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Biological Conservation 150 (2012) 33-41



Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Pollution impacts on bird population density and species diversity at four non-ferrous smelter sites

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ARTICLE INFO

Article history: Received 12 December 2011 Received in revised form 10 February 2012 Accepted 5 March 2012

Keywords:
Air pollution
Forest birds
Heavy metals
Population density
Species diversity

ABSTRACT

Non-ferrous smelters pose a potential hazard for breeding bird populations, but comprehensive analyses of the impacts on bird population densities around smelter sites are currently lacking. We measured with point counts bird population densities around four smelter sites in Russia (Monchegorsk, Karabash and Revda) and Finland (Harjavalta) to explore the relationships between bird population density/species diversity and exposure level quantified by the potentially bioavailable copper concentrations in forest litter. Total bird densities, bird biomasses and species diversities decreased in the vicinity of all three Russian smelters. In Harjavalta, there were no pollution-related trends in total bird density or biomass, although species diversity (species number and Shannon's index) decreased towards the pollution source. In general, the four smelters showed negative effects on bird populations in decreasing order of impact as follows: Monchegorsk > Karabash > Revda > Harjavalta, reflecting the amount of current and past emissions and consequent habitat change at each site. Our results suggest that around copper-nickel and copper smelters the pollution impact on bird diversity is accelerated when the litter copper level exceeds 1000 μg/g. However, even though bird densities and diversities reflected the exposure levels in our study, they were not associated with litter copper concentrations in a strictly dose-dependent manner, indicating that copper itself is not a primary cause for the changes in bird communities, but rather the combined effect of multiple pollutants on birds and especially on the resources necessary for breeding, such as food and suitable habitat.

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1. Introduction

Point sources of metals, such as non-ferrous smelters, pose a wide-ranged hazard for local breeding bird populations. Several studies have demonstrated detrimental effects on breeding performance of birds inhabiting smelter sites (Belskii et al., 1995; Eeva and Lehikoinen, 1996; Janssens et al., 2003; Nyholm, 1994). High emission levels may also negatively affect the local survival of breeding birds (Eeva et al., 2009b). At some level, the metal emissions are therefore likely to have detrimental effect also on population numbers. Gilyazov (1993) found that the density of typical forest birds was decreased by 80% at a heavily polluted area around a Russian copper-nickel smelter complex at Monchegorsk in the beginning of 1990s. Belskii and Lyakhov (2003) documented a decrease of c.a. 40% in total bird densities around a Russian copper smelter at Revda. On the other hand, Eeva et al. (2002) showed that population densities of only six out of 37 forest bird species responded negatively to the environmental pollution at a moderately polluted area around a copper–nickel smelter complex in Harjavalta, Finland. All the studies, however, suggest that responses are species-specific and in great deal due to secondary effects of pollution-related habitat changes. Despite multiple analyses of the effects of metal emissions on surrounding biota (Kozlov et al., 2009), comprehensive analyses on the relationships between emission levels and bird population densities are still lacking. However, owing to a large number of smelter and mining sites around the world, such studies would be well justified. For example, there are currently 99 operating copper smelters in the world, 34 of which in Europe (http://mrdata.usgs.gov/mineral-resources/copper-smelters.html). Still it is not well known how population densities and species diversity of birds are connected to ambient exposure levels and which species-specific traits are important in determining the susceptibility to pollution.

By using a standard sampling procedure we measured bird population densities around three Russian non-ferrous smelters (Karabash, Revda and Monchegorsk) to explore the relationships between bird population densities/species diversity and exposure levels. For each site we simultaneously measured the potentially bioavailable concentrations of metals in forest litter to make a di-

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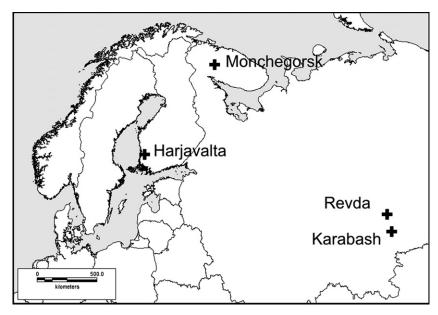


Fig. 1. A map showing the locations of four smelter sites where bird population densities were measured.

rect link between population density/diversity and local exposure level. The three data sets from the Russian smelter sites are here analyzed together with one collected earlier around a Finnish copper-nickel smelter (Harjavalta) by using the same methods (Eeva et al., 2002). Although having a similar type of emission source, the four smelter sites differ from each other by their pollution history, composition and amount of emissions, habitats and species composition. This allows testing how general the impacts of smelters on bird populations are. The aims of the current study are: (1) to assess how long-term pollution has affected the density, species diversity and biomass (s.l. productivity) of breeding bird populations at smelter sites, (2) to get information on which and what kind of species are sensitive to the pollution around smelters, (3) to evaluate how well the bird density and diversity reflect the local exposure levels (litter copper concentrations) across different smelter sites. Furthermore we explore the effects of some possibly confounding habitat characteristics on bird density and diversity. The last point is complicated by the fact that long-term pollution has also changed habitats (vegetation) around the point-sources (Kozlov et al., 2009). However, here we are not aiming to make a strict separation between direct toxic effects and more indirect effects (e.g. habitat and food), but just to take account of most obvious habitat variables associated with total bird densities and species diversities in addition to the pollution levels.

2. Methods

2.1. Study areas

The data was collected at four boreal non-ferrous smelter areas (Fig. 1), Harjavalta (Southern Finland, 61°20'N, 22°10'E), Karabash (Southern Urals, Russia, 55°27'N, 60°13'E), Monchegorsk (Kola Peninsula, Russia, 67°56'N, 32°49'E) and Revda (Middle Urals, Russia, 56°51'N, 59°53'E). The four smelter sites clearly differ from each other as regards to characteristics of the surrounding forests and emissions (summarized in Table 1). For example, the aerial dust emissions varied from 50 t/a (Harjavalta) to 13800 t/a (Karabash) among the smelters in the beginning of 2000s. Consistently, the area of industrial barrens (i.e. bleak open landscapes evolved due to deposition of airborne pollutants, with only small patches of vegetation surrounded by bare land) varied from less than 50 ha

at Harjavalta to 21000 ha around Monchegorsk (Table 1; Kozlov and Zvereva, 2007). The peak metal concentrations in topsoil of most contaminated sites at all four smelter sites exceed 10000 µg/g (Kozlov and Zvereva, 2007), i.e., being even higher than the metal content in ores. The history of industrial development, amounts of emissions of principal pollutants, extent of the contaminated territory and brief outline of environmental research conducted at these smelter sites are reviewed in Kozlov et al. (2009). Some cavity-nesting insectivorous birds breeding in the vicinity of the smelters have been found to suffer from lowered breeding success and reduced survival, both due to direct toxic effects of pollution and due to indirect effects of altered habitats and disrupted food webs (Belskii et al., 2005; Eeva et al., 2005, 2009b; Gilyazov, 1993).

2.2. Point counts

Relative bird densities were estimated by point counts, using the method of Koskimies and Väisänen (1991) for counting breeding land birds. The data from Harjavalta was collected in 2001 (see Eeva et al., 2002), while the other areas were sampled in 2009 (Karabash and Monchegorsk) and 2010 (Revda). In each study area we selected 10-14 sites representing different stages of pollution-induced deterioration of the forest habitat typical of the region (see Table 1). The care was taken to include both the unpolluted sites and the sites that have experienced the highest level of the pollution load, and to select sites so that they uniformly cover the entire range of pollution levels. More details on the methodology of site selection are given in Vorobeichik and Kozlov (2012). At each site we selected 2-4 sampling plots (coordinates and distances from the polluter are given in Appendix A), the distance between the plots being always more than 250 m to avoid counting the same birds twice (see Koskimies and Väisänen, 1991). In reporting the results we follow the nomenclature of the AERC Western Palearctic list (Crochet et al., 2010).

The censuses were carried out between 4:00 and 9:00 a.m., avoiding windy and rainy days (no rain or mist, temperature >6 °C, wind <5 m/s). Each plot was censused for 5 min. For each species, the numbers of observed individuals or active nests were recorded. Observations were interpreted as breeding pairs by following the rules of Koskimies and Väisänen (1991). Shortly, breed-

Table 1Upper part: the major habitat characteristics, pollution history and type of emissions for the four smelters where birds were censused for this study. Lower part: information on point counts.

·	Harjavalta	Karabash	Monchegorsk	Revda
Primary habitat	Pine forest with mixed spruce and birch	Birch forest with mixed pine	Spruce forest with mixed birch and pine	Fir and spruce forest with mixed birch and pine
Smelter type	Copper-nickel	Copper	Copper-nickel	Copper
Pollution started	1944	1910	1938	1940
Major heavy metals emitted (in decreasing order)	Cu, Zn, As, Ni	Zn, Pb, Cu, As	Ni, Cu, Co, As	Cu, Pb, Zn, As
Dust emissions (t/a) ^a	50	13800	9100	7300
Copper emissions (t/a) ^a	7.4	340 ^b	827	207
Lead emissions (t/a) ^a	0.7	92	No data	302
SO ₂ emissions (t/a) ^a	3002	71900	43900	52800
Barren area (ha) ^c	<50	<1000	21000	<300
N of study sites	14	10	10	10
N of counting points	28	40	40	40
N of point counts	112	160	160	160
Census period	21st May-21st June	20th May-12th June	8th-26th June	16th May-9th June
Census year	2001	2009	2009	2010
Observer	J. Sjöholm	E. Belskii	A. Gilyazov	E. Belskii

^a Aerial emissions from the industrial enterprises of the area in 2001. Source: Kozlov et al. (2009).

ing pair equals to: seen or heard male, male-female pair, single female, brood or active nest. Each plot was counted once a week, four times per season. Temporal replicates were taken to reduce the bias caused by changing singing activities during the course of spring. For each species and counting plot, the maximum density among four successive counts was used as a dependent variable in analyses. Numbers of study sites, counting plots and censuses, together with counting periods and observers are shown for each area in Table 1.

2.3. Bird density, diversity and biomass

Bird densities were calculated from the point count data using the formula of Järvinen (1978): D (pairs/km²) = $3Nc^2/\pi$, where N = number of pairs per counting plot and c = species-specific constant that corrects for the differences in detectability (value *k* from column C in Järvinen and Väisänen, 1983). For the two species (Cuculus saturatus and Zoothera dauma) not included in the list of Järvinen and Väisänen (1983), we used the constants of two similar species, Cuculus canorus and Turdus philomelos, respectively. However, it should be noted that despite applying the detectability constants our bird density estimates should be considered as relative ones, not absolute densities (see Järvinen and Väisänen, 1983). Species-specific density estimates were not calculated for those species we had fewer than 15 observations. These species are, however, included in the calculations of total bird density, biomass and species diversity. A full list of species and the numbers of observations for each counting point are given in Appendix A.

Besides the species number we used Shannon diversity index as a measure of bird diversity. Shannon indices ($H = -\Sigma [p_i \times \ln p_i]$, where p_i = the proportion of ith species of the total density) were calculated from the detectability corrected density estimates, not from the original counts. For plots with no birds H was set to 0. Since the sampling effort per plot was strictly standardized in our study and birds were clearly not randomly distributed over the study areas, the rarefaction method was not applied in a comparison of species diversities (see Gotelli and Colwell, 2001).

Bird densities were further transformed to total bird biomass (kg/km²) by multiplying plotwise species-specific density estimates by species-specific body mass. Since the density estimates denote bird pairs, the values were further multiplied by number 2. Bird body mass data were gathered from Vinogradova et al. (1976) and Cramp and Perrins (1993).

2.4. Heavy metal levels and habitat variables

Five pooled samples of forest litter were taken at each site (each of them composed of five individual samples) to measure concentrations of primary metal pollutants. Samples were crushed to pieces no more than 2 mm and metals were extracted with 5% HNO₃ for 24 h (the litter to acid ratio was 1:10 by weight). This method was preferred because it gives an estimate of the potentially bioavailable concentrations, rather than total concentrations which are of lower ecotoxicological importance. Metal concentrations were measured with an AAS 6 Vario atomic absorption spectrometer (Analytik Jena, Germany) at the Institute of Plant and Animal Ecology (Yekaterinburg, Russia) which belongs to an inter-calibration network. As a control sample for the heavy metal analyses we used a standard soil sample (OK E.TEP-5) worked out in order to provide inter-laboratory comparative tests by the Ural Scientific Research Institute for Metrology (UNIIM) and produced by the Urals plant for chemical reagents. Standard solutions were prepared from liquid standards (SS 7836-2000) produced by the Urals plant for chemical reagents. Complete results of these analyses will be published elsewhere. Here we have chosen to use the litter copper concentration (µg/g, d.w.) as a measure of the exposure level because copper was the only major metal pollutant common for all polluters (Table 1). Earlier studies have demonstrated that copper correlates well with other smelter emissions, including sulfur dioxide, within all four impact zones studied by us (data summarized by Kozlov et al., 2009). We use the litter copper concentration (µg/g, d.w.) as a measure of the exposure level in the statistical analyses.

Some basic habitat characteristics were further measured at each counting plot. These include a relative tree species composition (%) and field layer vegetation coverage (%) within a census plot. In Harjavalta, the latter was measured in 2009 and only for 9 sites. For the analyses, the tree species were combined into four groups: (1) birch (including Betula sp.), (2) spruce/fir (including Picea sp. and Abies sp.), (3) pine (including Pinus sylvestris) and (4) others (including various deciduous trees: Populus sp., Salix sp., Sorbus sp., Tilia sp., Larix sp., Alnus sp. and Prunus sp.). We also measured the basal area (BA (m^2/ha); with a relascope at 1.3 m height) and average height (H (m)) of tree trunks in the sampling plots. These were used to calculate a rough estimate of timber volume (V (m^3/ha)) for each plot, by using the Smalian's equation: $V = (BA \times H)/2$ (Avery and Burkhart, 1994).

b Data from year 2003. Source: Kozlov et al. (2009).

c Kozlov and Zvereva (2007).

2.5. Statistics

The statistical analyses were performed with a statistical software SAS 9.2 (SAS, 2008). We analyzed variation in the bird density and diversity data in two ways: relative to the distance to the pollution source and relative to the actual pollution levels (litter copper concentrations) together with the habitat variables. Analyzing the associations with distance in addition to metal concentrations is reasonable for assessing whether the changes in bird communities are indeed spatially associated with the point sources of pollutants, but especially because litter metal levels in a particular year do not necessarily reflect a cumulative long-term effect of multiple pollutants on environment and biota. Spearman correlations between distance and density for individual species are shown in an electronic Appendix B. Univariate tests for among-site variation are further presented for each area in the Appendix C.

We first explored, separately for each area, the associations of bird densities, diversities and biomasses with logarithmic distance (log₁₀ km) to the pollution source by GLMM models where study site was used as a random factor to control for the non-independence of individual counting plots within each site. Logarithmic distance was used because aerial heavy metal emissions from point sources, as well as their impacts on biota, typically follow logarithmic spatial distribution. The fit of the models to data was checked each time from the χ^2/df value, and normality of model residuals was checked with Shapiro-Wilk tests. Biomass was log₁₀-transformed prior the analysis to normalize distributions. For the two non-normally distributed variables (bird density and species number) we used negative binomial error

Because the proportions of four tree species groups are intercorrelated and do not vary independently, we used compositional principal component analysis (PCA) to calculate uncorrelated principal components (PCs) from the tree species data. Before the PCA, a central log-ratio transformation ($x = ln[x/\overline{x}_g]$; $\overline{x}_g = geometric$ mean of a proportion) was made for the proportions to allow a multivariate analysis on compositions (see Aitchison 1986). The first (PC1, eigenvalue = 1.25) and second (PC2, eigenvalue = 1.12) principal components explained together 59% of the variation in the data. PC1 can be interpreted to indicate variation along a coniferous - deciduous axis and PC2 along a barren - luxuriant axis. These two principal components were used as independent variables in subsequent models.

The relationships of bird densities, diversities and biomasses with litter copper concentrations and habitat characteristics were analyzed from the combined data of all areas with GLMMs using site as a random factor in the models. The independent variables in the models were: area, litter copper concentration ($log_{10} \mu g/g$), area \times litter copper, timber volume (\log_{10} m³/ha), field layer vegetation coverage (%) and 1st and 2nd principal components calculated from tree species composition data (see above). Distance to the pollution source was not included in these models because it was rather strongly correlated with the litter copper concentrations. The habitat variables did not show strong correlations to each other (in all cases $r_s < 0.35$) and were included in the same model. Non-significant terms (with $\alpha = 0.1$) were dropped from the models one-by-one, starting from interactions. Dropped terms were then introduced back to the reduced model and kept if significant. Degrees of freedom were calculated with Kenward-Roger method. In the case of significant interaction with copper concentration and area separate GLMMs were further ran for each

Spatial autocorrelation was further tested for the residuals of all full non-spatial models with Moran's I coefficient (Dormann, 2007), but in no case was the correlation significant and non-spatial covariance structure was used in all models.

Table 2 Generalized linear mixed models (GLMMs) for the relationships between logarithmic (log₁₀) distance to the smelter with bird densities (pairs/km²), bird biomass (log₁₀ kg/ km²), species numbers, and Shannon diversities of the breeding bird communities at four smelter areas (n = number of counted plots).

Area	n	Solution	$F_{ m df}$	р
Harjavalta (14 sites)			
Total density ^a	28	y = -0.097x + 6.825	$0.90_{1,26.0}$	0.35
Log biomass ^b	28	y = 0.012x + 1.666	$0.02_{1,12.1}$	0.88
N of species ^a	28	y = 0.224x + 2.836	$4.80_{1,13.1}$	0.047
Shannon index ^b	28	y = 0.278x + 2.397	$6.55_{1,12.2}$	0.025
Karabash (10 sites)				
Total density ^a	40	y = 1.119x + 4.948	$12.0_{1,8.5}$	0.0078
Log biomass ^b	40	y = 0.558x + 0.756	14.7 _{1,8.1}	0.0049
N of species ^a	40	y = 1.119x + 1.142	14.3 _{1,8.7}	0.0047
Shannon index ^b	40	y = 1.434x + 0.353	$23.0_{1,8.2}$	0.0013
Monchegorsk (10 sit	tes)			
Total density ^a	40	y = 2.528x + 1.394	$7.49_{1,7.8}$	0.026
Log biomass ^b	40	y = 0.638x + 0.145	$12.7_{1,8.0}$	0.0074
N of species ^a	40	y = 1.575x - 0.352	21.6 _{1,4.8}	0.0063
Shannon index ^b	40	y = 1.531x - 0.661	29.7 _{1,8.1}	0.0006
Revda (10 sites)				
Total density ^a	40	y = 0.514x + 5.993	21.3 _{1,8.1}	0.0017
Log biomass ^b	40	y = 0.245x + 1.154	19.8 _{1,8.1}	0.0020
N of species ^a	40	y = 0.271x + 2.404	$10.6_{1,7.8}$	0.012
Shannon index ^b	40	y = 0.308x + 2.025	20.4 _{1,8.1}	0.0019

^a GLMM with log link function and negative binomial error distribution. Study site was used as a random factor.

b GLMM with identity link function and normal error distribution. Study site was

3. Results

3.1. Total densities and biomass

The total bird densities decreased towards the pollution source in all areas, except in Harjavalta where the bird densities did not significantly vary among sites (Appendix C), and rather showed a tendency of being slightly higher near the pollution source (Table 2; Fig. 2a). The bird densities in the vicinity of the pollution source were 8% in Monchegorsk, 21% in Karabash, 49% in Revda and 110% in Harjavalta of those found in the most distant sites of each area (calculated from the equations in Table 2). The two Uralian sites, Revda and Karabash, showed relatively similar responses, the total densities being strongly decreased in the vicinity of the smelters, and approaching levels of the unpolluted area from 4 km (Revda) to 9 km (Karabash) from the smelters (Fig. 2a). In Monchegorsk, the densities are depressed over a much larger area, until c.a. 20 km from the smelter. The most northern area, Monchegorsk, showed expectedly much lower overall bird densities than the other areas. Correspondingly, the bird biomass decreased significantly towards the three Russian smelters, but not the Harjavalta smelter (Table 2; Fig. 2b). The bird biomass in the vicinity of the pollution source was 17% in Karabash, 22% in Monchegorsk, 46% in Revda and 97% in Harjavalta of those found in the most distant sites of each area (calculated from the equations in Table 2).

3.2. Species diversity

The number of bird species observed per counting plot decreased towards all the smelter sites, but the proportional reduction varied among areas (Table 2; Fig. 2c). The species numbers in the vicinity of the pollution source were 20% in Monchegorsk, 21% in Karabash, 69% in Revda and 80% in Harjavalta of those found in the most distant sites (calculated from the equations in Table 2). In Monchegorsk, a strong negative impact extended up to 11-20 km from the smelter (Fig. 2c). At all four smelters also the Shan-

used as a random factor.

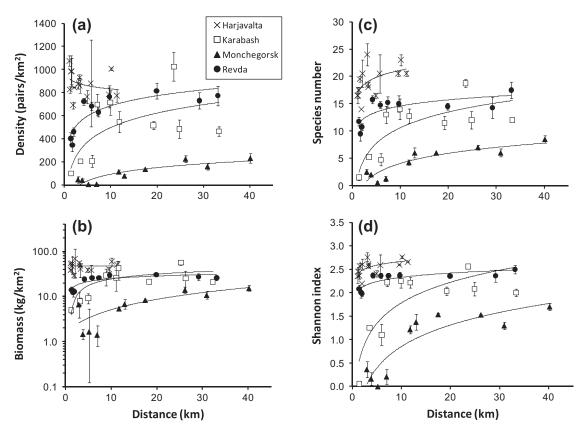


Fig. 2. Mean (±SE) total bird densities (a), total bird biomass (b), species numbers (c), and Shannon diversities (d) in pollution gradients of four smelters, with logarithmic regression lines. Site estimates are based on standardized point counts where bird numbers were counted for 5 min at each plot (Harjavalta: 2 plots/site, others: 4 plots/site). Each point was counted four times per season and the maximum value for each species was used to calculate density estimates.

non diversity index was lower near the pollution source than in most distant sites (Table 2; Fig. 2d).

3.3. Associations with metal levels and habitat variables

Bird density, biomass and diversity were generally negatively associated with forest litter copper concentrations but the strength of the association varied among the smelter areas (Table 3). Bird densities decreased with increasing litter copper load in Monchegorsk, Karabash and Revda (Table 3, Fig. 3a), while in Harjavalta there was no significant association between bird density and copper load (GLMM: $F_{1,16.0} = 1.09$, p = 0.31; Fig 3a). Total bird densities were positively associated with field vegetation coverage, timber volume, and PC2 of tree composition (Table 3). A positive relationship between PC2 and density suggests that luxuriant forests support higher bird densities than barren ones (primarily pine forests). The total bird biomass showed much the same pattern as density, except that it was not significantly related to field layer coverage (Table 3, Fig. 3b).

Species number decreased with increasing pollution load in all the Russian areas, but the reduction of species along with increasing copper levels was stronger in Karabash and Monchegorsk as compared to Revda (Table 3, Fig 3c). In Harjavalta this relationship was negative too, but only marginally significant (GLMM: $F_{1,9,1} = 4.13$, p = 0.073; Fig 3c). Species number was further positively associated with timber volume, PC1 of tree composition and field vegetation coverage, the latter effect not being statistically significant (Table 3). A positive relationship with species number and PC1 suggests that deciduous forests support higher bird densities than coniferous ones.

Shannon index showed relatively similar trends as the species number, values decreasing strongly with increasing copper load in Monchegorsk and Karabasch, and more gently in Revda and Harjavalta, the relationship being only marginally significant in the last area (GLMM: $F_{1,7.0}$ = 4.99, p = 0.061; Fig 3d). At the Russian sites, reduction in species diversity seems to be accelerated when litter copper concentrations exceed 1000 μ g/g (Fig. 3d). Notably, equally high copper loads in Revda and Karabash seem to lead to stronger reduction in diversity in Karabash. Shannon index was further positively associated with field vegetation coverage and timber volume, but not with tree species composition (Table 3).

As a post hoc test we further explored whether the variation in productivity (bird biomass) would explain the variation in species diversity (Shannon index). This was done by adding biomass to the final model derived for the Shannon index (shown in Table 2) as a further explanatory factor. Shannon diversity was strongly positively related to bird biomass (GLMM: $F_{1,111.1} = 49.8$, p < 0.0001; Fig. 4), but even after including biomass in the model the other explanatory factors remained significant: litter copper level (GLMM: $F_{1,55.0} = 14.2$, p = 0.0004), interaction between area and litter copper level (GLMM: $F_{3,39.0} = 4.19$, p = 0.011), field layer vegetation coverage (GLMM: $F_{1,127.0} = 5.63$, p = 0.019) and timber volume (GLMM: $F_{1,103.8} = 6.36$, p = 0.013).

3.4. Species-specific responses

Of the species for which we could calculate the density estimates, 67% in Monchegorsk, 53% in Karabash and 48% in Revda showed smaller densities in the heavily polluted zone as compared to the unpolluted zone (Appendix B). One species, *Anthus trivialis*, showed significantly higher density in the heavily polluted area of Revda, but decreased density in the heavily polluted area of Karabash. In Harjavalta, 20% of the species showed a decreasing trend while 9% of the species significantly increased in numbers towards

Table 3The associations of pollution level (bioavailable litter copper concentration) and habitat characteristics (field layer vegetation coverage, timber volume, and 1st and 2nd principal components of relative tree species composition) with total bird density, total bird biomass, species number and Shannon's diversity index. Non-significant (at α = 0.1) terms were dropped from the generalized linear mixed models (GLMMs) one-by-one. Final models are shown in bold. N = 138 plots.

Source of variation	Density ^a (pairs/km ²)		Biomass ^b (log ₁₀ kg/km ²)		Species number ^a (species/plot)		Shannon index ^b	
	$F_{ m df}$	р	$F_{ m df}$	p	$F_{ m df}$	р	$F_{ m df}$	р
Area	2.493127.0	0.063	3.13 _{3,40.6}	0.036	2.26 _{3,25.4}	0.11	1.213,39.0	0.32
Litter copper (log ₁₀ μg/g d.w.)	12.5 _{1127.0}	0.0006	24.0 _{1,42.8}	<0.0001	23.4 _{1,39.2}	<0.0001	20.8 _{1,54.0}	<0.0001
Area × litter copper	9.933127.0	<0.0001	6.663,39.4	0.0010	6.363,30.6	0.0018	5.573,40.0	0.0027
Field coverage (%)	$9.56_{1127.0}$	0.0024	$1.76_{1,87.2}$	0.19	2.941,34.5	0.096	8.18 _{1127.4}	0.0050
Timber volume (log ₁₀ m ³ /ha)	16.3 _{1127.0}	<0.0001	3.52 _{1,47.0}	0.067	12.6 _{1,49.8}	0.0009	$6.10_{1106.8}$	0.015
Tree species composition, PC1 (coniferous vs. deciduous)	$0.21_{1126.0}$	0.65	$0.72_{1114.7}$	0.40	4.561,98.8	0.035	$0.04_{1120.2}$	0.84
Tree species composition, PC2 (barren vs. luxuriant)	$8.49_{1127.0}$	0.0042	7.09 _{1,86.1}	0.0093	$0.85_{1,54.1}$	0.36	$0.06_{1126.0}$	0.81

^a GLMM with log link function and negative binomial error distribution. Study site was used as a random factor.

the smelter. The three hole-breeding species (*Parus major*, *P. caeruleus*, *Phoenicurus phoenicurus*) increasing in numbers towards the Harjavalta smelter are all partly human associated birds, the numbers indicating the higher degree of human inhabitation in the vicinity of the smelter in this area. Similar, though not statistically significant, trends were observed in some other human-associated species like *Passer domesticus*, *Turdus pilaris*, *Corvus monedula*, and *Pica pica*.

The species decreased in the polluted areas are ecologically rather diverse, including both migratory and sedentary, and on the other hand, insectivorous and granivorous species. Notably, 50% of the negatively affected species represent ones typical to relatively luxurious spruce/fir dominated forests. Such are e.g. *Turdus philomelos, T. merula, Erithacus rubecula, Regulus regulus, Phylloscopus trochiloides, Certhia familiaris, Ficedula parva* and *Pyrrhula pyrrhula*. In some cases the effect on individual species varied among the study areas. For example *E. rubecula* showed strongly reduced densities at Harjavalta and Karabash, but not at Revda, which might be associated with relatively better field layer vegetation coverage in the polluted sites of Revda, likely favoring this ground-feeding bird.

4. Discussion

The four smelters showed negative effects on total bird densities, bird biomasses and species diversities in a decreasing order of impact as follows: Monchegorsk > Karabash > Revda > Harjavalta, thus following the order based on the emission levels and extent of industrial barrens around these polluters (Table 1). In Monchegorsk the negative effect clearly extends farther (up to 20 km) from the smelter than in other sites. The SO₂ and metal emissions have been very high in this area, the former approaching or exceeding 300000 t/a in the 1970s (Kozlov et al., 2009). Heavy pollution exposure has created an industrial barren around the smelter, surrounded by a zone of dead or dying forest up to c.a. 10 km distance (Kozlov et al., 2009). Furthermore, the Norwegian spruce, one of the dominant coniferous trees in the area, is relatively sensitive to air pollution (Sazonova and Olchev, 2010), further extending the habitat change relatively far from the smelter. Bird densities were studied around Monchegorsk smelter also in 1977–90 (Gilyazov, 1993). At that time total bird density of the most polluted area was 13% and species number 34% of that in the remote control area. The figures were still lower in the current study (8% and 20%, respectively), indicating that despite the considerable reduction in emissions from 1980s to 2000s the bird populations have not yet recovered in this area. The lack of recovery may be explained by the continuing decline of forests around Monchegorsk due to very slow process of leaching of toxic metals from the contaminated soils (Zverev, 2009). Even if the forest would start to recover, there would be a long time lag for many resources that are essential for birds, such as tree holes for cavity-breeding species (Vesk et al., 2008). The list of decreased species in the earlier study resembles that of the current one, consisting primarily of species typical of coniferous northern taiga forests, such as *P. phoenicurus*, *T. iliacus*, *T. philomelos* and *P. trochilus*.

Bird densities and diversities were strongly reduced also in the most polluted zones around Karabash and Revda smelters, the negative impact being stronger and extending farther around the Karabash smelter. Dust and SO₂ emissions from the two smelters have been at similar levels in 1980s but metal emissions have been markedly higher in Karabash (Kozlov et al., 2009). In 1990s and 2000s, however, the metal emissions have been higher in Revda, typically showing relatively high proportion of lead (litter concentrations shown in: Smorkalov and Vorobeichik, 2011). The impact of pollution could be expected to be stronger in Revda due to more pollution-sensitive spruce/fir forest of the area, as compared to pine and birch dominated forests of Karabash. However, the negative effect on bird density and diversity extended farther and was much stronger in Karabash, likely due to higher metal and SO₂ emissions in the past, which have caused severe habitat changes such as heavy destruction of field layer vegetation near the smelter (Kozlov et al., 2009). Bird censuses have been made in Revda area also in 1991–2001 (Belskii and Lyakhov, 2003). During that period the bird density in the coniferous forests of the most polluted area was 54% of those in the unpolluted area, the figure being similar to the one (49%) in the current study. Correspondingly, the species number of the most polluted area was 78% of that in the unpolluted area in the earlier study (Belskii and Lyakhov, 2003), and 69% in the current study. The list of decreased species was again similar between the earlier and the current study, both including e.g. P. trochiloides, R. regulus, F. parva, F. hypoleuca, P. pyrrhula, T. iliacus, T. philomelos and Z. dauma. The only species that showed significantly higher densities in the polluted area of Revda in our study, A. trivialis, was more abundant in the polluted area also in the previous study in Revda (Belskii and Lyakhov, 2003) as well as in a study of Flousek (1989) from a heavily acidified forest area. There are no earlier studies on bird densities in Karabash, but population densities of small mammals were found to be strongly reduced within 10 km distance from the smelter (Mukhacheva et al., 2010).

Although individual species showed negative or positive density gradients in Harjavalta, there was no significant spatial trend in total bird density. This is likely due to relatively smaller emissions as compared to the Russian smelters but also due to the fact that Harjavalta smelter is located at an immediate vicinity of the town centre. Many bird species show positive spatial correlation with human settlements (Pautasso and Dinetti, 2009). Although forest floor vegetation is scanty in the most heavily polluted sites of Harjavalta, nearby gardens offer several bird species more luxu-

^b GLMM with identity link function and normal error distribution. Study site was used as a random factor.

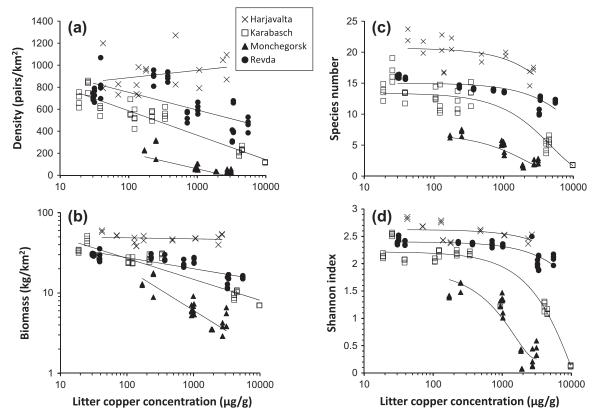


Fig. 3. The relationships between total bird densities (a), total bird biomass (b), species numbers (c), and Shannon diversities (d) with litter bioavailable copper concentrations in pollution gradients of four non-ferrous smelters, with logarithmic (a and b) or exponential (c and d) regression lines. The values are estimates from the models presented in Table 3 (*N* = 138 plots).

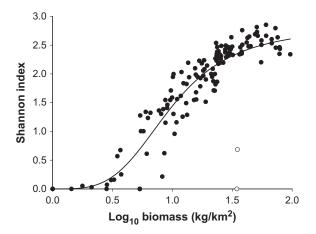


Fig. 4. The relationship between total bird biomass and Shannon diversity, with a logistic sigmoidal regression line. Two deviating points indicated with open circles are the ones from the Monchegorsk area where only a herring gull (*Larus argentatus*) with no or only one other species was observed.

rious patches of vegetation due to human activity, such as soil liming. In Harjavalta, the species showing decreased numbers near the smelter were mainly those associated with spruce forests. Spruce is less abundant in the polluted area of Harjavalta due to natural soil quality (primarily sandy soils), but also due to its relatively high sensitivity to air pollution (Sazonova and Olchev, 2010; Slovik, 1996; Vike, 1999). Reported dust emissions from Harjavalta smelter have been less than 5% of those from the Russian smelters during the 2000s. Relatively smaller emissions together with human-related mosaic habitat structure near the pollution source likely

explain the lack of effect on total bird densities in this area. Species number and bird diversity, however, were slightly decreased in the vicinity of this smelter too.

Decreased population densities of breeding birds in polluted sites may be an outcome of inferior reproductive success, increased mortality or lack of suitable resources (food and/or habitat) for breeding. Decreased breeding success has been documented for several hole-breeding insectivorous birds around the three smelters included in our study: Monchegorsk (Gilyazov, 1993), Revda (Belskii et al., 2005) and Harjavalta (Eeva et al., 2009a; Eeva and Lehikoinen, 1996). In Harjavalta, one key element explaining poor breeding success in the metal polluted area is the lack of suitable invertebrate food for birds, and especially scarcity of calcium-rich food items necessary for the needs of breeding females (Eeva and Lehikoinen, 2004). Small passerines need extra calcium during their breeding and the lack of calcium-rich food, such as snails, has resulted in inferior breeding success in acidified or metal polluted areas (Bureš and Weidinger, 2000; Eeva and Lehikoinen, 2004; Graveland and Drent, 1997). Poor snail availability may limit bird reproduction and bird densities also in forests with naturally low snail abundance (Rosenvald et al., 2011; Tilgar et al., 2002; Wilkin et al., 2009). However, despite markedly decreased breeding success, the population density of some common forest passerines, such as P. major, P. caeruleus and F. hypoleuca, were not decreased around Harjavalta smelter, most likely due to the most heavily polluted area being relatively small as regards to efficient dispersal capacity of birds (see Eeva et al., 2008). A reduced reproductive output can thus be compensated for by immigration. In the case of Harjavalta, the human settlement where birds are fed during winter also makes the polluted area relatively attractive for some wintering birds, such as tits.

Our results suggest that around copper-nickel and copper smelters the pollution impact on bird diversity is accelerated when the forest litter copper level exceeds 1000 $\mu g/g$. On average, this level of pollution was associated with c.a. 40% decrease in ground layer vegetation and 84% reduction in timber volumes. In a study of Salemaa et al. (2001) the ground layer vegetation was considered to be moderately damaged at the soil copper levels of $1500-2500 \mu g/g$ and heavily damaged at the concentrations above 3000 µg/g. Heavily damaged ground layer vegetation was typical especially around Karabash and Monchegorsk smelters, both showing strong impacts on bird populations. Scanty field layer vegetation and decreasing timber volume/forests cover reduce shelter for birds and also likely have negative effects on their food resources (Eeva et al., 2005). Pollution exposure around smelters generally increases openness and patchiness of forest habitats (Belskii and Lyakhov, 2003). A study of Zuckerberg and Porter (2010) suggests that probability of existence of forest birds strongly decrease below a species-specific threshold in forest coverage. Decreased forest cover may though favor the bird species normally associated with open and light forests, such as A. trivialis and P. phoenicurus (Cramp and Perrins, 1988; see also Flousek, 1989). At an extreme case, however, forests will die and forest birds disappear (Flousek, 1989; Gilyazov, 1993).

Our analysis indicated that despite a strong association between productivity (biomass) and diversity there are additional effects of pollution on species diversity besides those via reduced bird biomass. This is likely due to a decreased number of species in heavily contaminated sites, which was observed at all the smelter sites. However, it must be recalled that our proxy variable for productivity, the biomass of breeding birds, does not only indicate local productivity but also immigration of birds which have a good capacity to move into the new areas, also to the relatively heavily polluted 'sink' habitats (Kozlov et al., 2005).

Although bird densities and diversities reflected the exposure levels in our study (see also Belskii and Lyakhov, 2003) they were not associated with litter copper concentrations in a strictly dosedependent manner. This was evident from greatly varying strengths of associations between density/diversity measures and copper levels among the four smelter sites. For example, despite that in Harjavalta there were relatively high litter copper levels, approaching those in the most heavily polluted sites of Monchegorsk, they were not associated with decreased bird density or biomass, and only weakly associated with bird diversity. Birds generally have a relatively good homeostatic control for essential trace elements such as zinc and copper, but some non-essential metals commonly emitted from the smelters, such as lead, are less well regulated (Berglund et al., 2010, 2011; Dauwe et al., 2000; Nyholm, 1995) and more potent pollutants for causing direct toxic effects. Relatively low lead emissions from Harjavalta smelter as compared to Karabash and Revda may partly explain the less severe impact on bird populations, and the studies measuring different physiological biomarkers of pollution have mostly failed to show any direct metal-related physiological effects in birds of Harjavalta (Eeva et al., 2000, in press; Koivula et al., 2011). Our study on bird population densities should, however, help in selecting potentially sensitive species for the future studies on possible toxic physiological effects at other smelter sites. Our results suggest that copper itself is not a primary proximate cause for the changes in bird communities, but rather the combined long-term effect of multiple pollutants on bird populations and especially on the resources necessary for breeding, such as food and suitable habitat.

Acknowledgements

The three referees are acknowledged for their effort to improve our manuscript. We thank Juha Sjöholm and Minna Takalo for performing the field work in Harjavalta, and V. Zverev for measuring habitat characteristics in Monchegorsk and Harjavalta. Esa Lehikoinen gave valuable advice in bird density analyses. Our study was financed by the Academy of Finland (to TE, Grant 8119367; to MK, Grant 8124152) and the Russian Foundation for Basic Research (to EB, Grants 08-04-91766 and 10-04-00146).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.03.004.

References

- Aitchison, J., 1986. The statistical analysis of compositional data. Monographs on statistics and applied probability. Chapman and Hall, New York.
- Avery, T.E., Burkhart, H.E., 1994. Forest measurements, fourth ed. McGraw-Hill Inc., New York.
- Belskii, E.A., Lyakhov, A.G., 2003. Response of the avifauna to technogenic environmental pollution in the southern taiga zone of the Middle Urals. Russ. J. Ecol. 34, 181–187.
- Belskii, E.A., Bezel, V.S., Lyakhov, A.G., 1995. Characteristics of the reproductive indices of birds nesting in tree hollows under conditions of technogenic pollution. Russ. J. Ecol. 26, 126–131.
- Belskii, E.A., Lugas'kova, N.V., Karfidova, A.A., 2005. Reproductive parameters of adult birds and morphophysiological characteristics of chicks in the pied flycatcher (*Ficedula hypoleuca* Pall.) in technologically polluted habitats. Russ. J. Ecol. 36, 329–335.
- Berglund, Å.M.M., Ingvarsson, P.K., Danielsson, H., Nyholm, N.E.I., 2010. Lead exposure and biological effects in pied flycatchers (*Ficedula hypoleuca*) before and after the closure of a lead mine in northern Sweden. Environ. Pollut. 158, 1368-1375
- Berglund, Å.M.M., Koivula, M.J., Eeva, T., 2011. Species- and age-related variation in metal exposure and accumulation of two passerine bird species. Environ. Pollut. 159, 2368–2374.
- Bureš, S., Weidinger, K., 2000. Estimation of calcium intake by Meadow Pipit nestlings in an acidified area. J. Avian Biol. 31, 426–429.
- Cramp, S., Perrins, C.M., 1988. The Birds of the Western Palearctic V. Oxford University Press, Oxford.
- Cramp, S., Perrins, C.M., 1993. The Birds of the Western Palearctic VII. Oxford University Press, Oxford.
- Crochet, P.-A., Raty, L., De Smet, G., Anderson, B., Barthel, B.H., Collinson, J.M., Dubois, P.J., Helbig, A.J., Jiguet, F., Jirle, E., Knox, A.G., Le Maréchal, P., Parkin, D.T., Pons, J.M., Roselaar, C.S., Svensson, L., van Loon, A.J., Yésou, P. 2010. AERC TAC's Taxonomic Recommendations. July 2010. www.aerc.eu.
- Dauwe, T., Bervoets, L., Blust, R., Pinxten, R., Eens, M., 2000. Can excrement and feathers of nestling songbirds be used as biomonitors for heavy metal pollution? Arch. Environ. Contam. Toxicol. 39, 541–546.
- Dormann, C.F., 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Glob. Ecol. Biogeogr. 16, 129–138.
- Eeva, T., Lehikoinen, E., 1996. Growth and mortality of nestling great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) in a heavy metal pollution gradient. Oecologia 108, 631–639.
- Eeva, T., Lehikoinen, E., 2004. Rich calcium availability diminishes heavy metal toxicity in Pied Flycatcher. Funct. Ecol. 18, 548–553.
- Eeva, T., Tanhuanpää, S., Råbergh, C., Airaksinen, S., Nikinmaa, M., Lehikoinen, E., 2000. Biomarkers and fluctuating asymmetry as indicators of pollution-induced stress in two hole-nesting passerines. Funct. Ecol. 14, 235–243.
- Eeva, T., Koivunen, V., Hakkarainen, H., 2002. Population densities of forest birds in a heavy metal pollution gradient. Avian Sci. 2, 227–236.
- Eeva, T., Ryömä, M., Riihimäki, J., 2005. Pollution-related changes in diets of two insectivorous passerines. Oecologia 145, 629–639.
- Eeva, T., Ahola, M., Laaksonen, T., Lehikoinen, E., 2008. The effects of sex, age and breeding success on breeding dispersal of pied flycatchers along a pollution gradient. Oecologia 157, 231–238.
- Eeva, T., Ahola, M., Lehikoinen, E., 2009a. Breeding performance of blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) in a heavy metal polluted area. Environ. Pollut. 157, 3126–3131.
- Eeva, T., Hakkarainen, H., Belskii, E., 2009b. Local survival of pied flycatcher males and females in a pollution gradient of a Cu smelter. Environ. Pollut. 157, 1857–1861
- Eeva, T., Rainio, M., Kanerva, M., Salminen, J.-P., in press. Plasma carotenoid levels are not directly related to heavy metal exposure or reproductive success in three insectivorous passerines. Environmental Toxicology and Chemistry, in press.
- Flousek, J., 1989. Impact of industrial emissions on bird populations breeding in mountain spruce forests in Central Europe. Ann. Zool. Fenn. 26, 255–263.
- Gilyazov, A.S., 1993. Air pollution impact on the bird communities of the Lapland biosphere reserve. In: Kozlov, M.V. (Ed.), Aerial Pollution in Kola Peninsula. Kola Scientific Centre, Apatity, pp. 383–390.

- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391.
- Graveland, J., Drent, R.H., 1997. Calcium availability limits breeding success of passerines on poor soils. J. Anim. Ecol. 66, 279–288.
- Janssens, E., Dauwe, T., Pinxten, R., Eens, M., 2003. Breeding performance of great tits (*Parus major*) along a gradient of heavy metal pollution. Environ. Toxicol. Chem. 22, 1140–1145.
- Järvinen, O., 1978. Estimating relative densities of land birds by point counts. Ann. Zool. Fenn. 15, 290–293.
- Järvinen, O., Väisänen, R., 1983. Correction coefficients for line transect censuses of breeding birds. Ornis Fennica 60, 97–104.
- Koivula, M.J., Kanerva, M., Salminen, J.P., Nikinmaa, M., Eeva, T., 2011. Metal pollution indirectly increases oxidative stress in great tit (*Parus major*) nestlings. Environ. Res. 111, 362–370.
 Koskimies, P., Väisänen, R.A., 1991. Monitoring Bird Populations. A Manual of
- Koskimies, P., Väisänen, R.A., 1991. Monitoring Bird Populations. A Manual of Methods Applied in Finland. Zoological Museum, Finnish Museum of Natural History, University of Helsinki, Helsinki.
- Kozlov, M.V., Zvereva, E.L., 2007. Industrial barrens: extreme habitats created by non-ferrous metallurgy. Rev. Environ. Sci. Biotechnol. 6, 231–259.
- Kozlov, M.V., Zvereva, E.L., Gilyazov, A.S., Kataev, G.D., 2005. Contaminated zone around a nickel-copper smelters: a death trap for birds and mammals? In: Burk, A.R. (Ed.), Trends in Biodiversity Research. Nova Science Publishers, pp. 81–101.
- Kozlov, M.V., Zvereva, E.L., Zverev, V.E., 2009. Impacts of point polluters on terrestrial biota. Springer, Dordrecht, Heidelberg, London, New York.
- Mukhacheva, S.V., Davydova, Y.A., Kshnyasev, I.A., 2010. Responses of small mammal community to environmental pollution by emissions from a copper smelter. Russ, J. Ecol. 41, 513–518.
- Nyholm, N.E.I., 1994. Heavy metal tissue levels, impact on breeding and nestling development in natural populations of pied flycatchers (Aves) in the pollution gradient from a smelter. In: Donker, M., Eijsackers, H., Heimback, F. (Eds.), Ecotoxicology of Soil Organisms. Lewis Publishers, Chelsee, USA, pp. 373– 382
- Nyholm, N.E.I., 1995. Monitoring of terrestrial environmental metal pollution by means of free-living insectivorous birds. Ann. Chim. 85, 343–351.
- Pautasso, M., Dinetti, M., 2009. Avian species richness, human population and protected areas across Italy's regions. Environ. Conserv. 36, 22–31.

- Rosenvald, R., Lohmus, A., Kraut, A., Remm, L., 2011. Bird communities in hemiboreal old-growth forests: the roles of food supply, stand structure, and site type. Forest Ecol. Manage. 262, 1541–1550.
- Salemaa, M., Vanha-Majamaa, I., Derome, J., 2001. Understorey vegetation along a heavy-metal pollution gradient in SW Finland. Environ. Pollut. 112, 339–350.
- SAS, 2008. SAS/STAT ® 9.2 User's Guide. SAS Institute Inc, Cary, NC.
- Sazonova, T.A., Olchev, A.V., 2010. The response of coniferous trees to industrial pollution in north-western Russia. The Open Geogr. J. 3, 125–130.
- Slovik, S., 1996. Early needle senescence and thinning of the crown structure of *Picea abies* as induced by chronic SO₂ pollution. 2. Field data basis, model results and tolerance limits. Glob. Change Biol. 2, 459–477.
- Smorkalov, I.A., Vorobeichik, E.L., 2011. Soil respiration of forest ecosystems in gradients of environmental pollution by emissions from copper smelters. Russ. J. Ecol. 42, 464–470.
- Tilgar, V., Mänd, R., Mägi, M., 2002. Calcium shortage as a constraint on reproduction in great tits *Parus major*: a field experiment. J. Avian Biol. 33, 407–413
- Vesk, P.A., Nolan, R., Thomson, J.R., Dorrough, J.W., Mac Nally, R., 2008. Time lags in provision of habitat resources through revegetation. Biol. Conserv. 141, 174– 186.
- Vike, E., 1999. Air-pollutant dispersal patterns and vegetation damage in the vicinity of three aluminium smelters in Norway. Sci. Total Environ. 236, 75–90.
- Vinogradova, N.V., Dolnik, V.R., Yefremov, V.D., Payevsky, V.A., 1976. Identification of Sex and Age in Passerine Birds of the USSR. Nauka, Moscow.
- Vorobeichik, E.L., Kozlov, M.V., 2012. Impact of point polluters on terrestrial ecosystems: methodology of research, experimental design, and typical errors. Russ. J. Ecol. 43, 89–96.
- Wilkin, T.A., Gosler, A.G., Garant, D., Reynolds, S.J., Sheldon, B.C., 2009. Calcium effects on life-history traits in a wild population of the great tit (*Parus major*): analysis of long-term data at several spatial scales. Oecologia 159, 463–472.
- Zuckerberg, B., Porter, W.F., 2010. Thresholds in the long-term responses of breeding birds to forest cover and fragmentation. Biol. Conserv. 143, 952–962.
- Zverev, V.E., 2009. Mortality and recruitment of mountain birch (*Betula pubescens* ssp *czerepanovii*) in the impact zone of a copper–nickel smelter in the period of significant reduction of emissions: the results of 15-year monitoring. Russ. J. Ecol. 40, 254–260.