE of Existence: Evolutionarily Distinct & Globally Endangered website (Zoological Society of London, 2008). Using the ED scores, we calculated the community evolutionary distinctiveness (CED) as the average ED for the entire assemblage (Morelli et al., 2016; Tucker et al., 2016).

2.3. Statistical analyses

A Mantel test was combined with Monte Carlo permutations (999

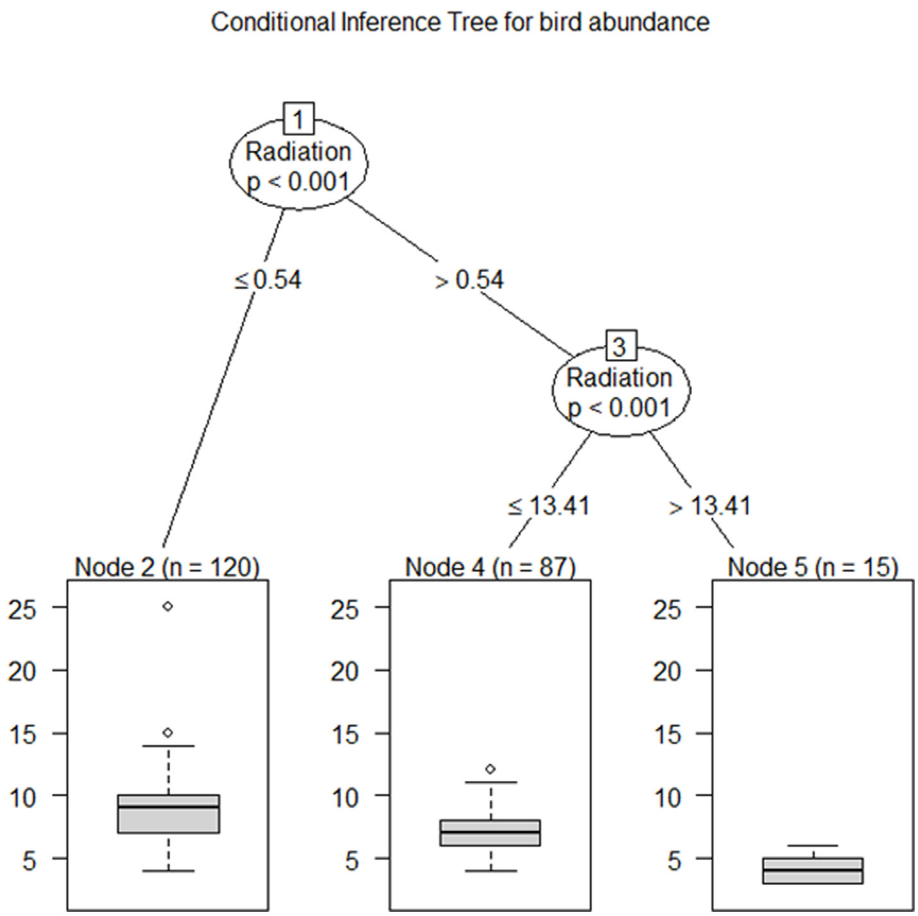

Fig. 3. Regression tree created with the environmental variables and the radiation level sampled in Chernobyl explaining the abundance of birds in communities. Under each branch, in the nodes 'n' is the number of sampling sites in the leaf (group); the values showed in the boxplots are the species richness for the group. Leaves of the tree indicate average catch weight per two of each group given the conditions and thresholds stipulated by the splits. The first split is for radiation level (0.54 μSv/h), and the second for radiation level (13.41 μSv/h).

randomizations) (Oksanen et al., 2016) to test for spatial autocorrelation in the data (Mantel, 1967; Legendre and Legendre, 2012). Generalized Linear Mixed Models (GLMM) were used to investigate the relationship between each bird diversity and community metric and radiation level, land use composition and year modelled as fixed effects, and site identity (point counts were repeated once per year during the three years of the study) as a random factor. Sampling sites were treated as statistically independent observations because the values of spatial autocorrelation were non-significant (e.g. data 2007: $r_M = 0.005$, $p = 0.387$). Models were fitted by restricted maximum likelihood (REML) using the package 'lme4' (Bates et al., 2014). Models were fitted assuming a Poisson distribution for bird species richness, log normal distribution for functional richness and normal distribution for community evolutionary distinctiveness, after having explored the distribution of variables (Box and Cox, 1964) using the package 'MASS' (Venables and Ripley, 2002), and 'glmmADMB' in R (Fournier et al., 2012; Skaug et al., 2013). Akaike's Information Criterion (AIC) was used to determine the model that 'best' explained variation in the data (Burnham and Anderson, 2002). An example of the equation of GLMM used for studying the response of bird species richness:

Model1 < - glmer(formula = Bird species richness ~ log (Radiation) + Farmland + Deciduous + Coniferous + Year + (1 | site), data = full dataset, family = "Poisson")

Finally, a classification and regression tree (RT) analysis (De'ath, 2002) was used to quantify thresholds of radiation levels and land use coverage affecting bird species richness, functional richness and community evolutionary distinctiveness. RT was performed filtering only data from 2007, because this was the year with higher radiation levels. RTs are leveraged in cases where the response variable is either continuous or numeric. It is a machine-learning method, which builds prediction models where data is split into multiple blocks recursively and the prediction model is fitted to each such partition (Breiman et al., 1984; De'ath, 2002; Prasad et al., 2006). The result of RT is a tree in which "leaves" (terminal groups of sites) are composed of subsets of sites selected to minimize the within-group sums of squares, but where each successive partition is defined by a threshold value of the explanatory variables (Borcard et al., 2011). RT was performed with the R package 'party' (Hothorn et al., 2006). All tests were performed with R (R Development Core Team, 2017).

3. Results

Ambient radiation levels decreased over the three years monitored in Chernobyl (Fig. S1, ESM). A total of 101 bird species were recorded during the three years of study (Table S2, ESM). Bird species richness and bird abundance were negatively associated with the levels of radiation, and decreased in the three consecutive years (Fig. 1, Table 1). However, the association was strongest during the first year (2007) (Fig. 1). Among the functional diversity indices, only "functional richness" was related to radiation, which also declined over the three consecutive years (Fig. 1, Table 1). The values of "functional evenness" and "functional divergence" in relation to radiation level were relatively constant during the three year study (Fig. 1). The "evolutionary distinctiveness" of bird communities was higher in the areas characterized by higher radiation levels (Fig. 1, Table 1).

Regression tree models of bird community metrics showed different responses for each metric per sampling site. Species richness was higher in bird communities with radiation levels lower than 0.7 μSv/h. In contrast, when radiation levels were higher than 16.67 μSv/h, bird species richness reached a minimum (Fig. 2). Bird abundance was higher in bird communities where radiation levels were lower than 0.54 μSv/h with minimum abundance in areas with radiation levels higher

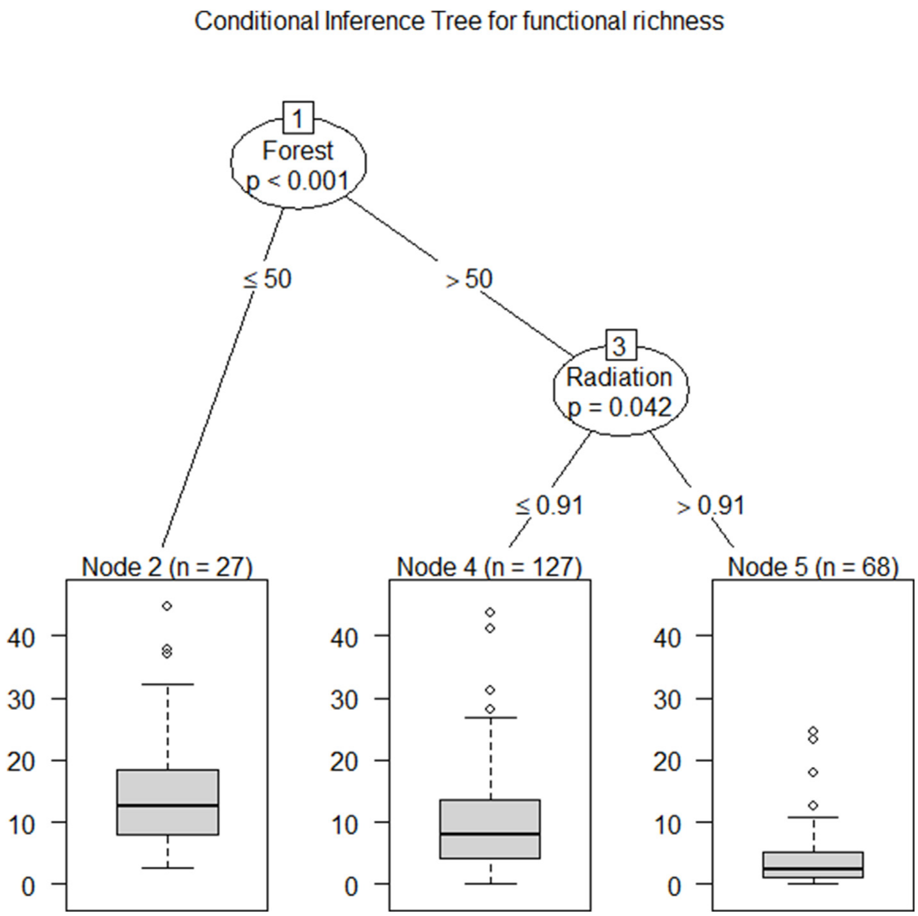

Fig. 4. Regression tree created with the environmental variables and the radiation level sampled in Chernobyl explaining the functional richness in bird communities. Under each branch, in the nodes 'n' is the number of sampling sites in the leaf (group); the values shown in the boxplots are the functional richness for groups. Leaves of the tree indicate average catch weight per two of each group given the conditions and thresholds stipulated by the splits. The first split is for forest coverage (50.00%), and the second for radiation level (0.91 μSv/h).

than 13.4 μSv/h (Fig. 3). Functional richness was affected by two variables: Forest cover and radiation level. Higher functional richness was found in bird communities in areas with forest cover lower than 50%. In areas with forest cover higher than 50%, functional richness was lower when radiation levels were higher than 0.91 μSv/h (Fig. 4). Finally, the average evolutionary distinctiveness of bird communities was highest in areas with forest cover exceeding 50% (Fig. 5).

4. Discussion

There is a small literature linking components of species richness to level of ionizing radiation at sites with nuclear accidents. This literature includes mainly studies at Fukushima (Garnier-Laplace et al., 2015; Møller et al., 2015b) and Chernobyl (Geras'kin et al., 2013, 2008). However, until now no studies addressed the association between radiation level and different components of avian community diversity, as taxonomic, functional and evolutionary diversity. Our study demonstrates a significant negative relationship between ambient levels of ionizing radiation, the number of species (richness) and the functional richness of a bird community at a given site. An association between species richness and functional richness is expected as these two metrics are not mathematically independent (Villéger et al., 2008). However, in this study species richness and functional richness were significantly but only moderately related ($R^2 = 0.4$, $t = 12.956$, $p < 2.2\text{e-}16$), and for this reason we have presented both results (i.e. the associations between background radiation and species richness and functional richness, respectively).

The observation that functional evenness and divergence were unrelated to radiation level, and were constant among years, suggests that the effect of radiation on bird community composition is mainly the result of effects on the number of species and the degree of niche space filled by species in the community (or functional richness) (Mason et al., 2005).

Bird communities characterized by the largest average community evolutionary distinctiveness were found in the study area where the levels of radiation were the highest. This is important because currently, ecologists recognize the importance of phylogenetic diversity measures to establish conservation priorities (EDGE of Existence, 2015; Isaac et al., 2007; Winter et al., 2013). In fact, some recent recommendations for nature conservation optimization encourage the use of measures of phylogenetic diversity together with species richness (Monnet et al., 2014; Winter et al., 2013). Here we used evolutionary uniqueness as a measure of evolutionary history, indicating the degree of isolation of species on a phylogenetic tree, and whether it represents uniquely divergent organisms (Isaac et al., 2007; Jetz et al., 2014). Furthermore, we have expanded this approach by inclusion of regression tree analysis. While we hypothesized that ambient radiation level affected community composition, we cannot dismiss the possibility that this effect arose as a consequence of other correlated factors. Indeed, areas with higher radiation levels also had the greatest forest cover, although this effect only accounted for 13% of the variance ($R^2 = 0.13$, $t = 3.571$, $p = 0.0004$). Thus we hypothesize that the positive association between radiation level and evolutionary distinctiveness of communities may be due, at least partly, to such a spurious correlation. This can only partly be the case because the negative relationship between ambient radiation and species richness is present both in forests and in open habitats. Thus, we suggest that this result may partly reflect the fact that bird communities with greater evolutionary uniqueness are found in areas with high forest cover (Fig. 4). In other studies we already found a positive association between the presence of big trees and size of forest patches and bird communities characterized by overall high evolutionary distinctiveness (Morelli, 2018; Morelli et al., 2017).

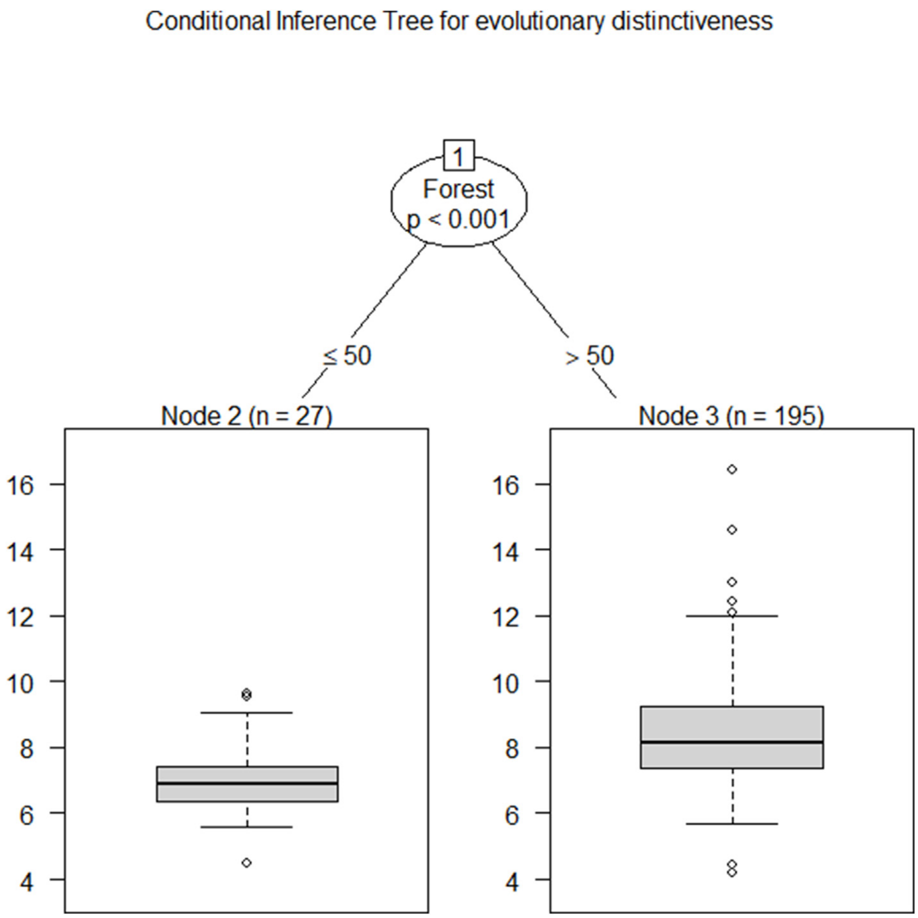

Fig. 5. Regression tree created with the environmental variables and the radiation level sampled in Chernobyl explaining the average evolutionary distinctiveness in bird communities. Under each branch, in the nodes 'n' is the number of sampling sites in the leaf (group); the values shown in the boxplots are the evolutionary distinctiveness for the group. Leaves of the tree indicate average catch weight per two of each group given the conditions and thresholds stipulated by the splits. The split is on forest coverage (50.00%).

Thus, we can hypothesize that the occurrence of some bird species characterized by a relatively high evolutionary distinctiveness score could be positively associated with the forest cover.

The findings reported here concerning bird community structure in radioactively contaminated areas may also have more global implications for biological conservation (Møller and Mousseau, 2011). We have previously related the abundance of birds around Chernobyl to dispersal distance and background radiation with population size increasing with longer dispersal distances (Møller et al., 2010). This is not surprising when considering that such dispersing species are likely to rescue local populations that serve as ecological "black holes" that trap immigrants in regions of low individual fitness due to the negative effects of mutation accumulation stemming from exposure to radioactive contaminants (Møller et al., 2010). In addition, background radiation was observed to have stronger negative impact on rare species and habitat specialists possibly because of the lack of an influx of dispersers that might otherwise moderate the mutational load imposed by radiation effects in small populations (Møller and Mousseau, 2011). Finally, species with high mitochondrial DNA substitution rate were found to be more likely to suffer population declines as a result of radiation exposure although interestingly, such species tended to have short breeding dispersal distances and relatively high subspecies richness (Møller and Mousseau, 2011). These findings may have significant implications for species richness, but also for taxonomic, functional and evolutionary diversity of bird communities facing changing ecological landscapes.

This study has a number implications for future research. First, we should test for changes in community structure over time, and even if background radiation levels decline as predicted from simple radioactive decay processes, we would expect the relative ranking of sites to be consistent for relationships between radiation and community structure. Second, we have collected similar bird community data in Fukushima, Japan, following the nuclear disaster there in March 2011. With data now available for 2011 to 2017 it will be possible to conduct analyses similar to those presented here for Chernobyl bird communities. We predict that similar changes in richess and diversity indices should also be apparent in Japan although changes in landscape are not as dramatic as those seen in Chernobyl given that the region was largely covered in forest even before the disaster, and only six years have passed since the nuclear accident. Third, we have documented a drop in ambient radiation by 35% during 2007–2015 (Fig. S1). If radiation is driving community structure, we should expect that change in community structure will be associated with change in ambient radiation. Fourth, recent forest fires have eliminated trees from large areas, but not significantly changed ambient radiation levels. This should provide an opportunity for disentangling the effects of radiation and forest cover on species richness. The main message here is that continued study of Chernobyl, and now also Fukushima, is likely to provide valuable insights to general processes influencing changes in population abundances and species richness of broad relevance for a planet undergoing rapid environmental changes in response to anthropogenic influences.

In conclusion, ionizing radiation from nuclear accidents has reduced the abundance, species richness and diversity of ecosystems. Here we analyzed taxonomic, functional and evolutionary diversity of bird communities in forested areas around Chernobyl. Species richness decreased with increasing radiation, as well as abundance of individuals. Functional richness, but not functional evenness and divergence, decreased with increasing level of ionizing radiation. Evolutionary distinctiveness of bird communities was larger in areas with higher levels of ionizing radiation. Regression tree models revealed that species richness was higher in areas with radiation level lower than 0.7 μSv/h.

In contrast, when radiation levels were higher than 16.67 μSv/h, bird species richness dropped to a minimum. These thresholds need to be considered and are very important for conservation management. Functional richness was related to both forest cover and radiation level. Larger functional richness was found in bird communities with forest cover higher than 50%. Finally, the average evolutionary distinctiveness of bird communities was higher in areas with forest cover larger than 50%. These findings imply that ionizing radiation interacts with forest cover to affect species richness and its component taxonomic, functional and evolutionary diversity.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jenvman.2018.05.032.

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