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Bird diversity and dissimilarity show contrasting patterns along heavy metal pollution gradients in the Urals, Russia

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Abstract

The effects of industrial pollution on bird diversity have been widely studied using traditional diversity measures, which assume all species to be equivalent. We compared species richness and Shannon index with distance-based measures of taxonomic, functional, and phylogenetic diversity (the abundance-weighted mean nearest taxon distances), which describe within-community dissimilarity at terminal branches. Analysis of dissimilarity can shed light on the processes underlying community assembly, i.e., environmental filtering decreases dissimilarity whereas competitive exclusion increases it. In the 2-year study near Karabash and Revda copper smelters in Russia, point counts of nesting birds and habitat descriptions were taken at 10 sites (40 plots) along each pollution gradient. The abundance and diversity of birds showed good repeatability in both regions. The total density of birds, number of species per plot, and Shannon diversity decreased at high toxic load in both regions. The taxonomic, functional, and phylogenetic nearest taxon distances showed the same pattern within regions. Species dissimilarity within communities increased with pollution in Karabash (due to loss of functionally similar species), but did not change in Revda (due to mass replacement of forest species by species of open habitats). Pollution-induced changes in bird communities near Karabash were greater due to the stronger deterioration of the forest ecosystems and less favorable natural conditions (more arid climate, lower diversity and vitality of the tree stand and understorey) compared to Revda. This study emphasizes the need for a multi-level approach to the analysis of bird communities using traditional indices of diversity, functional, taxonomic, or phylogenetic distances between species and environmental variables.

Keywords Heavy metals · Boreal forest · Bird community · Taxonomic diversity · Functional diversity · Phylogenetic diversity · Nearest taxon distance

Introduction

Studies of communities have advanced recently after the application of a multifaceted approach to biodiversity. Natural communities are analyzed with respect to their taxonomic, functional (trait), and phylogenetic diversity (Faith 1992; Hooper et al. 2005; Pavoine and Bonsall 2011; Petchey and

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Gaston 2006). Taxonomic diversity deals with both species and higher taxa. Functional diversity is related to the functional role of the species (organisms) in ecosystems, whereas phylogenetic diversity reflects the evolutionary history of the community. Among these indices, the functional diversity of a community is the most studied with respect to species response to environmental gradients, ecosystem function, and nature conservation (Cadotte et al. 2011; Dehling et al. 2014; Edwards et al. 2013; Petchey et al. 2007; Tilman 2001). In earlier studies, all species were assumed to be equivalent. Thus, traditional diversity measures operate only with the number of species and their relative abundances (species richness, Shannon diversity index or other metrics). The transition from traditional diversity indices to the new ones is based on the distances between species in a multidimensional space or in a tree (phylogram).

Calculation of phylogenetic distances between species is complicated by the absence of a single generally accepted phylogenetic tree of birds. This forces the researchers to

average the phylogenetic distances across thousands of phylogeny subsets (Jetz et al. 2012) or to recreate a consensus tree, which requires much computational effort. The task can be simplified when using the taxonomic tree. The taxonomic classification of birds was elaborated before the implementation of molecular methods and is widely used to date (with minor modifications concerning status of single species). The taxonomic tree reflects classification of species according to their similarity and relationships (Mayr 1968, 1969) on the basis of comparative morphological, embryological, cytological, and other data. The species arrangement in a hierarchy of higher categories allows for formalization of calculation the distances between species. Therefore, taxonomic diversity can be estimated much easier compared to the phylogenetic one that makes the former more affordable in policymaking for biodiversity conservation.

The analysis of different facets of diversity allows an understanding of the mechanisms of community assembly and ecosystem function as well as to predict their natural and human-induced dynamics. This approach has been used in studies of spatio-temporal variation of bird communities under climate fluctuations, natural gradients, and different land use regimes including agriculture, forest logging, and habitat fragmentation (Dehling et al. 2014; Devictor et al. 2010; Edwards et al. 2013; Flynn et al. 2009; Luck et al. 2013; Newbold et al. 2013; Petchey et al. 2007). Industrial pollution is a widespread phenomenon in highly developed countries. It affects all components of natural ecosystems resulting in their deterioration to industrial barrens in extreme cases (Kozlov and Zvereva 2007). Along pollution gradients, habitat quality varies greatly over small spatial scales (from a few up to dozens of kilometers), which facilitates the study of diversity patterns and community assembly processes. The variations of bird communities along industrial pollution gradients have been studied only with respect to abundance and traditional diversity indices (species richness and Shannon diversity) (Alaya-Ltifi and Selmi 2014; Belskii and Lyakhov 2003; Eeva et al. 2002, 2012; Flousek 1989). It was shown that industrial pollution causes deterioration in forest ecosystems and affects the food supply and nesting habitats. Consequently, generalists replace specialized species, and species of open habitats replace forest species.

In this study around two Russian copper smelters, we analyzed pollution-related variability of forest bird abundance and diversity. Considering strong pollution-induced changes in community composition, we expected that industrial pollution also affected the taxonomic, functional, and phylogenetic distances between species within bird communities. Particularly, we expected selection of a few tolerant species with similar habitat preferences in polluted areas and therefore the reduction of functional distances between species within

the community. At the same time, phylogenetic distances between species in polluted areas can increase or decrease depending on the species composition in a given community. By studying traditional diversity indices (species richness and Shannon diversity) as well as the distance-based indices of taxonomic, functional, and phylogenetic diversity, we tested the hypothesis that each facet of the diversity adds new information about the community response to the environmental stress. If so, different diversity measures were expected to change differently along the pollution gradient. Since the distance-based indices take into account species identity they were supposed to be more informative and show stronger association with environmental stress as compared to traditional diversity measures. Among the distance-based indices, the functional diversity was expected to be more conservative due to redundancy in natural communities, i.e., functional similarity between distant taxa. Community structure is the result of different ecological processes, most important of them were called "environmental filtering" and "limiting similarity." In the first case, environment selects for species with traits allowing for survival in specific conditions. This results in the reduction of functional diversity, especially at extreme values of environmental gradients (e.g., Seymour et al. 2015). In the second case, biotic factors such as competition prevent coexistence of species with similar ecological requirements resulting in high functional diversity (MacArthur and Levins 1967). In order to determine the main drivers of the community assembly processes (environmental filtering vs. limiting similarity), we compared the observed pattern of functional diversity to a pattern expected by chance. Taking into account the strong detrimental effects of pollution on forest vegetation, we expected environmental filtering to be a major determinant of taxonomic, functional, and phylogenetic diversity of birds in the areas subjected to industrial pollution.

Investigations around two copper smelters (Karabash and Revda) allowed us to test for the generality of conclusions. Both smelters emit the same pollutants (heavy metals and SO_2), which allowed a comparison between the pollution levels in these regions. However, the regions differ in industrial history, annual emissions and climate and ecosystem characteristics. This is why we expected to detect both general and region-specific effects of the pollution. Previous 1-year point censuses in these regions showed negative effects of the industrial pollution on forest bird density and community structure (Belskii and Belskaya 2013a; Eeva et al. 2012). By analyzing data collected for 2 years, we estimated the repeatability of the results within each region. We used the heavy metal concentrations in the forest litter to link bird density and diversity to toxic load. To ascertain key variables affecting bird communities, we calculated the associations of bird abundance and diversity with habitat characteristics. So, aims of the study were (1) to assess how industrial

pollution has affected the abundance and diversity in the breeding bird communities; (2) to compare pollution-related patterns in different diversity measures; (3) to reveal species-specific responses to pollution; (4) to determine key habitat characteristics affecting bird communities; (5) to estimate between-year repeatability and region-specific effects of the pollution.
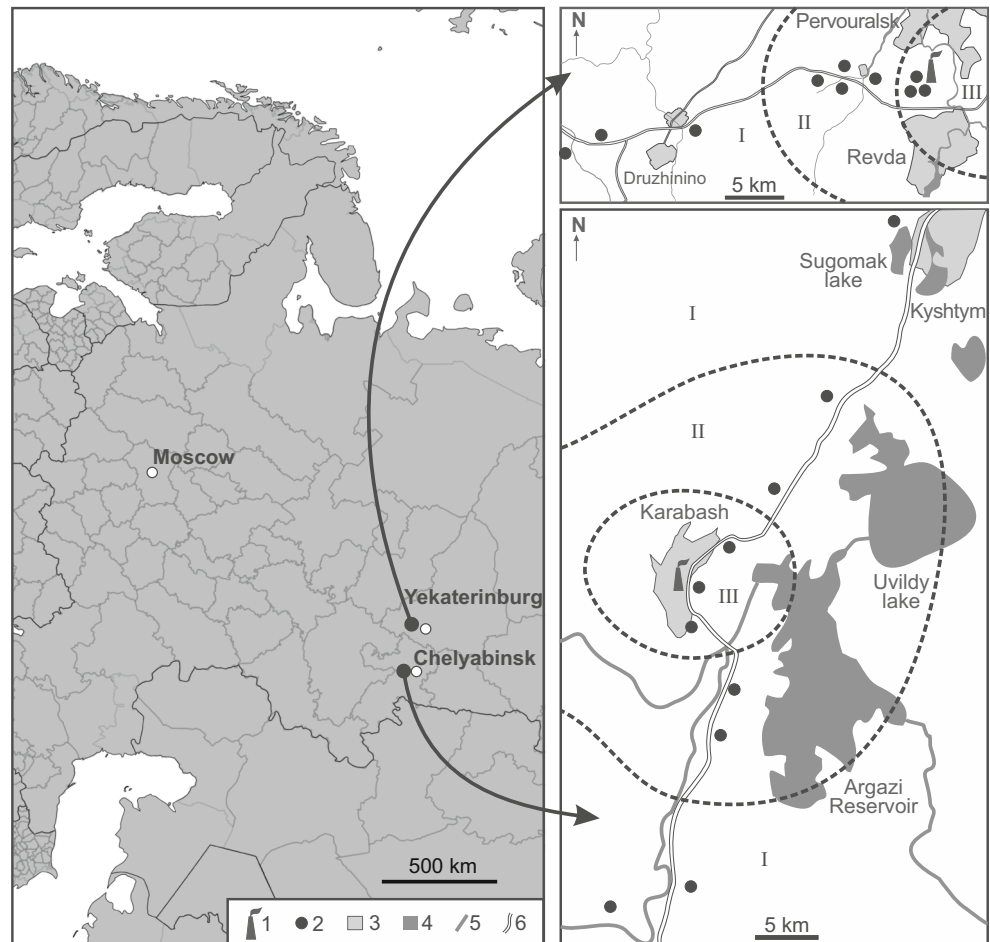
Material and methods

Study regions

The study was performed in two boreal regions with large copper smelters (Fig. 1), Karabash (Southern Urals, Russia, 55° 27′ N, 60° 13′ E, years 2009 and 2014) and Revda (Middle Urals, Russia, 56° 51′ N, 59° 53′ E, years 2010 and 2013). The distance between the enterprises is 155 km. Both smelters are strong sources of sulfur dioxide and polymetallic dust. Total emissions in 2009–2012 were relatively stable in Karabash (13,200–16,100 t/year) and decreased in Revda (from 21,700 to 2900 t/year) (Alexandrov 2013; Department of Rospotrebnadzor in Chelyabinsk oblast 2014). Karabash lies in a valley directed meridionally and is surrounded by hills up to 600 m high. This region, covered with a pine-birch forest, is located on the border between southern taiga and the forest–steppe. The area closest to the Karabash smelter is a large industrial barren, where natural vegetation and soil have almost completely disappeared (Kozlov et al. 2009). The region surrounding Revda belongs to the southern taiga subzone with primary spruce/fir and secondary birch/aspen forests.

The investigations were carried out near Karabash in a birch forest (with dominating *Betula pendula* Roth) and near Revda in a spruce-fir forest (*Picea obovata* Ledeb. and *Abies sibirica* Ledeb.). In each of the two regions, 10 study sites were established within a 1–33-km range from the smelters (Fig. 1). The sites were chosen to cover the entire pollution gradient and represent different stages of forest habitat deterioration: from background area (i.e., unpolluted) to industrial barren. At each site, we selected four sampling points with the distance between them more than 250 m to avoid counting the same

Fig. 1 Locations of study sites (black circles) along pollution gradients in two regions. Dashed concentric lines denote different stages of forest habitat deterioration (schematic): I—unpolluted, II—moderately polluted, and III—heavily polluted areas. Legend: 1, copper smelter; 2, study sites; 3, settlements; 4, lakes; 5, rivers; 6, roads

birds twice. The surroundings of each point (for at least 50 m) are of the same habitat type (Koskimies and Väisänen 1991). The same points were sampled each year. The observation circle around a point is referred to hereafter as a sampling plot.

Habitat characteristics

At each sampling plot, we measured the basic habitat characteristics. The stand basal area (m^2/ha) was measured with a relascope at 1.3 m. The height of the top tree canopy was estimated as a mean of the five highest trees within 50 m from a point by the angle of elevation method with a SILVA Clino Master height-meter (Silva, Sweden). Stand composition (rounded to the nearest 10%), cover of the tree canopy, understorey, and field layer were determined visually. In total, in each region, 40 sampling plots (10 sites) were described.

Pollution level

The concentrations of the primary pollutants (Cu, Pb, and Cd) in the forest litter were used to assess the pollution level (Smorkalov and Vorobeichik 2011; Vorobeichik and Pishchulin 2016). Although heavy metals comprise 3–4% of the total emissions, they correlate with other toxicants and can be used to estimate the toxic load (Kozlov et al. 2009). Furthermore, heavy metals accumulate in the soil and reflect contaminant exposure due to long-term deposition. The metal concentrations had nearly the same range in both study regions, which enabled the analysis of the combined data set. To estimate the pollution level, we performed principal component analysis (PCA) with $\log_{10}$-transformed concentrations of Cu, Pb, and Cd in the forest litter. The first principal component explained 98.9% of the variation in the data and was used as a variable representing the toxic load on the ecosystem at each site. The factor loadings equaled 0.995, 0.996, and 0.992 for Cu, Pb, and Cd, respectively.

Point counts

The nesting bird population was censused by one observer (Belskii E.) near Karabash from 20th May–12th June, 2009 and 14th May–4th June, 2014, while near Revda from 16th May–7th June, 2010 and 18th May–16th June, 2013 four times per season at each point with an approximately weekly interval. Point counts (Järvinen 1978; Järvinen and Väisänen 1983) were carried out between 5:00 and 10:00 a.m., local summer time, avoiding windy and rainy days (no rain, temperature > 6 °C, wind < 5 m/s). Each point was censused for 5 min. The number of point counts was 160 per year in each region. For each species, the number of observed individuals or active nests were recorded. We considered a seen or heard male, a male–female pair, a single female, a brood or an active

nest to be a breeding pair (Koskimies and Väisänen 1991). For each counting plot, the maximum density of a species among four successive counts was used in further analyses.

Bird density

Bird densities were calculated from the point count data using the formula of Järvinen (1978): D (pairs/km^2) = $3Nc^2/\pi$, where N = number of pairs per counting plot and c = species-specific constant that corrects for the differences in detectability (value k from column E in Järvinen and Väisänen 1983). The total bird densities and diversity indices were calculated for each plot, year and study region. In total, 640 data sets were analyzed (2 years in two regions, 10 sites in each region with four counting plots per site, four counts per plot with a 6 or 7-day interval).

Statistical analysis

Two traditional diversity measures were calculated: species richness and Shannon diversity index. To test for the repeatability of the results, that is to check for the dependence of abundance and diversity on the year, we performed a two-way ANOVA with the independent variables "Site" and "Year," in each study region separately. Post hoc comparisons between years at each site were performed with a Tukey test. The differentiation between local communities along the pollution gradient was estimated using Whittaker's beta-diversity index $\beta w = (S/\alpha) - 1$, where S is the species number for the entire study region (gamma-diversity) and α is the mean number of species per site (alpha-diversity). In each region, the data from the 2 years were averaged. In order to estimate the variations of the number of closely related species along pollution gradients, we calculated linear regression of species-to-genera and species-to-families ratios on the toxic load in Karabash and Revda. The differences between regions in the slopes of regressions were performed with F-test (Zar 2010).

Three facets of bird diversity were analyzed by taking into account taxonomic, functional, and phylogenetic distances between species. We used the abundance-weighted mean nearest taxon distance (MNTD$_{Ab}$) as a measure of diversity. This index is among those that characterize the divergence within a community, i.e., taxonomic, functional, and phylogenetic differences between taxa in a community (Webb et al. 2002). In contrast to the other divergence metrics, MNTD$_{Ab}$ captures the terminal tree structure (Tucker et al. 2017).

To assess the taxonomic diversity, we used the nomenclature of "The Birds of the Western Palearctic" (Cramp and Perrins 1977–1994). The nearest taxonomic distance equals the minimum path between the two species on the taxonomic tree (Faith 1992). For example, the distance between two species of the same genus is one, between two species of the same subfamily is two and so on. We used the following taxonomic

categories: species, genus, subfamily, family and order. For the phylogenetic diversity estimation, we used the global phylogeny of birds v2.III published by Jetz et al. (2012). The phylogenetic distance between species was averaged across 10,000 subsets of complete phylogenies, compiled in a Bayesian framework (Jetz et al. 2014) with topology constraints based on Hackett et al. (2008). The phylogenetic distances were square root transformed as suggested by Letten and Cornwell (2015). Functional diversity was estimated with 19 traits related to the species' morphology, demography, habitat, foraging activity, diet composition and migratory status (Table 1). Most traits used in this study were proposed by Petchey et al. (2007) and Devictor et al. (2010). The egg volume was calculated using the formula $V = 0.51 \times L \times B^2$, where L is the length and B is the diameter of the egg (Hoyt 1979). Gower's generalized coefficient was used to calculate the functional dissimilarity between species (Pavoine et al. 2009) and the principal coordinates analysis (PCO) was used to explore and visualize the obtained dissimilarity matrix. The contribution of each variable to the global distance was calculated as a correlation coefficient between the squared pairwise distances defined by the kth variable and the global squared distances defined by the mixed-variables coefficient of distance (Pavoine et al. 2009). To quantify the correlation between the taxonomic, functional, and phylogenetic distances, we applied the Mantel test (using Spearman's correlation coefficient, and the significance of the statistic was evaluated with 10,000 permutations).

We analyzed the pollution-related variations in the habitat characteristics and bird diversity metrics using a multiple regression with "Toxic load" (the first principal component of the metals in the forest litter) and "Study region" as independent variables. The site was used as a statistical unit ($n = 10$ in each region). The data normality was examined with the Kolmogorov–Smirnov test. Values of taxonomic, functional, and phylogenetic $MNTD_{Ab}$ at the industrial barren near Karabash were considered as outliers and therefore were removed from the analysis. Therefore, for $MNTD_{Ab}$ $n = 9$ sites near Karabash and $n = 10$ sites near Revda. The association of the diversity measures with habitat variables were analyzed using multiple regressions with stand basal area, cover of understorey, cover of field layer and tree diversity (Shannon index) as independent variables. The correlation between the predictor variables was weak ($r < 0.35$). A plot was used as a statistical unit in the analyses ($n = 40$ in each region). We tested residuals of the models for autocorrelation calculating Moran's I values and their p-values with Monte Carlo methods using 199 permutations. Spatial autocorrelation was observed only for the total density of birds in Karabash. In this case, spatial autoregression (SAR) was used. The calculations were carried out in the Spatial Analysis in Macroecology (Rangel et al. 2006) software publically available at http://www.ecoevol.ufg.br/sam. To analyze the species-specific responses to pollution in each region, we calculated the Spearman correlation coefficient between the population densities of the most common species and toxic load. The species with at least 15 observations per year were included in this analysis.

When analyzing the dependence of bird diversity indices on the toxic load, we explored which model fitted better to the data: linear or quadratic one. The best model was selected on the basis of likelihood ratio test and

Table 1 Functional traits used to estimate functional diversity of bird communities

Trait type	Trait	Type of variable	Source
Morphology	Body mass	Quantitative, continuous	(Cramp and Perrins 1977–1994)
	Egg volume	Quantitative, continuous	
Demography	Modal clutch size	Quantitative, integer	
	Maximal number of breeding cycles per season	Quantitative, integer	
	Generation length (years)	Quantitative, continuous	(BirdLife International 2017)
Preferred habitat	Forest, forest edge, open, synanthropic	Ordinal	(Cramp and Perrins 1977–1994)
Nest location	Canopy, hole, understorey, ground	Ordinal	
Foraging method	Pursuit, gleaning, pouncing, grazing, digging, hammering, scavenging, probing	Binary (multi-choice nominal)	
Diet components	Invertebrates, birds/mammals, reptiles/amphibians, fish, other vertebrates, carrion, fruits, nectar, seeds, other plant material	Proportion (fuzzy)	(Wilman et al. 2014)
Foraging substrates	Water around surface, ground, understorey, midhigh, canopy, air	Proportion (fuzzy)	(Wilman et al. 2014)
Activity period	Diurnal, crepuscular, nocturnal	Ordinal	(Cramp and Perrins 1977–1994)
Migratory status	Resident, nomadic, short-distant, long-distant	Ordinal	

Akaike Information Criterion (AICc). To test the hypothesis on the equivalence of diversity indices (i.e., similar trends along a pollution gradient and equal resolution), we used ANOVA with heteroscedasticity consistent standard errors (hc3 covariance matrix; Long and Ervin 2000) and tested the significance of the "Site × Index" interaction. To estimate the effect size of the interaction term we used a partial eta squared (η^2) (Fritz et al. 2012).

To determine the assembly rules of the local communities, we calculated the standardized effect size (SES) as a measure of the degree of within-community taxonomic, functional and phylogenetic differentiation. To calculate an expected $MNTD_{Ab}$, we set up null models by randomly sampling n species from the regional species pool for each plot with n species. An independent-swap algorithm was used to maintain species richness and frequency of species occurrence (Gotelli 2000), and 10,000 random communities were drawn. The mean of the null distribution was then subtracted from the observed $MNTD_{Ab}$ value and divided by the standard deviation of the null distribution, to yield the SES. $SES > 0$ indicates processes limiting species similarity (e.g., competition between species), while $SES < 0$ indicates environmental filtering.

All calculations were performed using the R v.3.2.3 software (R Core Team 2017) with additional packages ade4 v.1.7–6 (Dray and Dufour 2007), adephylo v.1.1–10 (Jombart et al. 2010), car v.2.1–5 (Fox and Weisberg 2011), heplots v.1.3–3 (Fox et al. 2016), picante v.1.6–2 (Kembel et al. 2010) and vegan v.2.4–3 (Oksanen et al. 2017).

Results

Pollution levels and habitat variables

Litter copper concentrations increased exponentially towards both smelters (Fig. S1). The copper concentrations were similar in both background areas but differed in the vicinities of the smelters, which reflected the higher toxic load near Karabash. The lead and cadmium concentrations followed the same pattern. The toxic load index showed a strong correlation with litter concentrations of heavy metals, e.g., copper (Fig. S2).

The toxic load had a negative effect on the characteristics of the tree stand and the field layer cover (Fig. S3, Table S1). The study region affected the tree height, stand basal area, understorey cover and tree species diversity. These parameters were lower in Karabash than in Revda. The dead stand basal area, top canopy and field layer cover did not depend on the region and toxic load. The "Region × Toxic load" interaction was significant for the dead stand basal area only. This index increased towards the Revda smelter and did not depend on the pollution in Karabash.

Community responses and repeatability

Total bird density and diversity did not depend on the year, which indicated the good repeatability of the results in both study regions. The sites differed in the total bird abundance (two-way ANOVA, Karabash: $F(9,60) = 22.76$, $p < 0.001$; Revda: $F(9,60) = 12.36$, $p < 0.001$), species richness (Karabash: $F = 30.32$, $p < 0.001$; Revda: $F = 11.33$, $p < 0.001$) and Shannon diversity (Karabash: $F = 61.88$, $p < 0.001$; Revda: $F = 9.05$, $p < 0.001$). The year affected significantly only the species richness in Revda ($F = 56.19$ $p < 0.001$). At the same time, the post-hoc tests showed no significant differences between the years at either site. The "Year × Site" interaction was insignificant in all cases ($0.40 \leq F \leq 1.31$, $0.25 \leq p \leq 0.93$), which indicated the same effect of the toxic load in different years. Since the effect of the year was insignificant, we averaged bird indices over the two years for further analysis.
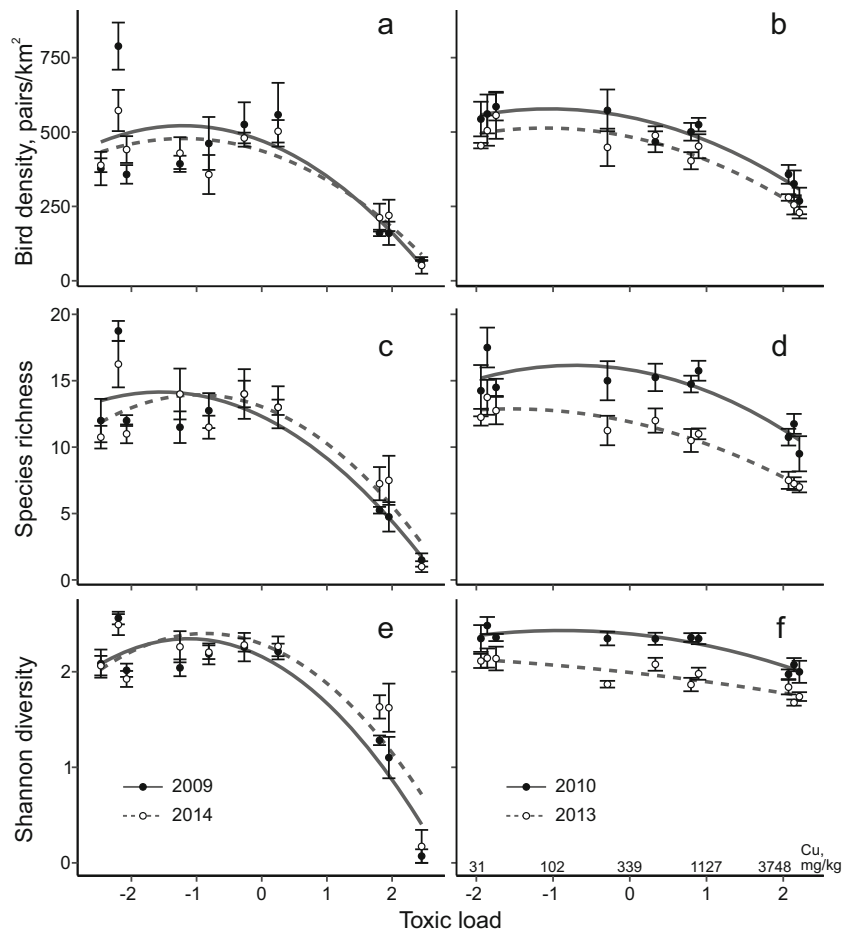
Total bird density, species richness and Shannon diversity decreased at high toxic load in both study regions (Table 2, Fig. 2), and the differences between the regions were significant for total density and species richness (Table 2). All interactions ("Region × Toxic load" and others) were insignificant in all indices. The number of closely related species, that is species of the same genus or family, was lower in heavily polluted sites compared to the background ones. The regression coefficients of the species-to-genera and species-to-families ratios on the toxic load were negative in both areas (Fig. 3). For

Table 2 The dependence of bird community characteristics on the toxic load and study region including interactions ($n = 10$ sites in each region, the data from the 2 years were averaged). Significant values ($p < 0.05$) are italicized

Source of variation	Total density, pairs/km^2		Species richness per plot		Shannon diversity	
	$F(1,15)$	p	$F(1,15)$	p	$F(1,15)$	p
Region	*17.67*	*0.001*	*16.21*	*0.001*	1.12	0.307
Toxic load	*63.12*	*< 0.001*	*29.05*	*< 0.001*	*10.10*	*0.006*
Toxic load^2	*8.48*	*0.011*	*10.94*	*0.005*	*4.74*	*0.046*
Region × Toxic load	1.31	0.271	3.61	0.077	3.45	0.083

F, F-ratio statistic; p, observed p value

Fig. 2 Total bird density (**a**, **b**), number of species per plot (**c**, **d**), and Shannon diversity (**e**, **f**) near Karabash (**a**, **c**, **e**) and Revda (**b**, **d**, **f**) copper smelters. Filled symbols and solid lines refer to the year 2009 in Karabash and 2010 in Revda, open symbols and dashed line refer to 2014 in Karabash and 2013 in Revda. Bars denote standard error
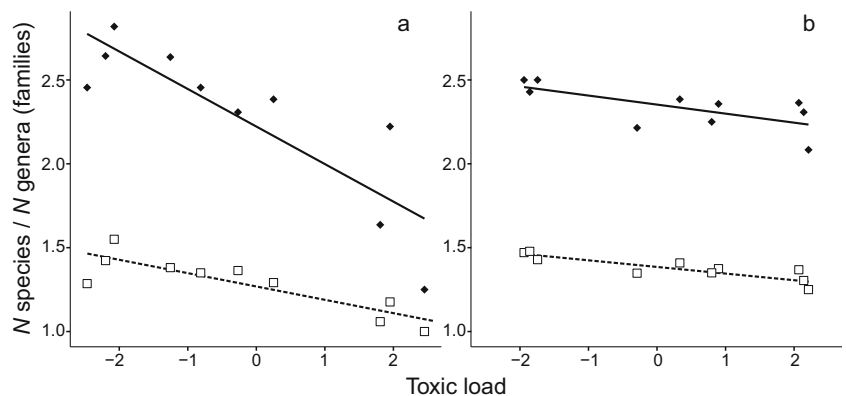
species-to-genera ratio in Karabash $B(\pm SE) = -0.079 \pm 0.017$ ($n = 10$, $p = 0.002$) and in Revda $B = -0.037 \pm 0.008$ ($n = 10$, $p = 0.001$). For species-to-families ratio in Karabash $B = -0.224 \pm 0.050$ ($p = 0.002$) and in Revda $B = -0.054 \pm 0.020$ ($p = 0.028$). The differences between regions in the slopes of regressions were significant: for species-to-genera ratio $F = 9.64$, $p < 0.005$, for species-to-families ratio $F = 5.70$, $p < 0.05$. The results indicate greater effect in Karabash compared to Revda.

Species-specific responses

Over 2 years 59 species were listed in Karabash and 52 species in Revda. The abundance correlated significantly with the toxic load in 1 of 15 common species (6%) in Karabash and 4 of 19 species (21%) in Revda (Table S2). All significant correlation coefficients were negative. Densities of the pied flycatcher *Ficedula hypoleuca*, red-breasted flycatcher *F. parva*, common chaffinch *Fringilla*

Fig. 3 Number of closely taxonomically related species (species per genus, dashed line, and species per family, solid line), along pollution gradients near Karabash (**a**) and Revda (**b**)

coelebs, willow tit *Parus montanus*, Eurasian bullfinch *Pyrrhula pyrrhula*, goldcrest *Regulus regulus*, song thrush *Turdus philomelos* and scaly thrush *Zoothera dauma* showed the strongest correlations with exposure. Most of these forest species disappeared in the vicinities of the smelters. Meanwhile, some species were observed only in heavily polluted sites with Cu litter concentrations exceeding 3000 mg/kg. They included mainly species of open habitats and synanthropic ones. In Karabash these were common swift *Apus apus*, black kite *Milvus migrans*, white wagtail *Motacilla alba*, northern wheatear *Oenanthe oenanthe* and Eurasian magpie *Pica pica*; in Revda these were common swift, European goldfinch *Carduelis carduelis,* yellowhammer *Emberiza citrinella,* white wagtail, spotted flycatcher *Muscicapa striata,* willow warbler *Phylloscopus trochilus,* Eurasian magpie and whinchat *Saxicola rubetra.* At the three heavily polluted sites in Karabash the bird community lost 31 of 54 species inhabiting the background area and acquired five species; in Revda the bird community lost 14 of 43 species inhabiting the background area and acquired nine species. Thus, the species loss in Revda was compensated for more $(9/14*100\% = 64.3\%)$ than in Karabash $(5/31*100\% = 16.1\%)$ (Fisher's exact test for differences between regions $p = 0.033$). Whittaker's beta-diversity index in Karabash (3.01) exceeded that of Revda (2.46), thereby indicating greater differentiation between local communities.

Distance-based diversity indices

For the estimation of taxonomic and phylogenetic mean nearest taxon distances ($TMNTD_{Ab}$ and $PMNTD_{Ab}$), we used the generally accepted taxonomy and phylogeny of the birds (see Material and methods). The correlation between these diversity indices equaled 0.95 ± 0.05 ($n = 39$) in Karabash and 0.91 ± 0.07 ($n = 40$) in Revda. This indicates good correspondences between classifications based on morphology and nucleotide sequences (Fig. S4). The correlation between taxonomical and functional diversity was weaker (Fig. S4) and equaled 0.86 ± 0.08 in Karabash and 0.69 ± 0.12 in Revda. This shows that taxonomically and phylogenetically distant species can possess similar functional traits. Different traits contributed differently to the functional distance between the species. The greatest correlations with the total distance ($r > 0.6$) were egg volume, diet and generation length followed by foraging method and body mass, while the nest location and clutch size were the least important (Fig. S5).

In accordance with the functional ordination of birds (Fig. 4), the first principal coordinate (PC) reflected the gradient from open to wooded habitats and the migratory status of species, while the second PC was mainly attributable to the differences in body size, generation length of birds and diet diversity. Note that the functional distances increased between larger species (e.g., black kite, common buzzard *Buteo buteo,* common raven *Corvus corax* and hooded crow *C. cornix*). In contrast, the smaller the species were and the more structured their habitat was, the more clustered the species were. In particular, the small species including tits Parus spp., goldcrest, Eurasian nuthatch *Sitta europaea*, Eurasian treecreeper *Certhia familiaris*, Eurasian siskin *Carduelis spinus*, Eurasian bullfinch and red crossbill *Loxia curvirostra,* were closely grouped due to their residence, ability to switch their diet from insects to seeds in winter and association with high forests that provide various microhabitats for nesting and foraging.

The taxonomic, functional, and phylogenetic mean nearest taxon distances increased with pollution near Karabash (Fig. 5). The regression slopes of these indices on the toxic load differed significantly from zero and equaled ($\beta \pm SE$) 0.80 ± 0.23 ($n = 9$, $p = 0.01$), 0.68 ± 0.28 ($p = 0.04$) and 0.85 ± 0.20 ($p = 0.01$), respectively. In contrast, these slopes did not differ from zero near Revda: 0.35 ± 0.33 ($n = 10$, $p = 0.32$), 0.46 ± 0.31 ($p = 0.18$) and 0.16 ± 0.35 ($p = 0.66$) for the nearest taxonomic, functional and phylogenetic distances, respectively. The interaction "Region × Toxic load" was significant for all these indices ($5.10 \leq F \leq 5.75$; $0.029 \leq p \leq 0.038$), thereby confirming their different patterns in each region.

The standardized effect sizes (SES) of the nearest taxonomic, functional, and phylogenetic distances did not differ between sites in both pollution gradients (Fig. S6). The slopes of the SES regression on the toxic load did not differ from zero in both regions ($0.14 \leq p \leq 0.80$). An environmental effect was observed only at particular sites. The functional clustering was registered at six plots out of 40 in Revda, and two plots in Karabash, thereby, indicating environmental filtering both at high and low loads (Fig. S6). Therefore, a random assembly of bird communities at most sites cannot be rejected.

Associations with habitat variables

The characteristics of the bird communities responded differently to habitat transformation. Specifically, the total density, species richness and Shannon diversity increased with the improvement of the vegetation cover; whereas, the taxonomic, functional and phylogenetic nearest taxon distances decreased in Karabash and did not change in Revda (Fig. S7). In both regions, traditional diversity indices and bird density depended on the stand basal area, field layer coverage or both. Among the distance-based indices, only the phylogenetic dissimilarity was related to the stand basal area in Karabash,
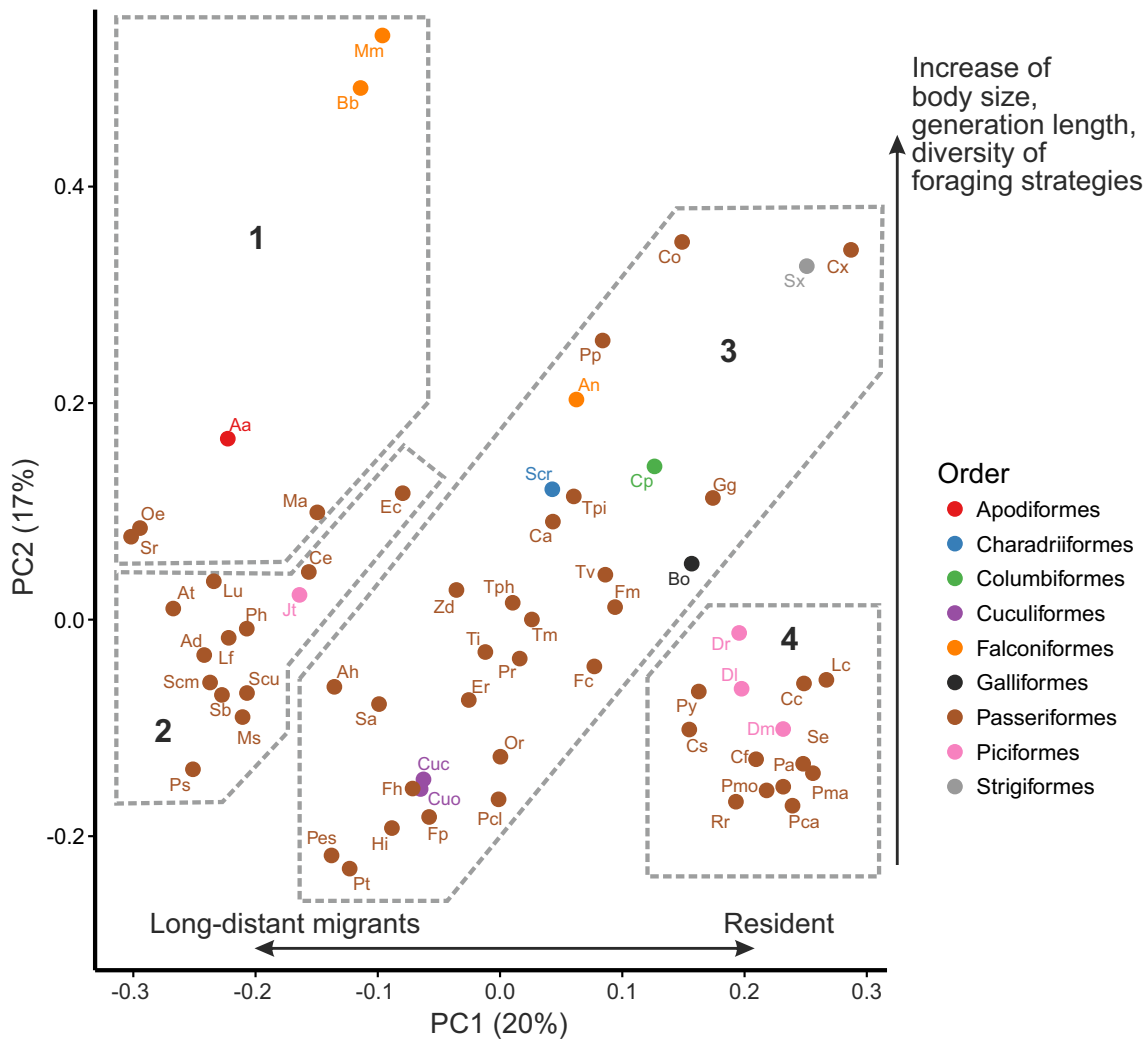
Fig. 4 Ordination of birds in relation to functional distances between species. Points indicate position of species in reduced-space ordination (PC, principal coordinates). Species that are ordinated closer together have smaller functional dissimilarity values than those ordinated further apart. Dashed areas denote preferred habitats: 1, open; 2, bush or forest edge; 3, sparse forest; 4, high forest. For species abbreviations, see Table S3

while the others were not associated with any of the vegetation indices. Associations of bird density and diversity with habitat variables were stronger in Karabash, where these variables explained 23–75% of the variance compared to 0–55% in Revda (Table 3).

Comparison of diversity indices

The comparison of pollution-related patterns of traditional diversity indices showed that the Shannon diversity index did not add new information to that provided by the species richness. The dependence of both indices on toxic load was similar (Fig. 2) and the interaction between them was insignificant (Table 4). At the same time, the patterns of the distance-based indices differed from traditional ones (Fig. 5). Interactions between these metrics were significant and explained 12–39% of the total variance (Table 4). The effect of the interactions in
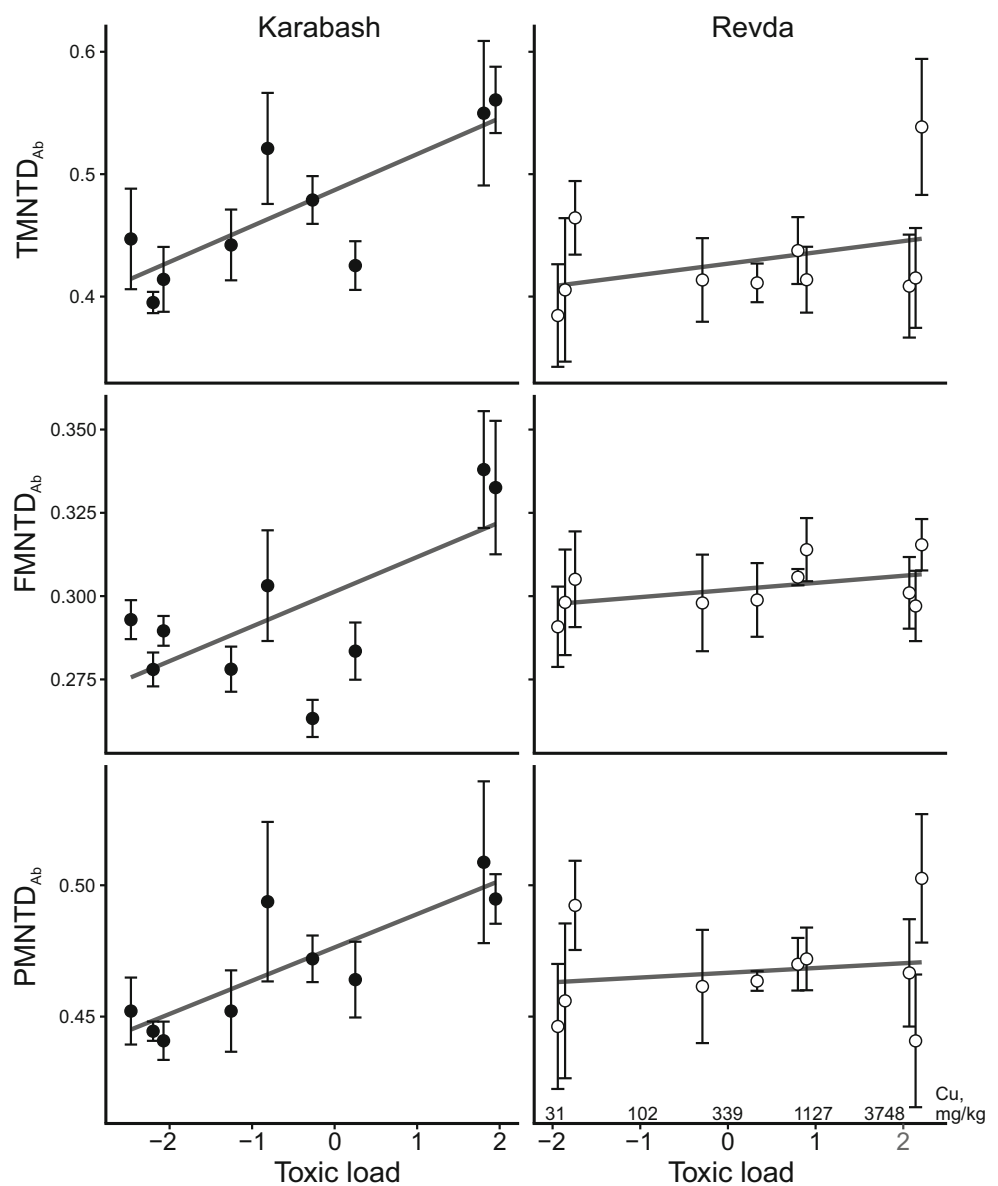
Karabash was greater than in Revda. However, the interactions between taxonomic, functional, and phylogenetic nearest taxon distances were insignificant, thereby indicating similar patterns along the pollution gradients.

The taxonomic and functional nearest taxon distances were not linearly related to species richness in Karabash (Fig. 6 for $FMNTD_{Ab}$). A pollution-induced reduction of species richness had a limited effect on the within-community differentiation when number of species was great or moderate. At low species richness decrease in the number of species was accompanied by a marked increase in dissimilarity.

Discussion

Comparisons between the 2 years, as well as between the current and earlier data (Belskii and Belskaya 2013a; Belskii

Fig. 5 Within-community taxonomic ($TMNTD_{Ab}$), functional ($FMNTD_{Ab}$), and phylogenetic ($PMNTD_{Ab}$) dissimilarity of birds (mean ± SE) along pollution gradients near Karabash (industrial barren excluded, left column) and Revda (right column) copper smelters

and Lyakhov 2003), showed good repeatability of the results. This indicates that the weather conditions in a particular year have a limited effect on the responses of birds to industrial pollution. The toxic load, i.e., the soil pool of heavy metals accumulated for years, decreases slightly if industrial emissions decrease (for Revda see Vorobeichik and Kaigorodova 2017), resulting in a slow recovery of polluted ecosystems.

Pollution-induced changes in bird communities in both study regions are similar to other areas subjected to industrial pollution (Alaya-Ltifi and Selmi 2014; Eeva et al. 2002, 2012; Flousek 1989), with decreased abundance, species richness and Shannon diversity. These effects are in parallel with a structural simplification of the forest ecosytems towards more open and less productive habitats, which was observed in both our study regions (Belskii and Belskaya 2013b; Eeva et al. 2012). The Karabash region showed a greater species richness

of birds compared to Revda, but lower total bird density, number of species per plot and Shannon diversity. Greater gamma-diversity in Karabash together with lower species richness per plot (alpha-diversity) indicates a greater differentiation of the local communities (beta-diversity) near Karabash than those near Revda. This may be due to the lower structural complexity of the Karabash forests (lower tree diversity, height, stand basal area and thickness of understorey, Table S1), which limits the alpha-diversity.

Despite different species compositions of birds and habitat characteristics (deciduous forest with sparser stand and understorey around Karabash vs. coniferous one around Revda), we observed almost the same species decline with pollution (Table S2). These are hole-nesters (pied flycatcher in both regions; great tit, willow tit and marginally great spotted woodpecker *Dendrocopos major* in Karabash; red-

Table 3 Associations of bird density and diversity with habitat variables (multiple regression, $n = 40$ plots in each region). Significant values ($p < 0.05$) are italicized

Indices	Stand basal area		Cover of understorey		Cover of field layer		Tree diversity (Shannon)		Whole model
	t	p	t	p	t	p	t	p	R^2
Karabash									
Total density[a]	0.89	0.379	0.50	0.622	*2.49*	*0.018*	− 0.48	0.636	*0.665*
Species richness per plot	*2.78*	*0.009*	1.29	0.206	*3.29*	*0.002*	− 1.12	0.273	*0.746*
Shannon diversity	*2.65*	*0.012*	*2.35*	*0.025*	*2.69*	*0.011*	− 1.98	0.056	*0.743*
TMNTD$_{Ab}$[b]	− 1.73	0.094	− 1.21	0.236	− 1.41	0.170	0.01	0.995	*0.307*
FMNTD$_{Ab}$[b]	− 1.38	0.177	0.26	0.795	− 1.77	0.088	− 0.27	0.789	*0.323*
PMNTD$_{Ab}$[b]	− 2.27	*0.031*	− 0.48	0.638	− 0.16	0.873	− 0.69	0.494	*0.229*
Revda									
Total density	*4.94*	*< 0.001*	0.89	0.381	*2.87*	*0.007*	0.75	0.456	*0.546*
Species richness per plot	*2.67*	*0.011*	1.81	0.079	1.95	0.060	0.26	0.800	*0.321*
Shannon diversity	*2.37*	*0.024*	1.32	0.195	1.94	0.061	− 0.22	0.827	*0.246*
TMNTD$_{Ab}$	− 0.96	0.345	− 1.60	0.118	0.81	0.422	0.46	0.647	0.076
FMNTD$_{Ab}$	0.03	0.976	− 1.05	0.303	− 0.28	0.781	− 0.12	0.908	0
PMNTD$_{Ab}$	− 0.04	0.968	− 1.29	0.205	0.79	0.438	0.21	0.839	0

[a] For total density in Karabash spatial autoregressive model was used

[b] For MNTD$_{Ab}$ in Karabash $n = 36$ with industrial barren excluded

breasted flycatcher and marginally coal tit *Parus ater* in Revda); common chaffinch, which prefers nesting on trees; and consumers of soil invertebrates, mainly earthworms (song thrush in both regions, and scaly thrush in Revda). In addition, species suffering from pollution include Eurasian bullfinch (prefers nesting on pollution-sensitive conifers), greenish warbler *Phylloscopus trochiloides* and Eurasian blackcap *Sylvia atricapilla* in Revda and common chiffchaff *Phylloscopus collybita* in Karabash. Most other mass species also tend to reduce their abundance with increased load. Only tree pipit *Anthus trivialis* tended to increase its density with pollution in Revda, as in spruce forests in Central Europe (Flousek 1989). This species of fringes and glades does not like thick dark coniferous forest, which becomes more sparse and favorable for the tree pipit due to pollution. In contrast, a light deciduous forest around Karabash with plenty of glades in unpolluted

areas is favorable for the tree pipit. In this region, a pollution-induced deterioration of vegetation, especially in the field layer, apparently is a reason for reduced density of this species. The observed responses to pollution agree with earlier results on the vulnerability of typical forest species, particularly, ground foraging European robin *Erithacus rubecula* and thrushes as well as crown foraging in conifers kinglets and tits and hole-nesting tits and flycatchers (Belskii and Belskaya 2013a; Belskii and Lyakhov 2003; Eeva et al. 2002; Flousek 1989; Tomek 1992).
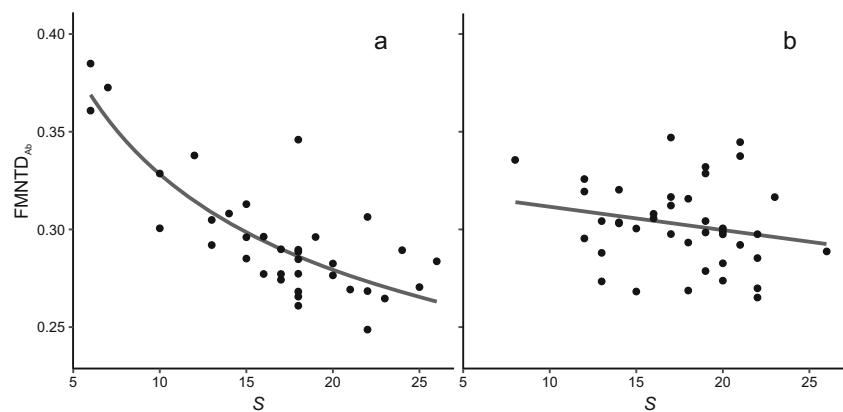
Species of open habitats, which increase in density with pollution, support the conclusion that pollution affects bird communities indirectly via habitat change. Long-distance migrants dominate the bird communities in both study regions. These species choose nesting sites according to their habitat preferences, as they are not able to assess the level of pollution.

Table 4 Proportion of the total variance (η^2) attributable to interaction between diversity indices near Karabash (above diagonal) and Revda (below diagonal). Significant interactions ($p < 0.05$) are italicized

Diversity index	S		H		TMNTD$_{Ab}$		FMNTD$_{Ab}$		PMNTD$_{Ab}$	
	η^2	p	η^2	p	η^2	p	η^2	p	η^2	p
S	–	–	0.003	0.672	*0.388*	*< 0.001*	*0.365*	*< 0.001*	*0.366*	*< 0.001*
H	0.001	0.827	–	–	*0.354*	*< 0.001*	*0.333*	*< 0.001*	*0.333*	*< 0.001*
TMNTD$_{Ab}$	*0.181*	*< 0.001*	*0.185*	*< 0.001*	–	–	0	0.941	0.001	0.848
FMNTD$_{Ab}$	*0.149*	*< 0.001*	*0.154*	*< 0.001*	0	0.971	–	–	0	0.911
PMNTD$_{Ab}$	*0.120*	*0.002*	*0.126*	*0.001*	0.002	0.694	0.002	0.693	–	–

S, species richness; *H*, Shannon diversity index; η^2, effect size; *p*, observed *p* value

Fig. 6 Association of functional
mean nearest taxon distances
(FMNTD$_{Ab}$) with bird species
richness near Karabash (**a**,
industrial barren excluded, $n =$
36) and Revda (**b**, $n = 40$)

The toxic effects on birds appear mainly during nesting. The poor reproduction of birds in polluted areas (Alaya-Ltifi et al. 2012; Belskii et al. 2005; Berglund and Nyholm 2011; Eeva and Lehikoinen 1995, 1996; Janssens et al. 2003; Nyholm 1994) is unlikely to affect the abundance of birds in subsequent seasons due to significant annual renewal of nesting populations in most species. Our data support the importance of habitat variables (especially the tree stand and field layer) for bird density and diversity. The latter are greater in more structured and diverse habitats providing birds with more diverse food and nesting sites (Cody 1974; MacArthur and Levins 1967). That is, the more diverse the habitat resources are, the greater the possibilities for divergence of niches of sympatric species and the more species that can coexist. Decreased bird density and diversity due to pollution in both our study regions is in good agreement with the deterioration of the forest habitat and simplification of its spatial structure.

A comparison of the two study regions showed that the pollution affected the bird density and diversity more strongly in Karabash than in Revda. We expected greater effects in coniferous forests (near Revda) than in deciduous forests (near Karabash) because coniferous forests are more vulnerable to industrial pollution (Sazonova and Olchev 2010). Differences between regions in habitat characteristics and pollution level may explain the observed effect. The Karabash region is located on the border between the southern taiga and forest–steppe with a drier and hotter climate compared to Revda, which is located farther north. The mean temperature of the vegetation period (April–September) in Karabash is 13.7 °C and in Revda 12.9 °C and precipitation is 231 and 264 mm, respectively. Measurements in July 2010 showed that the soil temperature near Karabash was 3 °C greater than that near Revda (Smorkalov and Vorobeichik 2011). Furthermore, the forest soils around Karabash are not as thick and are more stony when compared to Revda (Kozlov et al. 2009). Apparently, less favorable climatic and soil conditions resulted in a lower tree height, stand basal area, tree diversity and lower understorey cover in Karabash (Fig. S3, Table S1). Undoubtedly, the simpler spatial structure of the habitats near Karabash determined

their lower ecological carrying capacity. In addition, the industrial emissions in Karabash remained stable over the study period, whereas in Revda they decreased significantly after the reconstruction of the enterprise. The large amount of the SO$_2$ not captured by the filters made the emissions in Karabash more toxic than in Revda. This resulted in a higher deterioration of the forest ecosystems around Karabash that peaked as a vast industrial barren with eroded soil and almost no vegetation. The barren area near Revda is much smaller (Kozlov et al. 2009). Thus, the greater effect of the pollution on birds in Karabash is consistent with the conclusion that the community under environmental stress (i.e., less favorable climatic and soil conditions) reacts more strongly to additional stress factors (i.e., pollution) (Helmus et al. 2010).

Pollution-related patterns differed in traditional and distance-based indices. Moreover, there were differences between the regions. Species richness and Shannon diversity decreased at severe pollution. At the same time, the distances between nearest neighbors increased near Karabash indicating increased pollution-induced within-community differentiation and did not change near Revda indicating stable dissimilarity between species (Fig. 5). Increases in MNTD$_{Ab}$ near Karabash indicated greater distances at the level of the terminal branches due to a loss of taxonomically, functionally and phylogenetically related species. The number of closely related species (species of the same genus or family) decreased towards the smelter (Fig. 3a). Closely related species disappear apparently due to a simplification of the habitat structure and decrease in the ecosystem productivity caused by pollution. A reduction in the resources available to birds results in higher competition between species, primarily between species with similar ecological characteristics and ecosystem functions. In polluted areas, functionally similar species disappear from the community first because of competition. In contrast, more complex and productive habitats distant from the smelters allow the coexistence of a larger number of functionally similar species. Thus, the decrease in the nearest taxon distances far away from the Karabash smelter agrees with the ecological niche theory predicting that the habitats with more

structured vegetation can support more bird species (Cody 1974; MacArthur and Levins 1967).

The elimination of closely related species towards the Revda smelter (Fig. 3b) was less pronounced when compared to Karabash (Fig. 3a). The loss of typical forest species in polluted area near Revda was lower than in Karabash and to a greater extent was compensated for by species from open habitats and forest edges thanks to the remaining field and shrub layers, which provide the necessary food supply and protection for nests. Most species of open habitats and forest edges are functionally similar (left part of the ordination plot, Fig. 4). They are small passerines, most are the long-distance migrants: Blyth's reed warbler *Acrocephalus dumetorum*, tree pipit, European goldfinch, yellowhammer, white wagtail, northern wheatear, common redstart *Phoenicurus phoenicurus*, willow warbler, whinchat, garden warbler *Sylvia borin* and common whitethroat *S. communis*. These species forage on shrubs, in grass, on the ground or in surface air (white wagtail) and nest on the ground or low in grass or bushes. Many species are able to use plant food (European goldfinch, yellowhammer, common redstart and typical warblers). The more functionally similar species appear in polluted areas, the fewer the changes in the functional nearest taxon distances in the community. So, along the pollution gradient in Revda, the bird community gained twice as many new species as in Karabash. Although taxonomic distances between species increase at the most polluted site in Revda, the functional dissimilarity remains at the same level (Fig. 6), which indicates a selection of functionally similar species (environmental filtering).

Note that the taxonomic and functional mean nearest taxon distances depend nonlinearly on the species richness in Karabash. At high and moderate species richness the taxonomic, functional and phylogenetic shortest distances vary less than the number of species (Fig. 6). That is, species elimination at low and moderate toxic loads is equally probable and not related to their taxonomic, functional and phylogenetic characteristics. This indicates functional redundancy in the bird communities of the background and slightly polluted areas. Only at high loads, when the species richness is low, closely related and functionally similar species disappear from the community first.

The formal test with the standardized effect size did not confirm the importance of environmental variables in the bird community assembly along the pollution gradients. The taxonomic, functional and phylogenetic structure of local communities in both regions did not differ from the random one, at almost all of the sites. This indicates that the environmental filtering and competition between species as a whole did not affect the bird community assembly. This conclusion is in conflict with considerable pollution-induced transformation of forest ecosystems in both study regions, which inevitably should result in selection of few tolerant species at high load.

Our results are consistent with the conclusions of other researchers that ecosystem disturbances do not always affect the functional diversity and structure of the bird communities. For example, the functional distances between bird species did not depend on the burn frequency in Amazonian forests subjected to fires. Furthermore, the community structure did not differ from that expected by chance (Hidasi-Neto et al. 2012), despite the fire affecting the bird diversity and abundance (Barlow and Peres 2004). These authors showed that bird communities differing in composition can be similar in functional diversity and structure, as observed in the heavily polluted area near Revda. The study of frugivorous bird assemblages in tropical Ands showed that species richness, functional richness and phylogenetic diversity decreased with increasing elevation while functional and phylogenetic distances between species increased (Dehling et al. 2014). In this study, the analysis of the nearest taxon distances did not reveal differences in the community structure from that expected by chance, while the mean pairwise distances between the species were more informative. Apparently, various indices differ in their ability to reflect changes in community structure.

A comparison of the traditional and distance-based diversity measures showed that their dynamics along the pollution gradient differed between the two groups of indices but not within them (Table 4). The three dissimilarity indices showed the same pollution-related dynamics because the functional characteristics are similar in closely related species, and the taxonomic and phylogenetic classifications largely coincide (Connolly et al. 2011; Gerhold et al. 2015). Thus, indices belonging to the same group produce similar results and the number of indices can be reduced without a loss of information. The taxonomic diversity is preferable over the phylogenetic one because of much easier calculation. The simpler approach might facilitate the use of bird communities as indicators of ecological changes.

Conclusion

An analysis of the abundance and diversity of forest birds along the pollution gradients in two regions showed good repeatability in the results, thereby indicating a weak dependence of the bird communities on the weather conditions of a particular year. The total density of nesting birds, number of species per plot and Shannon diversity of local bird communities in Karabash were on average less than those in Revda, despite the greater gamma-diversity. In both study regions, the total bird density, species richness and Shannon diversity decreased at high toxic load. Species dissimilarity within local communities increased with pollution in Karabash due to a loss of functionally similar species, but it did not change in Revda, which is likely due to a mass replacement of forest species by species of open habitats and forest edges.

Pollution-induced changes in the bird communities near Karabash were greater than those near Revda due to a stronger deterioration in the forest ecosystems and less favorable natural conditions (more arid climate, less diversity and vitality of the tree stand and understorey). In both regions, there was evidence for taxonomic, functional and phylogenetic redundancy in bird communities far away from the pollution sources, thereby indicating stable ecosystems with complex structure and productivity high enough for the coexistence of similar species. Our study emphasizes the need for a multi-level approach to the analysis of bird communities when using traditional indices of diversity, measures based on functional, taxonomic or phylogenetic distances between species and environmental variables.

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