Null model analysis of spatial species associations in spruce, tree line and dwarf-pine bird assemblages in the High Tatras, the Western Carpathians

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Abstract

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Jared Diamond proposed several assembly rules based on the assumption of competitive interactions among species. The first Diamond's rule proposes that communities are formed of certain permissible combinations of species that can co-exist. The fifth assembly rule states that some pairs of species never co-occur, forming so called "checkerboard" or complementary distributions. The objective of this study was to test these propositions on spruce, tree-line and dwarf-pine bird assemblages censused by the fixed radius point count method in the High Tatras, Slovakia. The null model simulations yielded no clear assembly patterns. The binary null models had tendency toward random associations, while quantitative null models suggested segregations. Presence/absence null models showed tendency toward random associations in post-breeding and breeding spruce bird assemblages, while quantitative null models yielded half random and half segregations in post-breeding season and all types of associations were detected during the breeding with slight prevalence of segregation. All binary tests indicated random associations in the post-breeding bird assemblages in the upper tree line and dwarf pine communities, whereas quantitative models showed prevalence of segregation. Binary models indicated slight prevalence of random associations in the breeding bird assemblages of the upper tree line and dwarf pine communities from territorial records and prevalence of segregation from all records. Quantitative models did not show consistent results in these habitat types detecting prevalence of segregations. In summary, the first Diamond's rule was not supported due to random patterns of unique species combinations and the fifth rule was supported partly by quantitative null model analyses.

Keywords

binary null models, bird communities, co-occurrence, quantitative null models, species associations

Introduction

Null model analyses of spatial and temporal species associations are commonly applied on testing hypothesis of compensatory dynamics and complementary distributions (e.g. Gotelli, 2000; Gotelli and McCabe, 2002; Ulrich and Gotelli, 2010; Korňan, 2013; Korňan and Kropil 2014). Compensatory dynamics and checkerboard distributions assume negative covariance of competing species in spatial and temporal patterns. These phenomena may be tested on the level of two or several species, guild/s, and assemblage or community.

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Compensatory dynamics and checkerboard distributions have played a crucial role in the development of competitive bird assemblage concepts (Lack, 1971; MacArthur, 1972; Cody, 1974; Diamond, 1975; see Wiens, 1989; Gonzalez and Loreau, 2009 for review). Initially, interspecific competitive interactions were viewed as the dominant force of nature driving spatiotemporal patterns and coexistence among species for decades. In the first half of 1980's, the competitionist view was heavily criticized (see Wiens, 1989 for review). At that time, bird community assemblage, began to be viewed as being much more complex, resulting from competition as well as many other processes, including food resource abundance, stochastic weather events, habitat change, winter mortality, predation, parasitism, other disturbances etc. later referred to "pluralistic concept" (Holmes et al., 1986; Wesołowski and Tomiałojć, 1997; Korňan, 2013; see Wiens, 1989; Brawn et al., 2001 for review). Thus, the pluralistic concept combines biotic and abiotic processes influencing survival of populations forming communities and operating on various temporal and spatial scales. Based on experimental evidence, however, some authors still consider interspecific competition as the primary factor (see Dhondt, 2012 for review). Moreover, competitionist view (complementary distribution) sensu Diamond's assembly rules was supported by community wide analyses of many taxonomical groups from compiled data matrices (Gotelli and McCabe 2002, Ulrich and Gotelli 2010). Furthermore, negative co-occurrence patterns revealed by null model analyses that support the competition theory were detected in wide range of assemblages, e.g. diatoms (Heino and Soininen, 2005), ants (Badano et al., 2005), fish (Bhat and Magurran, 2007), bird (Sarà et al., 2006), and small mammals (Abu Baker and Patterson, 2011). In contrast, other authors reported opposite results also from compiled data matrices of wide range of taxonomic groups (Schluter, 1984; Houlahan et al., 2007). In addition, a number of other studies analysing various taxonomic group assemblages, e.g. zooplankton (Jenkins, 2006), crustaceans (Sfenthourakis et al., 2006), fish (Perez-Neto, 2004), birds (Gotelli et al., 1997, Feeley, 2003, Wang et al., 2011), and carnivores (Šálek et al., 2014), detected prevalence of random or positive species associations in co-occurrence patterns tested out by various null models and indices.

The results to date are contradictory, and discussion on the relative importance of interspecific competition continues. Nevertheless, other community processes e.g., unique habitat associations, limited dispersal, historical and evolutionary processes that prevent species co-occurrence may generate negative species associations, as well as missing species combinations (Ulrich and Gotelli, 2007). The topic of general validity of competition processes in complementary distribution patterns remains unresolved and further studies and needed.

The primary objective of this study is to test Diamond's first and fifth assembly rules (Diamond, 1975, p. 344) on the data set of breeding and post-breeding bird assemblages in spruce, upper tree line and dwarf pine bird assemblages. The first and fifth Diamond's assembly rules states: "(1) If one considers all species combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature. (5) Some pairs of species never coexist, either by themselves or as part of a larger combination." The working questions for our research were as follows: The first objective of our research was to determine whether the spatial and abundance patterns of birds in our study supported the role of interspecific competition, as proposed by Diamond. Are the studied bird assemblages formed by specific species combinations under interspecific competition assumptions that permit specific community structure? Do the spatial patterns observed in our study system support assumption of complementary (checkerboard) distribution? We applied binary and quantitative null models and co-occurrence indices to test these hypotheses on assemblage level.

The study was conducted in three main types of habitat during breeding and post-breeding seasons. The second objective is to test effect of habitat type and season on assembly patterns. Because habitat and seasonal effects can influence bird assemblage structure and assembly rules, we proposed two hypotheses: (1) More structured assembly patterns (negative associations) should occur in the breeding season because of the territorial patterns exhibited by birds at that time. Conversely, random species associations are more likely to occur in the post-breeding period when birds do not defend territories and move more opportunistically. (2) Bird assemblages of spruce forests should indicated stronger assembly coming from species competitive interactions than those in dwarf pine habitats. This is due to higher species richness and mean population and total assemblage densities in spruce communities. Consequently, we assume stronger tendency toward complementary distribution (segregation, negative species associations) in spruce communities than dwarf pine and upper tree line communities, in which we expect tendency toward disassembly (random species associations).

Material and methods

Study area

The research was performed in the High Tatras, the Western Carpathians, North-central Slovakia. The bird point count transects were conducted in the Furkotská, Mlynická and Mengusovská valleys in the wider area

of Štrbské pleso ski resort. Air temperatures in July average about 10 and 12 °C. Mean annual precipitation varies between 1,200-1,600 mm. Snow cover lasts 140–200 days in a year (Miklós et al., 2002).

The study area is covered by spruce, upper tree line and dwarf pine communities. Spruce forest were dominated by Norway spruce (*Picea abies*), with an admixture of European larch (*Larix decidua*) and Rowan (*Sorbus aucuparia*). Upper tree line communities consisted of Dwarf pine (*Pinus mugo*), Swiss pine (*Pinus cembra*), European larch and Norway spruce with an admixture of Common aspen (*Populus tremula*) and Goat (Pussy) willow (*Salix caprea*). Dwarf pine communities were composed of dwarf pine with some Norway spruce, Swiss pine, Goat willow and Common aspen. The study area is covered by continuous forest cover and was in some places affected by damaging windstorm in 2004.

Bird counts

Birds were counted by the fixed-radius point count method in post-breeding season in 2008 and breeding season in 2009 (Bibby et al., 2000). Count point radius of 50 m was used in spruce communities, while radius of 100 m was applied for counting in tree-line and dwarf-pine communities. Radius of 50 m is generally recommended for closed habitats such as forests, whereas radius of 100 m is suitable for open habitats such as meadows, pastures, etc. Radius of points was estimated by eye. During bird counting, all visual and acoustic records of birds were positioned into standardized field sheets. Distances of calling birds were not included into the analyses of population abundances by detectability functions that could increase accuracy of estimates. For presence/absence data this procedure is not necessary. Count points were positioned by a GPS apparatus. Minimum distance between count points was at least 200–300 m estimated by walking. Population and total assemblage densities were computed from all samples (pooled data) for each habitat. Primary data sets are archived by the first author and are available upon request.

During post-breeding season, birds were counted along four point transects. The first transect (transect A, 7 points) was located along the ski chairlift cleared corridor beginning in Štrbské pleso and ending on Solisko. This transect intersected spruce (three points), upper tree line (two points) and dwarf pine communities (two points). The second transect (transect B, 6 points) was located in upper tree line (one point) and dwarf pine communities (five points) in broader area of Solisko. The third transect (transect C, 8 points) was set in spruce (four points) and upper tree line communities (four points) in the area of Solisko. The fourth transect (transect D, 9 points) was situated along the

tourist trail Štrbské pleso – Popradské pleso (red line) crossing mainly spruce forest (seven points) less upper tree line (one point) and dwarf pine communities (one point). In total, two to five samples (counts of all points per transect per season) were carried out on these transects (Fig. 1). Two standardize sampling effort, we used only two samples per season around same dates, i.e. 12–13 July 2008 and 1–2 August 2008 between 4:03 and 10:00 Central European Time (CET). Bird counting was conducted by both authors, each two transects.

During breeding season, bird counts were carried out in the period from 20 May 2009 to 20 July 2009 on four point transects. Birds were sampled four times per breeding season on all transects. Three samples were conducted in the mornings between 4:52 and 10:29 CET and one bird count was in evening between 16:27 and 20:56 CET. The first transect (transect A) was located along the ski chairlift cleared corridor beginning in Štrbské pleso and ending on Solisko. This transect had seven points and crossed three habitat types: spruce forest (three points), upper tree line communities (two points), and dwarf-pine communities (two points). Bird sampling was carried out on this transect in the following dates 20 May, 17 June, 3 July and 20 July. The second transect (transect E) was located along the tourist trails beginning at the inn Chata pod Soliskom toward the Furkotská valley (blue line) and from the crossing point in the Furkotska valley toward Štrbské pleso (yellow line). The second transect had five count points, out of which two points were in upper tree-line community and three points in dwarf-pine community. The bird counting was carried out on 22 May, 17 June, 30 June and 6 July. The third transect (transect F) lay in Mlynická valley and consisted of five count points spread in spruce forest. The bird counting was conducted on 20 May, 1 July, 8 July and 18 July. The fourth transect (transect G) was set along the tourist trail Štrbské pleso – Popradské pleso (red line) consists of 13 count points, out of which eight were located in the spruce forest, three were in upper tree line communities and two points were in the dwarf-pine communities (Fig. 1). Bird counting was performed on 21 May, 19 June, 1 July and 19 July. Bird counting in the breeding season was performed only by MK.

Data matrix preparation

Data matrices were separately constructed for post-breeding season 2008 and breeding season 2009 in MS Excel 2007. Each type of bird assemblage was characterized by pooled data of all points of this habitat type from all transects. One type of data matrix was prepared for post-breeding data from all record. Two types of data matrices were prepared for breeding data. The first data matrix type was set up from all records (territorial song, non-territorial call, visual records), whereas the second
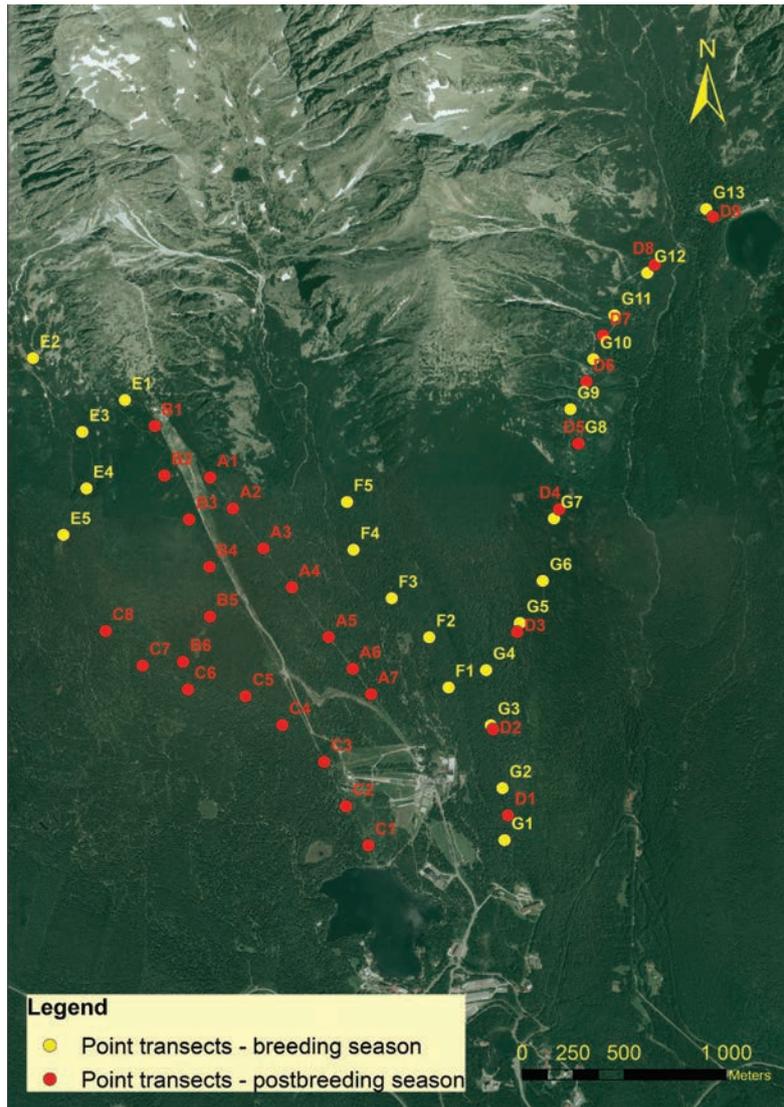
Fig. 1. Map of bird count point transect locations in the study area.

data matrix type was constructed only from territorial records. We expected clearer patterns of complementary distribution in territorial matrices because these data covered birds that presumably bred in the given points, whereas matrices with all records also contained non-breeding individuals (floaters, juveniles) that did not have to necessarily show spatial interactions due to spatial movement. Territorial records consisted only of counts of singing territorial (stationary) males. All matrices were composed of species abundance values (whole integers) per 50 m or 100 m radius point samples. The binary data matrices were constructed from the quantitative data matrices simply by transforming quantitative information into binary code (as either present or absent).

Two matrices were prepared for post-breeding season bird assemblages. One matrix described upper tree line (8 points) and dwarf pine (8 points) communities (24 species × 16 points) and one matrix for spruce com-

munities (16 species × 14 points). Two breeding data matrices (15 species × 14 points, 19 species × 14 points) was prepared for dwarf-pine (7 points) and upper tree line samples (7 points) and two matrices (16 species × 16 points, 21 species × 16 points) was constructed for spruce communities.

Statistical analyses

In order to test species co-occurrence patterns in spatial data sets in the simplest form, four binary (presence/absence) indices were used – number of checkerboards (CHECKER), variance ratio (V-ratio), checkerboard score (C-score) and number of unique species combination (COMBO). The number of checkerboard index counts the number of species pairs in the data matrix forming perfect checkerboards (Diamond, 1975; Gotelli, 2000). The second applied index for testing species association is variance ratio (Schluter, 1984;

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GOTELLI, 2000). The index is based on computation of the ratio of the variance in total species number in point samples to the sum of the variances of the individual species (SCHLUTER, 1984). Similar to CHECKER is the checkerboard score (STONE and ROBERTS, 1990; GOTELLI, 2000). This index examines checkerboard patterns, or lack of them, over all pairs of sites (STONE and ROBERTS, 1990). The index number of species combinations was proposed by PIELOU and PIELOU (1968) in order to test for a number of specific species combinations in a community structure. GOTELLI and MCCABE (2002) argue that this index is directly designed to test Diamond's first and second assembly rules.

To test species covariation from quantitative data matrices, three quantitative covariance metrics – quantitative number of checkerboards (CA_{ST}), quantitative number of aggregations (AA_{ST}), and the Chao's index of similarity for n communities (MA) were used in null model analyses. The quantitative index number of checkerboards is the analog of the presence/absence checkerboard index with abundance or density data (ULRICH and GOTELLI, 2010). The second applied metric for measuring quantitative species association was the number of quantitative aggregations. The index is a count of aggregated species by site 2×2 submatrices in the matrix (ULRICH and GOTELLI, 2010). The third used matrix was the Chao's index (CHAO et al., 2008; ULRICH and GOTELLI, 2010). The index values in communities driven by competition processes should be significantly lower than in randomized data matrices by null models.

Binary null models are designed for analyses of binary (presence/absence) matrices. A total of nine null model solutions is possible to apply for analysis of presence/absence data matrices (GOTELLI, 2000). We applied only null models with best statistical properties regarding low rates of statistical Type I and Type II errors. Low Type I error rate means that the algorithm does not have high rate of identification of random matrices as structured, whereas the low Type II error rate indicates that the algorithm does not have high rate of classification of structured matrices as random. Only two binary null models, SIM2 (row sums fixed and column equiprobable constrain) and SIM9 (sums of rows and columns fixed constrain), had acceptable statistical error rates (GOTELLI, 2000). The algorithm SIM9 was not applicable for simulations by V-ratio index.

We used same statistical criteria as described above for selection of optimal quantitative null models algorithms with low rates of statistical errors. The optimal solution based on wide diagnostic testing of null model algorithms and indices by ULRICH and GOTELLI (2010) for analyses of quantitative data matrices are algorithms IT (aa) and IA (rc). Algorithm IT assigns individuals randomly to matrix cells with probabilities proportional to observed row and column abundance totals until, for each row and column, total abundances are reached (ULRICH and GOTELLI, 2010). Algorithm IA reassigns all individuals randomly to matrix cells with probabilities proportional to observed row and column abundance totals until the matrix-wide total number of individuals is reached (ULRICH and GOTELLI, 2010). This algorithm can generate matrices with empty rows or columns.

Binary null model analyses were performed in the numerical package ECOSIM 7.0 (GOTELLI and ENTSMINGER, 2001) and quantitative null model analyses were done in TURNOVER 1.1 (ULRICH, 2010). Sequential swap randomization algorithm was used for randomizations of the original data matrices by binary null models. Since we were interested in the variance of these indices to the both sides, i.e. we searched for segregation as well as for aggregation patterns in species distribution, two-tailed tests were used to test for significance of the observed index values. Two-tailed tests in binary analyses and one-tailed tests (package limitation) in quantitative analyses were applied with the aim to test all possible outcomes (negative, positive, and random associations) of null model analyses. We used 10,000 iterations in all simulations and statistical threshold level was set on $\alpha = 0.05$.

Results

Characteristics of bird assemblages

During the breeding season (all records), we detected a total of 21 bird species at 16 points in spruce communities. The bird assemblage was dominated ($x \geq 5\%$) by Common chaffinch *Fringilla coelebs* (22.6%), Coal tit *Periparus ater* (15.9%), Goldcrest *Regulus regulus* (13.5%), Eurasian robin *Erithacus rubecula* (11.5%), Eurasian treecreeper *Certhia familiaris* (7.5%), and Eurasian siskin *Carduelis spinus* (5.6%). The total breeding bird assemblage density was estimated on 200.5 ind./10 ha. Post-breeding season bird assemblages in spruce forests were species poor, with only 16 bird species were detected in 14 bird count points in 2008. In total, six species – Coal tit (28.6%), Goldcrest (19.1%), Crested tit *Lophophanes cristatus* (10.2%), Common crossbill *Loxia curvirostra* (8.8%), Spotted nutcracker *Nucifraga caryocatactes* (8.2%), and Common chaffinch (6.8%) were classified as dominants. The total post-breeding bird assemblage density was estimated on 133.7 ind./10 ha.

Species richness of the breeding bird assemblage of the dwarf pine and upper tree line communities was 19 species from pooled data from 14 points (all records). Dunnock *Prunella modularis* (31.1%), Common chiffchaff *Phylloscopus collybita* (13.0%), Common chaffinch (9.3%), Eurasian blackcap *Sylvia atricapilla* (8.5%), Eurasian robin (6.7%), Willow warbler *Phylloscopus trochilus* (6.7%) and Goldcrest (5.2%) were the dominant species in the assemblage. The total

breeding bird assemblage density was estimated on 61.4 ind./10 ha. Post-breeding bird assemblage of this habitat had pooled species richness 24 species from 16 points. The post-breeding bird assemblage was dominated by five species: Common crossbill (32.9%), Spotted nutcracker (16.1%), Common chiffchaff (11.8%), Coal tit (9.1%) and Lesser redpoll *Acanthis cabaret* (6.5%). The total density of the post-breeding bird assemblage of dwarf pine and upper tree line communities was estimated on 37.0 ind./10 ha.

Null model analyses

Spruce bird assemblages
The results of binary null model simulation by SIM2 algorithm and four co-occurrence indices showed half random associations and half positive associations (Table 1) in post-breeding bird assemblage of spruce forest point samples. Only random associations were detected in the same assemblage when tested by SIM9 algorithm and three indices. Null model analysis by IT (aa) algorithm and three species association indices of spruce bird assemblage detected 67% of random patterns and 33% segregations (Table 2). IA (rc) algorithm in simulations by the same indices and the bird assemblage showed opposite patterns (67% segregations, 33% random associations). Null model simulations by SIM2 and SIM9 algorithms and all indices detected random associations in all cases when testing breeding bird assemblage of spruce forest from territorial or all records (Table 1). Simulations by IT (aa) algorithm and three indices of breeding bird assemblage of spruce forest from territorial records indicated dichotomous patterns (aggregation, segregation, and random associations). Each index yielded different association result (Table 2). Two segregations and one random association were detected from the same assemblage from all records. IA (rc) algorithm showed consistent pattern for territorial and all records regarding the species association output related to index type, however, again each index revealed different associations (aggregation, random, segregation).

Dwarf pine and upper tree line bird assemblages
Null model analysis by SIM2 and SIM9 algorithms and four indices of dwarf pine and upper tree line post-breeding bird assemblages indicated random associations in all cases (Table 1). Simulations by IT (aa) and IA (rc) algorithms and three indices of dwarf pine and upper three line bird assemblage yielded 67% of negative associations and 33 % random associations (Table 2). The simulations by both algorithms of dwarf pine and upper three line assemblages showed identical results for all combination of algorithm and index.

Co-occurrence pattern simulation results of dwarf pine and upper three line breeding bird assemblages differed when considering combination of individual

algorithms and indices (Table 1). Testing of species associations by SIM2 algorithm and four indices showed consistent pattern for territorial and all records when considering combination of individual algorithms and indices (67% positive associations, 33% random associations). Yet, simulations by SIM9 algorithm and three indices detected 67% of random associations and 33% of segregation when analyzing territorial records. Simulations by the same algorithm and indices from all records showed opposite pattern (67% of segregations, 33% random associations). Results of null model simulations by IT (aa) and IA (rc) algorithms indicated the consistent results in testing dwarf pine and upper tree line breeding bird assemblages for territorial and all records for all combinations of algorithm and index (Table 2). Nevertheless, IT (aa) algorithms detected four segregations and two random associations, whereas IA (rc) algorithms revealed four segregations and two aggregations.

Discussion

Design of null models

We selected binary (presence/absence) and abundance null models with lowest rate of statistical Type I and Type II errors (GOTELLI, 2000; ULRICH and GOTELLI, 2010), thus results should have acceptable statistical power. Another problem is the size of data matrices. We used six data matrices (24×16, 16×14, 15×14, 19×14, 16×16, 21×16) that are relatively small enhancing only low statistical power of analysis (GOTELLI and MCCABE, 2002). This can be possibly one of the causes of high rate of nonsignificant results (community disassembly). Low sample size from upper tree line and dwarf pine communities caused that we have to combine these two habitats into one data matrix. This was the only way to include these two habitats in the null model analyses. The main reason of low sample sizes was the small size of the research area, in which it was impossible to obtain more bird counts samples. Combining dwarf pine and upper three line communities into one data matrix created a natural ecological gradient, since these two habitats are floristically and structurally more similar then spruce forests.

Null model outcomes and possible scenarios

Post-breeding bird assemblage of spruce, upper tree line and dwarf pine communities analyzed by binary null models showed no assembly because 71% of simulations of spruce forest and 100% of simulations of upper tree line and dwarf pine bird assemblage indicated random associations. The simulations of the index number of species combinations revealed random associations in all cases. Therefore, the results do not support

Table 1. Results of the binary null model analyses by the SIM2 (row sums fixed and column equiprobable constrain) and SIM9 (sums of rows and columns fixed constrain) algorithms with four indices (CHECKER – number of binary checkerboards, Combo – number of unique species combinations, C-score, V-ratio) of post-breeding and breeding bird assemblages of spruce, upper tree line and dwarf pine communities in the High Tatra Mts. Observed values of individual indices, their simulated values (10,000 iterations), statistical probability at $\alpha = 0.05$ (two-tailed test), and the types of detected species associations are given. Explanations: Obs. – observed value of an index, Sim. – mean of the simulated values of an index, P1 – left tail probability (observed <= expected), P2 – right tail probability (observed >= expected).

Site/index	CHECKER				Combo				C-score				V-ratio			
	Obs.	Sim.	P1	P2	Obs.	Sim.	P1	P2	Obs.	Sim.	P1	P2	Obs.	Sim.	P1	P2
Post-breeding season																
SIM2 algorithm																
Spruce communities	38	45.32	0.0565	0.9615	14	13.94	1.0000	0.9387	4.53	5.54	**0.0122**	0.9881	2.22	1.00	0.9963	**0.0044**
Dwarf pine and upper tree line communities	171	176.05	0.2177	0.8208	16	15.95	1.0000	0.9519	3.79	4.04	0.1262	0.8766	1.57	1.00	0.9359	0.0763
SIM9 algorithm																
Spruce communities	38	38.53	0.5299	0.6120	14	13.89	1.0000	0.8902	4.53	4.31	0.9509	0.0537	–	–	–	–
Dwarf pine and upper tree line communities	171	167.00	0.8638	0.1863	16	15.91	1.0000	0.9081	3.79	3.75	0.6918	0.3219	–	–	–	–
Breeding season																
SIM2 algorithm																
Territorial records																
Spruce communities	50	50.17	0.5081	0.5984	15	15.19	0.5965	0.8150	3.25	3.60	0.1336	0.8710	1.40	1.00	0.8913	0.1414
Dwarf pine and upper tree line communities	41	39.70	0.6816	0.4329	13	13.84	0.1491	0.9923	3.05	4.55	**0.0006**	0.9994	2.78	1.00	0.9998	**0.0002**
All records																
Spruce communities	81	79.04	0.6876	0.3966	15	15.77	0.2142	0.9817	3.68	3.41	0.8791	0.1257	0.79	1.00	0.3298	0.7304
Dwarf pine and upper tree line communities	68	65.58	0.7335	0.3500	14	13.97	1.0000	0.9692	3.26	4.50	**0.0006**	0.9994	2.95	1.00	1.000	**0.0001**
SIM9 algorithm																
Territorial records																
Spruce communities	50	47.63	0.8928	0.1960	15	15.23	0.6029	0.8495	3.25	3.21	0.6799	0.3430	–	–	–	–
Dwarf pine and upper tree line communities	41	31.06	0.9968	**0.0058**	13	13.44	0.4799	0.9215	3.05	2.85	0.9694	0.0354	–	–	–	–
All records																
Spruce communities	81	81.22	0.5490	0.5889	15	15.80	0.1863	0.9879	3.68	3.52	0.9307	0.0741	–	–	–	–
Dwarf pine and upper tree line communities	68	52.94	0.9986	**0.0018**	14	13.89	1.0000	0.8868	3.26	3.03	0.9885	**0.0126**	–	–	–	–

Table 2. Results of quantitative null model analyses by the IT (aa) and IA (rc) algorithms with three indices (CA_{ST} – number of quantitative checkerboards, AA_{ST} – number of quantitative aggregations, MA – Chao's index of similarity of n communities) of post-breeding and breeding bird assemblages of spruce, upper tree line and dwarf pine communities in the High Tatra Mts. Observed values of individual indices, their simulated values (10,000 iterations), statistical one-sided probability at $\alpha = 0.05$ are given. The abbreviations of the algorithms and indices given in parenthesis follow TURNOVER 1.1 manual (ULRICH 2010).

Site/index	CA_{ST} (WCS)			AA_{ST} (Wtog)			MA (Chao)		
	Observed	Simulated	P	Observed	Simulated	P	Observed	Simulated	P
Post-breeding season									
IT (aa) algorithm									
Spruce communities	0.06	0.04	0.0800	0.11	0.13	0.2110	0.26	0.51	**0.0024**
Dwarf pine and upper tree line communities	0.03	0.02	**0.0274**	0.05	0.08	**0.0006**	0.20	0.52	**0.0002**
IA (rc) algorithm									
Spruce communities	0.06	0.05	0.4000	0.11	0.13	**0.0176**	0.26	0.48	**0.0016**
Dwarf pine and upper tree line communities	0.03	0.03	0.1812	0.05	0.08	**0.0002**	0.20	0.51	**0.0002**
Breeding season									
IT (aa) algorithm									
Territorial records									
Spruce communities	0.03	0.06	**0.0008**	0.05	0.12	**0.0002**	0.54	0.61	0.1768
Dwarf pine and upper tree line communities	0.04	0.06	0.0522	0.11	0.17	**0.0004**	0.49	0.69	**0.0070**
All records									
Spruce communities	0.04	0.06	0.0682	0.06	0.11	**0.0002**	0.66	0.63	0.3966
Dwarf pine and upper tree line communities	0.05	0.06	0.1598	0.12	0.15	**0.0144**	0.45	0.69	**0.0006**
IA (rc) algorithm									
Territorial records									
Spruce communities	0.03	0.07	**0.0002**	0.05	0.12	**0.0002**	0.54	0.60	0.1766
Dwarf pine and upper tree line communities	0.04	0.07	**0.0002**	0.11	0.17	**0.0002**	0.49	0.69	**0.0044**
All records									
Spruce communities	0.04	0.06	**0.0002**	0.06	0.10	**0.0002**	0.66	0.62	0.2262
Dwarf pine and upper tree line communities	0.05	0.07	**0.0002**	0.12	0.15	**0.0002**	0.45	0.68	**0.0022**

assumptions of Diamond 1 assembly rule. Quantitative null models applied for analysis of post-breeding bird assemblage of these two groups of habitats detected 50% segregations and 50% random associations for spruce bird assemblages and 67% segregations and 33% random associations. These patterns do not indicate clear assembly organization for these assemblages. However, there was a tendency toward segregations in dwarf pine and upper tree line communities, which supports the hypothesis of complementary distribution.

Binary null model analysis of the breeding bird assemblage of spruce forest from territorial and all records indicated random associations in all cases. The results for the dwarf pine and upper tree line bird assemblages were contradictory both for territorial and all records because all types of associations were observed. However, as before, random association prevailed in territorial records (57%) and all records (43%) showing tendency toward disassembly. Diamond 1 and 2 assembly rules were not supported due to random patterns of species combination index for all bird assemblages including territorial and all record samples in all cases. Quantitative null model analyses of spruce forest bird assemblage failed to support any clear assemblage organization pattern. Positive, negative and random associations occurred in even proportion except simulation by the IT (aa) algorithm of all records in which two random associations and one segregation occurred. Breeding bird assemblage of dwarf pine and upper tree line communities from territorial and all records revealed prevalence of segregation (67%) against random (17%) and positive associations (17%). This result supports complementary distribution hypothesis. Over all, the results of null model simulation did not yield any clear assembly patterns. In fact, binary null models had tendency toward random associations, while quantitative null models toward segregations.

Assembly rules are defined as the patterns mediated by interactions between species; these patterns if detected are evidence of competition, allelopathy, facilitation, mutualism and all other biotic interactions that affect real ecological communities (WILSON, 1999). Interspecific competition in communities can also be minimised by resource partitioning patterns along several axes: food, spatial, temporal, and thermal (e.g. LUISELLI, 2006; KORŇAN and ADAMÍK, 2007). In the next section, we primarily focus on spatial patterns of assemblages. DIAMOND (1975) proposed concept of assembly rules, e.g. checkerboard distribution, forbidden species combinations, incidence function, and established the notion that interspecific competition is the main natural mechanism driving these assembly rules. Coming from an example of a game board for draughts or checkers consisting of alternating squares of different colours, DIAMOND (1975) defined „checkerboard distribution" in which a member of a pair of species occupies only one colour that means, translating to real

nature, occupying different islands or spots in environment by only one species from the pair. The idea of checkerboard distribution was transferred to spatiotemporal patterns of communities that are known as complementary distribution and compensatory dynamics and has become one of the most widely tested concepts in ecology (CONNOR et al., 2013).

Studies of complementary distribution revealed contradictory results. Earlier, SCHLUTER (1984) meta-analyzed 37 presence/absence spatial matrices from various taxonomical animal groups by simple variance ratio test and came to conclusion that positive associations are the rule in nature while negative ones are uncommon, suggesting that complementary distribution were rare. More recently, GOTELLI and MCCABE (2002) conducted a meta-analysis of 96 data sets from studies reporting spatial distribution of various plant and animal taxonomic groups with application of binary null model (SIM9, fixed row and column totals) and three indices (number of checkerboards, C-score, and number of species combinations). They detected fewer species combinations, more checkerboard species pairs, and less co-occurrence in the analyzed matrices than expected by chance, thus supporting the concept of Diamond's assembly rules and complementary distribution. An even more recent meta-analysis of 149 spatial empirical abundance matrices and 36 interaction matrices collected from published papers and posted data sets showed that more 80% of these matrices were significantly segregated when analyzed by abundance IT null model with Chao's similarity index and variance ratio (ULRICH and GOTELLI, 2010). Negative species association were, in addition, reported in other studies analyzing e.g. diatom, ant, fish, bird, and mammal assemblages (KOBZA et al., 2004; BADANO et al., 2005; HEINO and SOININEN, 2005; SARÀ et al., 2006; ABU BAKER and PATTERSON, 2011). In contrast, there are numerous other studies from different taxonomic groups that detected prevalence of random or positive species associations carried out by various null models and metrics (e.g. FEELEY, 2003; PEREZ-NETO, 2004; SFENTHOURAKIS et al., 2006; JENKINS, 2006; WANG et al., 2011; CONNOR et al., 2013; ŠÁLEK et al., 2014). ULRICH and GOTELLI (2010) argue that prevalence of positive associations by the variance ration index in the studies of SCHLUTER (1984) and HOULAHAN et al. (2007) could be a result of improper statistical design. In fact, their analyses assumed equivalence of sites or times in the matrices in probability of occurrence of individuals of different species. ULRICH and GOTELLI (2010) point out that correct approach is to use the IT algorithm that preserves the columns totals for abundance incorporating differences in suitability or conditions among sites or times.

The meta-analyses results seem convincing, nonetheless they are not. After all, segregation results of null model analyses should be taken only as a signal of competition due to the fact that other community processes

e.g., unique habitat associations, limited dispersal, historical and evolutionary processes that prevent species co-occurrence may generate negative species associations and missing species combinations as well (Ulrich and Gotelli, 2007). Our study is purely based on species covariance and does not have experimental nature. To distinguish among these community processes, we would have to perform a well-designed field surveys and experiments that would enable us prove the mechanism of assembly processes.

Scale effects

Interspecific competition can operate on several spatial levels in different way and different assumptions can be drawn from microhabitat to landscape scale in relation to null model analysis design. Interference and exploitation competition can operate on the level of a single tree. An excellent example of the interference competition and predation risk effects is the guild of foliage gleaners of boreal forest, in which feeding position on a tree (leaves, twigs, branch, trunk) is influenced by dominance status of tit species (see review in Dhondt, 2012, p. 108–113). This model of species packing and resource partitioning enables co-existence of tits on microhabitat scale. Bird point counts on 50 or 100 m radius circular plots and consequent binary null models are not able to detect such interaction due too large scale at which they are conducted. In this case, species packing causes presences on a point sample, thus causing aggregation. Nevertheless, quantitative null models should be able to detect competitive interaction even in this case because exploitation and interference competition should effect population growth parameters that should be reflected in abundance changes among tit species on count point level (Dhondt, 2012).

Segregation at larger spatial scales such as bird count area scale or landscape scale might be divided into two not necessarily exclusive patterns. The first is spatial turnover, where species replace each other across a spatial gradient (Leibold and Mikkelson, 2002). The second is a checkerboard pattern, the mutual exclusion of species without clearly defined spatial gradients. This pattern is predicted by the principle of competitive exclusion (Diamond, 1975). Spatial turnover may be reflected in spatial patterns of density gradient turnover among competing species not necessarily by presence/absence turnover. The first model would be hardly detected by binary null models, while the second model as well as the presence/absence checkerboard pattern meets the assumptions of binary null model analysis. Quantitative null models are sensitive to changes in abundance, and thus are suitable for detection of segregation in all described cases. Based on above, we consider spatial scale of 50 and 100 m radius bird count plots fully appropriate for estimating bird abundance and conducting null model analyses on local and regional scale.

We are fully aware that our results can be only interpreted in the given temporal and spatial scale and generalizing the conclusions on macroecological scale (continental or range scale) could be misleading because other mechanisms and processes may operate on such scales (Fisher et al., 2010). One year snap shot data of climax forest breeding bird assemblages can give a general picture of species and quantitative structure of the assemblage based on long term monitoring data from Slovakia and Poland (Korňan, 2013; Wesołowski et al., 2015).

Patterns of diversity can be properly interpreted only within the broad context of regional and historical influences (Ricklefs, 2004). Based on Ricklefs' notion (2004), past concept of communities should be understand as a point of overlapping regional species distributions. Patterns and processes of these local distributions can be properly understood only by considering interaction within the region as a whole. Coming from this notion, Ricklefs (2008) "disintegrated" previous ecological community concepts based heavily on point studies and asserted that distribution of species within a region is more fundamental biologically than the coexistence of many species at a point. Furthermore, he called for urgent need of macroecological studies on several spatial scales to properly understand processes operating at these scales and forming community patterns.

Habitat and season heterogeneity

The hypothesis that random associations of post-breeding bird assemblages should prevail due to opportunism and movement patterns was strongly supported by binary null models. This pattern was even more straight forward in the matrix of dwarf pine and upper tree line communities that showed pure random association in all analyses. Quantitative null models showed more contradictory results. Simulations of spruce forest bird assemblage by two algorithms and three indices indicated half random associations and half segregations. It is impossible to compare the results with similar studies worldwide since we did not find in the scientific databases such as Web of Science and SCOPUS any studies of bird species associations focused on post-breeding season and analysed with similar methods. The segregation pattern could have been caused by a random segregation pattern of the data matrix that could have resulted from randomly assembled bird assemblages randomly forming segregation pattern as a result of opportunistic movement of birds. If we have more data matrices from this habitat type then it would be possible to draw more general conclusions.

The prediction that species more diverse spruce forest bird assemblage during the breeding season should show the structured assembly pattern then species poorer assemblages of dwarf pine and upper tree line communities was not supported by the null model analyses outcomes. Simulations by both algorithms and indices showed very dichotomous results indicating all types of

associations (aggregation, segregation, random association). Surprisingly, null model analysis of upper tree line and dwarf pine bird assemblages yielded strong prevalence of negative species associations, even though random and positive association were also detected. This finding might have been partly caused by the natural habitat gradient between dwarf pine and upper tree line communities causing increased microhabitat heterogeneity that could effect spatial distribution of species. For instance, Chiffchaffs and Willow Warblers were associated with the presence of deciduous trees, Coal Tits and Crested Tit with the presence of spruce, Chaffinch with presence of trees, etc., while other species were more evenly distributed in dwarf pine communities e.g., Water Pipit *Anthus spinoletta* and Dunnock, this could possibly form a checkerboard pattern due to habitat heterogeneity. Of course, to prove this explanation, we would need to sample habitat structure in detail and map breeding territories of birds and analyse territory associations in relation to habitat structure.

Our study of bird species associations of dwarf pine and upper tree line bird assemblage is the first attempt to describe such patterns in communities above upper tree line in mountains. As in many other major topics in ecology, the issue of complementary distribution will not be solved in near future and the continuing controversy will probably persist for many future years. Overall, role of interspecific competition as a primary factor driving spatiotemporal dynamics of communities remains open. From current empirical evidence we can conclude that communities occupying arid and tropical zones exhibited tendency toward segregation (Ulrich et al., 2012). Patterns in arctic environment are still poorly studied.

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