Long-term Effects of Rewilding on Species Composition: 22-years of Raptor Monitoring in the Chernobyl Exclusion Zone

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Abstract

Large-scale rewilding has been proposed as an effective method to combat the global biodiversity crisis, although there is a lack of data to support this. Rewilding generally refers to a process that allows nature to recover by reducing human interference, without the predefined end-goal that more traditional restoration projects usually have. The Chernobyl Exclusion Zone (CEZ) is perhaps the most famous example of passive rewilding (rewilding with little or no management), but until now, most research has focussed on the impact of radiation on wildlife rather than rewilding. Here, we analyse species composition change of raptors in the Belarusian CEZ over a twenty-two year period, starting twelve years after the accident, alongside national raptor monitoring data. Generalist and farmland-associated mesopredators, super-abundant at the beginning of our study, strongly declined, as open habitats (former agricultural land) rewetted or became overgrown. Increase in waterlogged areas saw wetland specialists increase in abundance, including two species locally extinct from the area before the accident: Greater Spotted Eagle (Endangered in Europe) and White-tailed Eagle. Greater Spotted Eagles are an indicator of wetland habitat quality, and whilst declining throughout Europe in recent decades, they have increased from zero to at least thirteen pairs, over the whole Belarusian CEZ. Our research is evidence that rewilding could be an effective way of restoring species and species interactions found in near-natural habitats, and if human interferences in ecological processes are reduced, *a priori* restoration goals and continued management are not always necessary to conserve threatened species.

Running title: Effects of Rewilding on Raptors

Keywords

Passive restoration, conservation, predators, birds, biodiversity, endangered species,

Implications for practice

Our work shows evidence that passive rewilding can return European lowland ecosystems to near-natural states in both habitat and species composition.

We show that passive rewilding can support recovery of species of conservation concern.

Passive rewilding can drive a change from generalist to specialist species due to habitat change and species interactions.

Monitoring over multiple decades of rewilding projects is needed in order to detect change at an appropriate timescale.

Introduction

Rewilding is a hotly discussed topic, with projects such as Knepp rewilding and Oostvardeplassen bringing widespread publicity. Rewilding refers to a process that allows nature to recover in an area by removing or reducing human interference, with the aim of increasing ecosystem functioning, biodiversity and resilience against perturbations (Perino et al. 2019). This can differ from more traditional conservation or restoration activities that involve managing or restoring an area to create a predefined habitat or ecosystem. Rewilding projects generally operate on a scale from virtually no human interference (passive rewilding) to constant management in order to promote natural processes. Cases of passive rewilding are rare, however, and on large-scales practically non-existent, with most large projects at least beginning with the goals and management inputs of a restoration project (Hayward et al. 2019).

Management can range from reintroducing locally extinct large herbivores or top-predators to provide important ecosystem functions (e.g. Yellowstone national park (Dobson 2014)), or using domesticated animals to provide similar functions such as grazing pressure (e.g. Knepp rewilding (Tree 2017)).

To evaluate the efficacy of rewilding as a biodiversity conservation tool, the impact on species assemblages needs to be quantified, with interspecific comparisons necessary to predict impacts across species with a diverse array of ecological niches (Jarzyna & Jetz 2017). Empirical studies on the effects of rewilding are surprisingly scarce, however, (Svenning et al. 2016), and the literature is dominated by reviews and opinions pieces, both positive and negative (Rubenstein & Rubenstein 2016; Nogués-Bravo et al. 2016; Corlett 2016; Van Meerbeek et al. 2019; Fernández et al. 2017; Perino et al. 2019).

Avian predators can be excellent indicators of ecosystem health due to their position at the top of the food chain and ecological specialisation, providing insights into the effects of habitat change (Burgas et al. 2014; Martín & Ferrer 2013). In this study, we analyse species composition change using a long-term data set of breeding raptor abundances from the Belarusian Chernobyl Exclusion Zone (CEZ). Since the reactor meltdown of Chernobyl nuclear power plant in 1986, human interference in Chernobyl and the surrounding 4700 km ^{2} of landscape has been heavily reduced. Before 1986, the area was largely a production landscape; housing large pig and cow farms, densely populated settlements and undergoing intensive arable agriculture. Since 1986, ecological research has largely focused on the potential negative effects of radiation on wildlife, within the affected area (Howard et al. 2010). Of this body of research, findings have been largely mixed, with both negative and null effects of chronic radiation exposure found (Beresford et al. 2019).

The nuclear meltdown and the subsequent annexing of the exclusion zone (CEZ) inadvertently led to a huge rewilding project. The natural return of wolves (*Canis lupus lupus*) and elk (*Alces alces*), and the reintroduction of Przewalski's (*Equus przewalskii*) and Bison (*Bison bonasus*) have has been well documented in the media, but until now, there has been little attempt to quantify and explain the impact of land-abandonment and reduction of human interference on the environment and wildlife, by the scientific community. There is only one research paper, to our knowledge, (Deryabina et al. 2015) documenting the impact on animal populations, finding large herbivore numbers and much higher wolf abundance than other nature reserves in the region.

Here, we present long-term breeding raptor data from a 147 km ^{2} study plot within the Belarusian CEZ; an area of former intensive agricultural land that has been abandoned for over thirty-three years (fig. 1). Sampling began twelve years after the Chernobyl accident, and we quantify raptor species composition and habitat change over the next twenty-two years. We relate these changes in raptor composition to sites across a gradient of human interference in Belarus, from heavily transformed sites, with high agricultural land cover to near-natural sites with high wetland cover. From these data we assess the impact of land-abandonment on raptor community composition, whether rewilding can be a viable alternative to more traditional restoration projects and the timescale such projects need to be monitored over.

Methods

CEZ study plot

We conducted our study in the 2162 km ^{2} Belarusian CEZ. Prior to the nuclear accident in 1986, the CEZ was largely used for intensive agriculture, facilitated by the drainage of natural wetlands and deforestation (Schlichting et al. 2019). Since 1986, the CEZ has been largely annexed to the public, resulting in much reduced human interference (Schlichting et al. 2019). Immediately after the accident, all locks on the drainage canals were closed and earthen dams were built where locks were insufficient to hold the water. Canals have also become blocked due to lack of maintenance and from damming by beavers. Management has also included planting of scots pine in some areas for commercial forestry and to sequester radiation. The near absence of human interference and management, combined with the blocking of drainage canals has resulted in large areas of natural succession of habitats, recolonisation by previously extinct species and rewetting of the area, facilitated by natural and human damning of rivers and canals (to reduce the spread of radiation) (Deryabina et al. 2015; Schlichting et al. 2019).

Our study plot was an area of 147 km2 in the North-East of the Belarusian CEZ (fig. 1). It is situated on the edge of the CEZ, bordered by intensive arable farmland. In 2008 the density of contamination of the territory with caesium^{137} was 10.8 to 54.0 Ci / km^2 and strontium 0.15 to 2.03 Ci / km2. The impact of radiation was not taken into account in this study as it has not been shown to have an effect on animal populations (Lyons et al. 2020; Deryabina et al. 2015).

Raptor surveys in the CEZ

Surveys of breeding raptors were carried out between 1998 and 2019. The entire 147 km ^{2} plot was surveyed in 1998, 2016 and 2019 from a network of fourteen elevated observation points, 2-3 km apart, with binoculars and a telescope (20-60x) (Dombrovski & Ivanovski 2005a). A reduced area of the main plot was surveyed in 2004 (120km^2/ seven points), 2007 (120km^2/ seven points), 2010 (95km^2/ seven points) and 2013 (120km^2/ nine points). Number of points do not equate equitably to area surveyed, as some observation points were on the edge of the study plot.

Points were located so that each sector of the plot was viewable from different sides and locations of breeding raptors were marked on a map after verifying from more than one tower. Duration of each observation at each point was at least 4 hours, with one point observed in one day, by one observer. Timing of observation was from 10:00 am to 3:00 pm, i.e. the time of main summer activity of birds-of-prey. On cloudy and rainy days counts would either be cancelled for the whole day, or would only start from the moment when permanent fine weather has re-established. The following parameters were recorded for each raptor sampled:

1) Species (all individuals were identified to species) and sex of bird (only possible for species with dimorphic plumage).

2) Distance to the observed bird, visually determined.

3) The azimuth at which the bird was observed, with the help of a compass with a scale division of 1–2 degrees,

4) Any features of bird behaviour e.g. Displaying behaviour, nest building, prey delivery.

5) All distinctive features of birds under observation were recorded (peculiar plumage, colour, absence of flight feathers and tail feathers) for their individual identification.

Birds were considered breeding or occupying a breeding territory if elements of nesting behaviour were observed (aerial display, aggressiveness towards larger species, bringing nest material or prey). This was largely determined by male behaviour, as females spend more time sitting on the nest incubating eggs or brooding chicks.

In many cases, the nest was found to increase accuracy of the breeding location, although this was not always possible. The search for nests was carried out primarily for the most numerous species in cases where the supposed nesting sites were very close to each other, to make sure that they were different pairs. For example, in 1998, half of inhabited nests of buzzards and common kestrel were found and two nests of a lesser spotted eagle. Since 2004, the buzzard population significantly decreased, and the search their nests to clarify their nesting density was carried out to a lesser extent.

We also searched nests of all *Clanga clanga* and *Clanga pomarina* to confirm their identification, as this can be difficult in the field, particularly those of mixed pairs. All individuals were subsequently identified to species. During 2019 we used camera traps on the nests for the same purposes. Borders of the presumed nesting ranges were mapped to prevent double counting of breeding birds, if the nest was not found. The land cover type around the nest was described e.g. forest or wetland type and these data were used for future land cover change analysis.

In 1998, 2016 and 2019 observations at each point were carried out twice: in mid-April to May and in June to July. The maximum number of breeding pairs observed was used for the analysis. In 2004, 2007 and 2013 single counts were carried out in June. By using the above methods we endeavoured to sample every breeding pair. However, non-soaring, forest dwelling species, such as Eurasian Sparrowhawk (*Accipiter nisus*), may have been undersampled.

Land cover change in the CEZ

Land cover change was estimated within and directly surrounding the study plot using the “remap” tool (Murray et al. 2018). Remap allows analysis of land cover type from cloud free composite images between 1999-2003 and 2014-2017. To map land cover change we first split land cover into four classes: forest, wetland, dry open and open sandy areas. We then used 855 (1999-2003) and 1145 (2014-2017) georeferenced training points (with a minimum of 55 training points of each class) identified from a mixture of aerial images and ground-truthing to identify the land cover classes. Ground-truthed points were gathered from extensive field notes collected by the first author (VD), whilst conducting field surveys, between 1999-2003 and 2014-2017 respectively. Each training point then samples a range of satellite datasets (predictors) from LANDSAT and USGS to train a random forest classifier. Once the random forest is trained, remap classifies all of the pixels present in a focal region into the map classes defined by the training set (Murray et al. 2018).

National raptor data

We used raptor abundance data from fourteen plots in Belarus to put species composition in the CEZ in a national context. Detailed methods can be found in Dombrovski & Ivanovski, (2005a). Briefly, surveys were conducted between 1999 and 2002, using similar methods to the CEZ study plot, with counts conducted from elevated points, with telescope and binoculars, twice during the breeding season. Data from twenty-five study plots were available, but so as to compare sampling plots with similar overall area, we discounted eleven plots from the analysis that were below 50 km ^{2} or above 200 km ^{2}. Land cover composition of these study plots was collected by combining topographic and forestry inventory maps, satellite images and ground-truthing when visiting study sites. Initially, land-use types were divided into 14 types (Dombrovski & Ivanovski 2005b), here for the purposes of simpler data presentation, we combined them into five different land-use types particularly relevant to the species in our study: dry forest (coniferous and deciduous non-flooded forest), wet forest (flooded deciduous forest), wetlands (mire, bog and floodplain meadows), agricultural and fellings.

Three species were removed from the analysis as they only appeared once in the data set (*Milvus milvus, Milvus migrans, Pandion haliaetus*) and one species as it only appears in the Northern part of Belarus, *Falco columbarius*.

Statistical analysis

We modelled change in raptor community composition from 1998-2019 by using a multivariate generalized linear latent variable model (gllvm) with the R package “gllvm” (Niku et al. 2019). Multivariate abundance data often has a strong mean–variance relationship, which if not accounted for, can introduce artefacts into the analysis (Wang et al. 2012). Generalized linear latent variable models allow similar model visualisations to traditional ordinal techniques such as NMDS, but have advantages, as they specify a statistical model for the data intended to capture key data properties, including the mean-variance relationship. Furthermore, diagnostic tools can be used to check model fit and model selection is possible through AIC (Niku et al. 2019).

To examine how raptor species composition changed in the CEZ over time, we modelled abundance of breeding pairs for each species for each site (year of data collection), with time as an explanatory variable (*abundance ~ time)*. The model was fitted with a negative binomial distribution with two latent variables, (the latent variables can be interpreted as a way of accounting for any residual covariation not explained by the covariates [Mehner et al. 2021]) and an offset (log (*area*)) to account for the different area of the study plot sampled between years.

We used a pure latent gllvm (no environmental variables) with three latent variables to compare raptor species composition in the CEZ to nineteen other sites situated throughout Belarus and show species associations with sites. We used gllvm as a model-based approach to unconstrained ordination by including latent variables in the model but no predictors (Hui et al. 2015; Walker & Jackson 2011). The latent variables are unknown and therefore assumed to be random, drawn from a bivariate, standard normal distribution and estimated simultaneously with the coefficients and row effects (Hui et al. 2015). Latent variables "can be thought of unmeasured environmental variables, or as ordination scores, capturing the main axes of covariation of abundance (after controlling for observed predictors)" (Niku et al. 2019). The corresponding ordination plot then provides a graphical representation of which sites are similar in terms of their species composition.

We modelled abundance of breeding pairs for each species for each site (each year of CEZ monitoring + national raptor monitoring sites). The site associated latent variable scores (row effect) then allow comparison of site similarity which was interpreted visually in an ordination plot. Individual species also get associated latent scores allowing for species association with specific sites, or groups of sites (Niku et al. 2019). We did not include land cover as an explanatory variable in our model as data collection methods were not comparable between the CEZ study plot and the other sites. We did, however, present land cover for national raptor monitoring site visually, in the ordination plot (fig. 5). Model selection for all gllvms was done by comparing AICc values with additional latent variables and model distributions using the "*anova*" function. Model fit was assessed by Dunn-Smyth residuals and a quantile–quantile plot with simulated point-wise 95% confidence interval envelopes (fig. S1 and fig. S2.).

To quantify positive and negative associations between raptor species in the CEZ study plot and national monitoring sites, we used factor loadings from the residual covariance matrix induced by the latent variables using the "*getResidualCor"* function. Latent variables induce correlation across response variables, and so provide a means of estimating correlation patterns across species, and the extent to which they can be explained by environmental variables. Information on correlation is stored in the factor loadings θj, so the residual covariance matrix, storing information on species co-occurrence that is not explained by environmental variables, can be calculated as $\Sigma=\Gamma\Gamma\top$, where $\Gamma=[\theta 1\ldots\theta m]'$. The getResidualCor function can be used to estimate the correlation matrix of the linear predictor across species, which was visualised using the corrplot package.

Results

Raptor composition in the CEZ from 1998-2019

During the twenty- two year study period, we recorded thirteen species of breeding diurnal raptors in our 147 km ^{2} study plot in the CEZ.

Species composition changed during our study period with some species declining and others increasing. Montagu's Harrier (*Circus pygargus*), Lesser Spotted Eagle (*C. pomarina*), European Honey Buzzard (*Pernis apivorus*) and Common Buzzard (*Buteo buteo*), species associated with dry forest and open habitats, all declined during our monitoring period (fig. 2). Numbers of pairs of Honey Buzzard, Common Buzzard and Eurasian Sparrowhawk declined dramatically from 1998-2004 from levels above the national mean, but then stabilised to near the national mean in later years of the study. Lesser Spotted Eagles experienced a continued decline from thirteen pairs in 1998 to just four in 2019 (Table SI1) and Short-toed Snake Eagle (*Circaetus gallicus*) also declined from three to one remaining pair in 2019. Breeding pairs of Northern Goshawk (*Accipiter gentilis*) also declined after the first sampling year, but numbers stabilised throughout the next eighteen years, although below the national mean.

Four species showed increases in number of breeding pairs during our study period: Greater Spotted Eagle (*C. clanga*), White-tailed Eagle (*Haliaeetus albicilla*), Marsh Harrier (*Circus aeruginosus*) and Eurasian Hobby (*Falco subbuteo*). Greater Spotted Eagle (*C. clanga*), White-tailed Eagle (*Haliaeetus albicilla*), and Eurasian Hobby (*Falco subbuteo*) were found at higher densities in the CEZ study plot than the national mean. Greater Spotted Eagle was possibly the most noticeable increase, from zero pairs breeding in 1998 to four pairs in 2019. Until 2000, Greater Spotted Eagle had been locally extinct in the

CEZ. Mixed pairs of Greater Spotted Eagle and Lesser Spotted Eagle also showed an increase throughout our study period, from zero in 1998 to two in 2019, reflecting the increase in Greater Spotted Eagles. Common Kestrel (*Falco tinnunculus*) abundance fluctuated within the CEZ, but remained considerably higher than the national mean.

The most numerous species in 2019 was still Common Buzzard and European Honey Buzzard, while the Lesser Spotted Eagle has been replaced by the Marsh Harrier and Eurasian Hobby.

From the coefficients of our gllvm, five species showed significant declines (95% CIs that did not cross zero): Montagu's Harrier, Lesser Spotted Eagle, European Honey Buzzard, Eurasian Sparrowhawk and Short-toed Snake Eagle. Greater Spotted Eagle and mixed pairs of Greater Spotted Eagle and Lesser Spotted Eagles showed significant increases in abundance. Other declining or increasing species (e.g. Marsh Harrier [increasing] and Common Kestrel [decreasing]) show near-significant changes in breeding pair abundance during our study period, with 95% CIs slightly overlapping zero. Large CIs are likely caused by the small sample sizes of each species and natural fluctuations in population, such as the relatively low abundance seen in the majority of species in 2013 (fig. 3). The spring of 2013 was unusually dry and the summer unusually wet, likely leading to unfavourable breeding conditions. Pairs may have failed to breed or abandoned breeding altogether that year.

Land cover change

Between 1999 and 2017, in our study plot and the surrounding area, wetland area increased by 680 % and forest by 14% (Table 1. and fig. 4). Open field decreased by 45 % and sand by 31 %. Our models of land cover showed an 86.5 % accuracy rate for the period 2014-2017 and 93.3 % accuracy rating for 1998-2001.

Raptor community change in the CEZ in a national context

From 1998 to 2019, raptor species composition in the CEZ study plot became more similar to sites throughout Belarus associated with wetland species (fig. 5). From the two primary latent variables, there was clustering of sites with high wetland cover, which were separated from sites with high agricultural and dry forest cover. The raptor species association with the latent variables was separated broadly into two groups comprising of wetland and bog associated species: Greater Spotted Eagle, White-tailed Eagle, Marsh Harrier, Short-toed Snake Eagle and Hen Harrier and forest associated and farmland species, Lesser Spotted Eagle, Common Buzzard, Honey Buzzard and Eurasian Sparrowhawk, Northern Goshawk and Eurasian hobby, Montagu's harrier and Common Kestrel. This reflects the change in species composition seen in the CEZ during the study period with forest and farmland associated species more common in 1998 and wetland species increasing in latter years. All study sites were large, > 90km ^{2}, and often contained multiple land-use types, which may have reduced the separation on the axes for certain species, particularly agricultural and dry-forest associated species (e.g. Montagu's Harrier and Northern Goshawk).

Similar relationships were also seen in the correlation analysis, with the wetland and bog associated species (Greater Spotted Eagle, White-tailed Eagle, Marsh Harrier, Short-toed Snake Eagle and Hen Harrier) positively associated with each other and negatively associated with the dry, open country species (Montagu's harrier, and Common Kestrel) (fig. 6).

Figure 5. Correlation plot of raptor species in the CEZ study plot across all years and raptor survey sites across Belarus. Red squares signify the intensity of a negative correlation and blue squares positive.

Discussion

Rewilding, or passive restoration, is becoming an increasingly employed method to deal with the global biodiversity and climate change crisis. However, long-term data on the impact of rewilding on faunal communities are scarce or non-existent (Svenning et al. 2016). Our data-set offers a rare exception, allowing us to quantify the effects of over thirty years of land-abandonment of an intensively farmed area, on raptor species composition. There were "winners" and "losers" in breeding raptors over the study period, while some species fluctuated after land-abandonment. Broadly, top-predators and wetland specialists, such as the Endangered Greater Spotted Eagle, increased in abundance, coinciding with an increase in wetland area as former fields became flooded due to the collapse of drainage canals. Generalist mesopredators and farmland specialists, such as the Common Buzzard, and Montagu's Harrier, at super-abundant levels at the beginning of our study (twelve years after the Chernobyl disaster), suffered sharp declines which levelled off after a number of years. Drier forest species, such as the Lesser Spotted Eagle showed continuous declines, which alongside the increase in abundance of Greater Spotted

Eagle shows the opposite relationship to the national trend. Over time, the raptor composition in the CEZ became more similar to other sites in Belarus with high wetland composition and natural habitat cover (mires and raised bogs) and less similar to habitats with high agricultural and dry-forest cover. The increase in abundance of specialist raptors in the CEZ at the expense of generalists, indicate the reversal of environmental degradation, in which generalists usually increase in abundance at the expense of habitat specialists (Devictor et al. 2008; Julliard et al. 2006). Overall, our study shows that rewilded areas have the potential to offer important refugia for species of conservation concern and return assemblages and habitats to those seen in native, near-natural landscapes.

Land cover and species composition change

Since 1986, with the reduction of human habitat management the study area underwent considerable land cover change. Between 1999 and 2017, wetland and bogs substantially increased in area (680%) as open fields rewetted (leading to their corresponding decrease in area). Forest also increased by 14 %. Although we do not have land cover data from before 1999, a previous study shows that between abandonment in 1986 and 1999 forest cover and wetland area increased (Bulavik et al. 2013). Rewetting was facilitated by the silting up and collapse of drainage canals, blocking of waterways by beavers, and the blocking of canals by humans to prevent the travel of radiation immediately after the Chernobyl accident, and to increase the resistance to fires (Bulavik et al. 2013). In 2019 the habitat more closely resembled near-natural areas in Northern Ukraine and Southern Belarus that undergo seasonal flooding events and contain Europe’s largest expanse of peatland bogs.

Overall, species composition changed from raptor communities more associated with agricultural or dry forest to those found in near-natural wetlands in the region. This saw species such as Montagu’s Harrier and Lesser Spotted Eagle replaced by Marsh Harrier and Greater Spotted Eagle. The colonisation of Greater Spotted Eagle and its continued increase in abundance is one of the most remarkable findings of our study. In 2019, there were four breeding pairs in the study plot and at least thirteen pairs present within the Belarusian exclusion zone (*own unpublished data*). This is contrary to national and global trends (Väli et al. 2010; Väli 2015), and to our knowledge, is the only recorded increase throughout the Greater Spotted Eagle distribution in recent history. Greater Spotted Eagles are classed as globally Vulnerable with less than 4500 pairs (Ferguson-Lees & Christie 2001) and Endangered in Europe, with between 770 and 1040 pairs remaining (BirdLife International 2017). The species has become extinct in Western Europe, and has tiny remnant populations in Poland, Estonia, Ukraine and Lithuania. Belarus, however, is relative stronghold with an estimated 120-160 pairs, although Greater Spotted Eagle numbers have declined considerably in the last twenty years (Dombrovski 2013). Greater Spotted Eagles are considered an indicator of wetland quality, and their decline has largely been attributed to the reduction and degradation of wetland habitats and disturbance from people (Dombrovski & Ivanovski 2005b). Another major threat is hybridisation with Lesser Spotted Eagles (Väli et al. 2010) which occupy drier habitats (Cramp et al. 1992). Lesser Spotted Eagle range has extended into Eastern Europe, coinciding with drainage of wetlands for agriculture and forestry (Väli et al. 2010).

White-tailed Eagle, another raptor sensitive to anthropogenic disturbance (Helander & Stjernberg 2003), also increased from one to two breeding pairs in our study plot. White-tailed Eagles were not breeding in the CEZ prior to the accident and were first reported in 1992 (A.Tishechkin, *personal communication*), increasing to at least twenty pairs in 2010 (Yurko 2016). Unlike Greater Spotted Eagle, this species is resident, needing a regular supply of large prey throughout the winter months. The increase in abundance of wolves and their prey species (e.g. Elk, Red Deer) in the CEZ (Deryabina et al. 2015) may provide White-tailed Eagles with carrion during winter (Schlichting et al. 2019) allowing them to survive throughout this period.

Greater Spotted Eagle and White-tailed Eagle can be seen as umbrella species for the wider conservation success of the CEZ. They rely on high abundances of other species of conservation importance, such as Great Snipe (*Gallinago media*), Corncrake (*Crex crex*) and an array of wader and waterfowl species that are indicators of wetland and forest quality (Sulkava, Tornberg, and Koivusaari 1997; Dombrovski 2010). Although changes in abundance in these species were relatively subtle in our study plot, the species' colonisation and change in breeding abundance in the wider CEZ indicates a “true” relationship.

Decline of farmland-associated raptors and mesopredators

The largest declining species in the period 1998–2019, were three widespread, myophagous species that prefer non-waterlogged and open or dry forest habitats for hunting (Montagu's Harrier, Lesser Spotted

Eagle and Honey Buzzard) (Cramp & Simmons, 1980). Common Buzzard abundance also decreased by more than 60% between 1998 and 2013, but saw increases in later years and which led to confidence intervals crossing zero in our statistical analysis over the whole study period. The decrease in abundance of these species occurred with a progressive reduction of open dry areas; previously agricultural fields. At the beginning of our research in 1998, the breeding densities of these species in the reserve were much higher than the average for the region, or Belarus as a whole (Dombrovski & Ivanovski 2005a). Unfortunately, we do not have data from the first twelve years after the accident, however, it is unlikely that such high abundances were present before the accident, since the region had a high density of human population and was intensively managed for agriculture and commercial forestry. Raptor mesopredator abundance may have rapidly increased in the first decade after the Chernobyl accident due to the preservation of favourable feeding conditions alongside the reduction in anthropogenic pressure (Nikiforov et al. 1995). In the absence of humans and large raptors, nest sites were likely not limited, and from 1993-1998 we found numerous Common Buzzard nests in clearly visible places - on narrow forest belts, along roads and on single trees. In later years, only pairs that nested in the forest were observed.

The reduction in preferred hunting grounds and mesopredator suppression by White-tailed Eagle and Greater Spotted Eagle may have contributed to the decline of these species (Jiménez et al. 2019; V V Yurko 2016; Kamarauskaitė et al. 2020). Short-toed Snake Eagle, a specialist predator of reptiles, also fell from three to one pairs, possibly due to competition with other increasing top predators. A White-tailed eagle was observed in the Ukrainian CEZ by camera-trap, predating a Short-toed Snake Eagle nest in 2020 (Simon, *personal communication* 2020) and Short-toed Snake Eagle remains have been found in Greater Spotted Eagle nests in Belarus (Dombrovski, *unpublished data)*.

We did not analyse fine-scale distributions of breeding raptors between years, due to small sample sizes, but we observed that the greatest changes in breeding densities of common raptors occurred in the centre or edge of plot furthest away from human habitation. Prior to the rewetting and overgrowth of former fields in our study plot, breeding density of Common and Honey Buzzard was high towards the middle of the CEZ. These areas showed the largest decrease in breeding density of these species in latter years, when overall breeding density decreased. Large, rarer species such as Greater spotted, White-tailed and Short-toed Snake Eagles did not display a similar pattern, and the appearance of new pairs occurred both on the periphery and inside the reserve, possibly explained by the comparatively large home ranges of these species.

Rewilding of the CEZ in a broader context

We show that rewilding has the potential to reverse the effects of anthropogenic land-use change without continued habitat management. Thirty three years after abandonment and aided by the initial blocking of drainage canals to prevent spread of radiation, the CEZ has undergone major land cover change. This is likely the main driver for the change in raptor community composition in the CEZ, particularly rewetting, shown by the increase in abundance of wetland specialists. An increase in the complexity of species interactions is also likely to have been important. For example, increase in White-tailed Eagle abundance may have been enabled through provisioning of carrion during lean winter months by wolves (Schlichting et al. 2019), and top-down control of mesopredators by other raptors likely impacted their abundance (Alston et al. 2019). Reduced human pressure, such as raptor persecution, road collision and physical disturbance may have also contributed to changes in raptor abundance (McClure et al. 2018), although it is difficult to ascertain how this affected species differently, species particularly sensitive to nest disturbance, such as Greater Spotted Eagles, may have more greatly benefited than less sensitive species.

Our research is evidence that rewilding could be an effective way of restoring species and species interactions found in near-natural habitats, and if human interferences in ecological processes are reduced, *a priori* restoration goals and continued management are not always necessary to conserve threatened species. Priority conservation species, such as Greater Spotted Eagles, showed considerable recovery, going against declining national and continental trends. To the best of our knowledge, this is the only documented conservation success for this species throughout its range. This coincides with increase in mammalian top-predators, such as a bear or lynx, which have colonised the CEZ since the accident (Shkvyria & Vishnevskiy 2012). Our study plot was situated on the edge of the CEZ, bordered by intensive arable farmland. This indicates that rewilding projects within heavily managed landscapes can be an effective restoration tool.

Finally, we stress the importance of long-term monitoring to evaluate results of rewilding projects. Several species took nearly twenty years to stabilise in breeding abundance, and some species (Lesser

Spotted Eagle, Greater Spotted Eagle) show continued changes. Focal species for conservation may also take time to respond; Greater Spotted Eagle, one of the key indicators for the conservation success of the CEZ, only began to colonise the area sixteen years after abandonment. Depending on the initial state of a rewilding project, it is likely that several decades will be needed to sufficiently assess changes in biodiversity, continued research in the CEZ, and in other long-term rewilding projects, globally is needed to effectively quantify the impacts of rewilding on biodiversity (Poorter et al. 2021).

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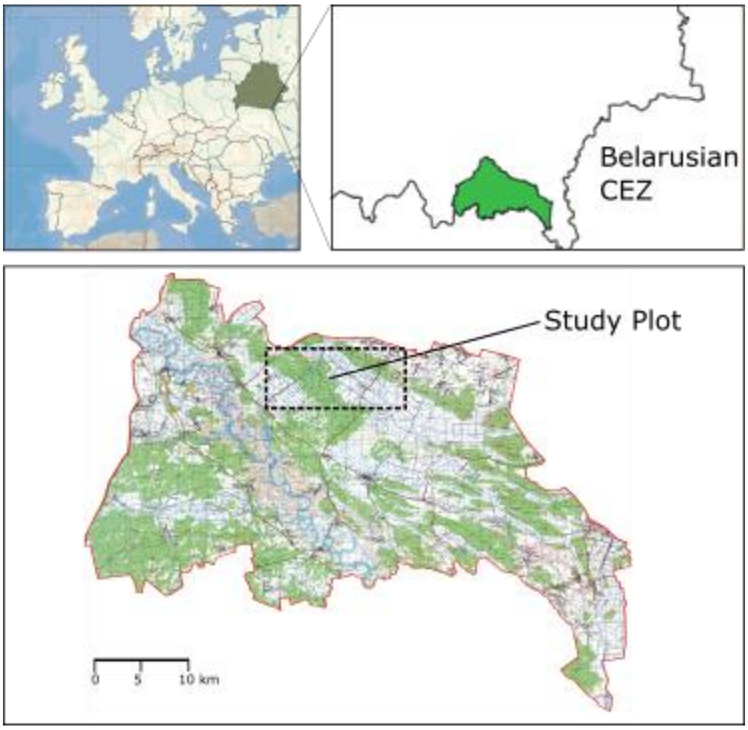

Figure 1. Location of study plot in the Belarusian Chernobyl Exclusion Zone.

Table 1. Land cover of the 147 km ^{2} and the surrounding area from remote-sensed data

Land cover	1999-2003 (km ^{2})	2014-2017(km ^{2})
Open field	158	86.5
Forest	104	118.6
Wetland	10	68.8
Sand	3.2	2.2

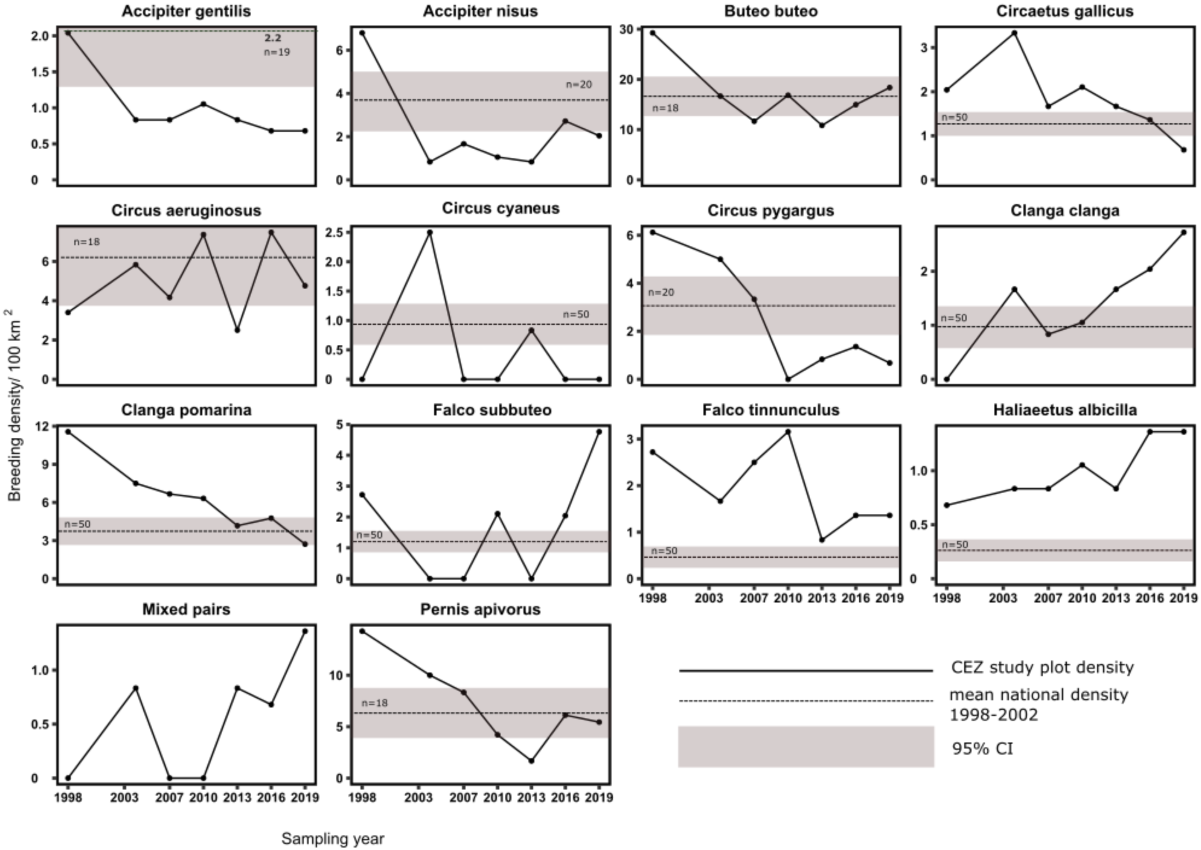

Figure 2. Density of breeding raptors / 100 km ^{2} plotted against sampling year. The dashed lines represent the mean density of the species, with 95 % CIs (grey bars) from national raptor monitoring sites over 60 km ^{2} from Dombrovski and Ivanovski, 2005a. Mean density of A. gentilis is presented numerically for clarity, and for A. gentilis and C. aeruginosus the upper confidence intervals are not entirely included. Sample sizes for means and CIs from Dombrovski and Ivanovski, 2005a differ between species as species considered as common were not recorded for many sites. Mixed pairs refer to C. clanga x C. pomarina. Mean density for national monitoring plots was not presented for mixed pairs as they were not recorded in Dombrovski and Ivanovski, 2005.

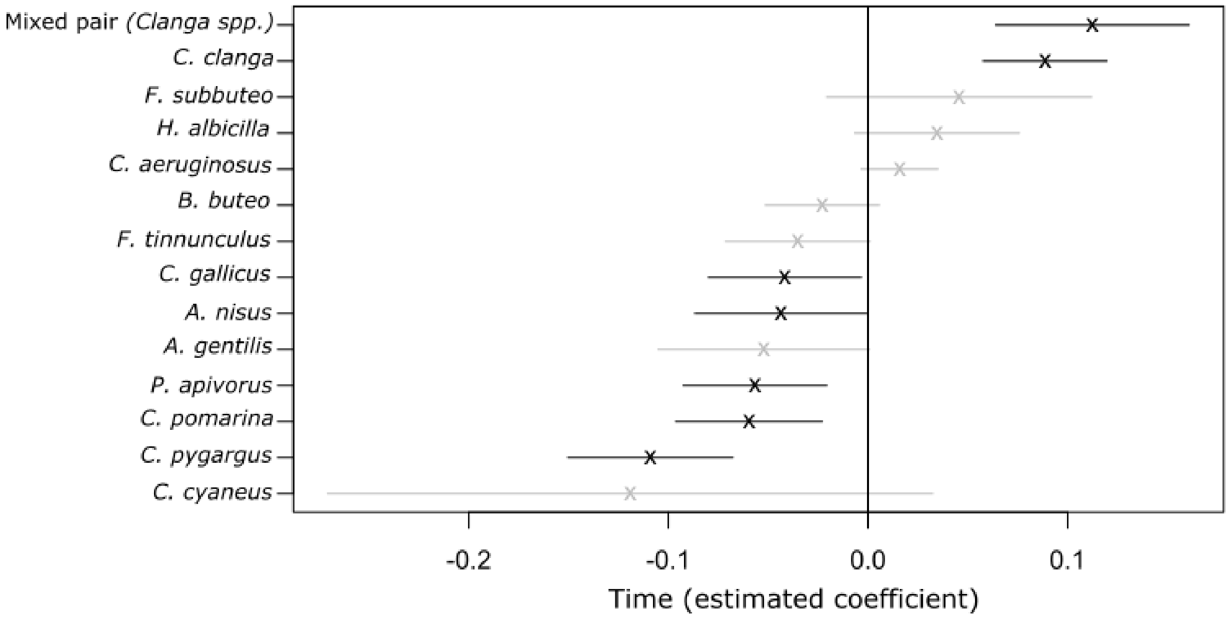

Figure 3. Coefficient plot from the gllvm, with change in raptor breeding pair abundance over the study period with time as an explanatory variable. The unit of change covariate equates to a multiplacative change of the species specific predicted mean. Error bars are 95% CIs. Plots in bold are those where the CIs do not cross zero.

Figure 4. Photos of wetland (a) and open field (b) habitats in the CEZ study plot. Evidence of White-tailed Eagle feeding on an Elk carcus killed by wolves (c) and a Greater Spotted Eagle chick in the nest (d) from the study plot.

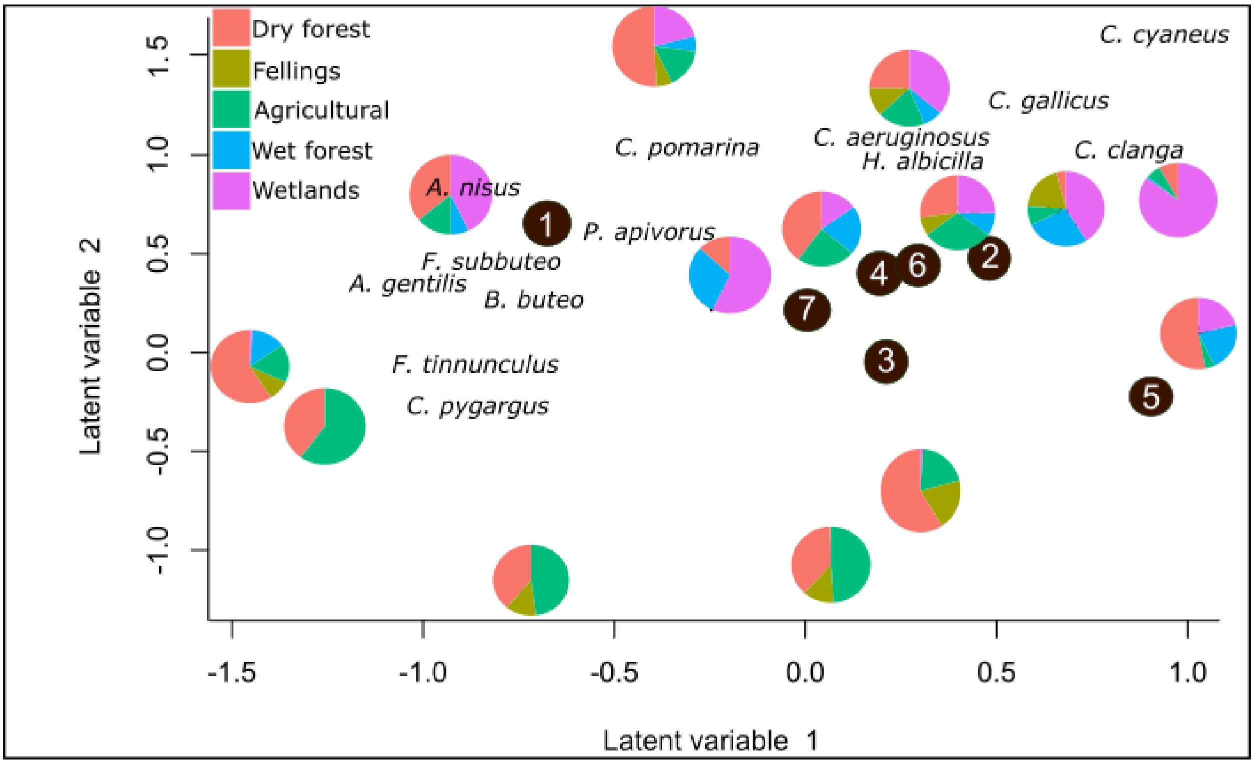

Figure 5. Ordination plot of the latent variables of sites, showing raptor composition from each sampling year from 1998-2019 (shown by the black circles: 1=1998, 7=2019) compared to other raptor monitoring sites in Belarus, represented as pie charts with segments representing percentage habitat composition. Species specific latent variables are also spotted so site association with specific species can be compared.

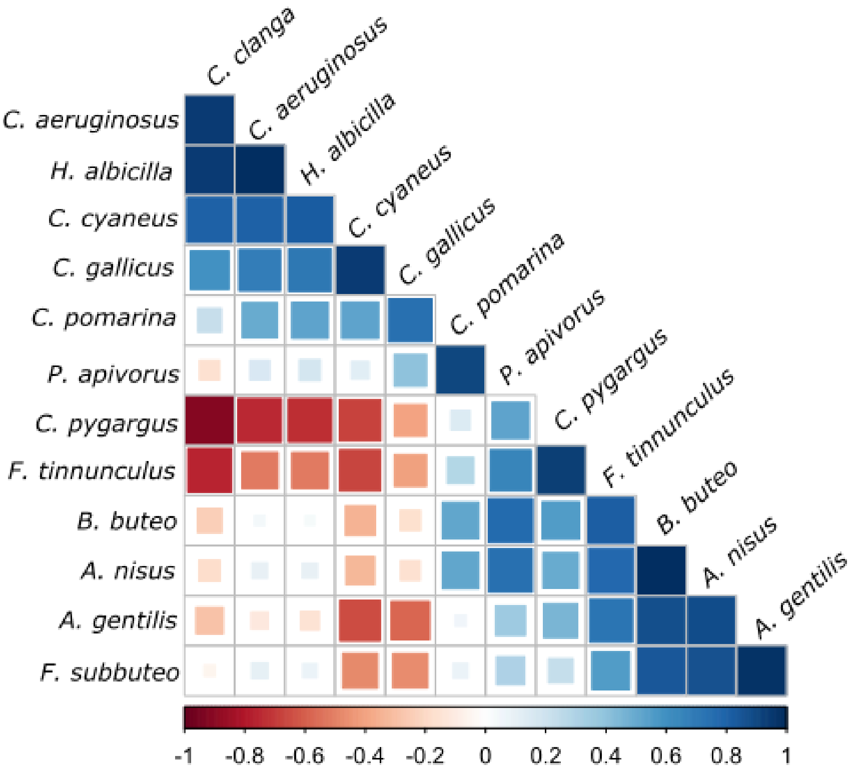

Figure 6. Correlation plot of raptor species in the CEZ study plot across all years and raptor survey sites across Belarus. Red squares signify the intensity of a negative correlation and blue squares positive.