



# Pairwise null model analyses of temporal patterns of bird assemblages contradict the assumptions of competition theory

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Received 13 November 2017; accepted 2 July 2018  
Available online 9 July 2018

## Abstract

Compensatory dynamics assume inverse patterns of population dynamics of species with similar ecological resource requirements (temporal segregation). The objective of this study was to test this hypothesis on temporal samples (10–57 years) of 19 breeding bird assemblages of various habitats. We used presence/absence null model (SIM2) in combination with the C-score and Sørensen indices. The C-score index estimates the average number of checkerboards for two species, while the Sørensen index measures the qualitative similarity of co-occurrence between two species in a time series. We used pairwise null model analysis to select significant species pairs based on three selection criteria: the standard confidence interval criterion, conservative empirical Bayes mean based criterion and confidence limit based criterion. Altogether, 21 402 species pairs were analysed. The SIM2 algorithm detected from 157 to 7 segregated pairs depending on the selection criterion. The number of significant negative pairs with possible biological significance (foraging guild membership, predator–prey interactions) was far lower and represented approximately 0.0–0.3% (4–65) of pairs in a matrix. Indeed, the number of detected negative associations depended on the selection criterion. Moreover, the number of segregated pairs was negatively related to the area of the census plots and fill of the species matrix. Our results underline the minor importance of interspecific competitive interactions in temporal patterns of bird assemblages. Instead, we suggest that stochastic factors, climate or heterospecific social information may lead to more or less synchronous dynamics of bird pairs.

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**Keywords:** Bird community; Co-occurrence; Compensatory dynamics; Species associations; Null model analyses; Pairwise analyses; Empirical Bayes approach; Presence/absence matrices

## Introduction

Testing community assembly patterns has become one of the major tasks in community ecology in the past decades (Weiher & Keddy 1999). The most influential assembly rule

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<https://doi.org/10.1016/j.baae.2018.07.001>

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remains Diamond's (1975) interspecific competitive model of community assembly (Gotelli & McCabe 2002). Diamond's assembly rule assumes a "checkerboard distribution," or negative co-occurrence patterns in spatial community organization. Negative co-occurrence patterns have become the most widely tested assembly rule in ecology. Paradoxically, to date, the checkerboard distribution remains unresolved (Connor, Collins, & Simberloff 2013).

J.M. Diamond's assembly rule principle, the checkerboard distribution, can be applied to temporal patterns. Compensatory dynamics involves repeated phases of population growth and decline among species in response to continuous environmental pulses (Gonzales & Loreau 2009). As part of competition theory, compensatory dynamics has been frequently tested in ecology (Gonzales & Loreau 2009). Many studies have found support for compensatory dynamics in several taxonomic groups. However, there is disagreement over the applicability of this concept in ecology (Houlahan et al. 2007; Gonzalez & Loreau 2009).

The development of species association (co-occurrence) indices and null models has played a crucial role in testing and searching for patterns that indicate both phenomena (Gotelli & Graves 1996). From a historical perspective, ecologists first developed presence/absence (binary) null models to test species associations from spatial and temporal datasets long before quantitative null models were available (Connor & Simberloff 1979; Gotelli & Graves 1996; Gotelli 2000; Ulrich & Gotelli 2010). From a methodological point of view, there are two distinct approaches in null model analysis for testing species associations: community (also referred to as the guild level) and pairwise approaches. Both approaches are based on the randomization of a whole community matrix; however, in community analyses, a co-occurrence index is computed for the entire matrix, while in pairwise analyses, an index is computed for individual pairs within the matrix. In addition, in pairwise analyses, the selection of significant pairs may follow several statistical criteria, e.g., the traditional confidence limit criterion, Benjamini and Yekutieli criterion, empirical Bayes mean criterion, and empirical Bayes confidence limit criterion, which differ in their false detection error rates (Type II error) and are listed from the most liberal to the most conservative (Gotelli & Ulrich 2010).

Complementary distribution (spatial negative species associations) has been widely tested in ecology, but evidence for this pattern is often contradictory. The prevalence of segregation has been reported in many community studies based on binary and quantitative null model analyses of data matrices from various taxonomic groups (e.g., Gotelli & McCabe 2002; Heino & Soininen 2005; Ulrich & Gotelli 2010; Abu Baker & Patterson 2011; Ulrich, Zalewski, & Uvarov 2012). Random or significant positive species associations (aggregation) have been, in contrast, described in other community studies with similar statistical designs (e.g., Feeley 2003; Perez-Neto 2004; Sfenthourakis,

Tzanatos, & Giokas 2006; Houlahan et al. 2007; Wang, Chen, & Ding 2011; Šálek, Červinka, Padyšáková, & Kreisinger 2014). In summary, community meta-analyses focus on testing complementary distributions using binary or quantitative datasets and reveal the prevalence of negative species associations (e.g., Gotelli & McCabe 2002; Ulrich & Gotelli 2010), whereas community meta-analyses, which test compensatory dynamics, yield opposite patterns (e.g., Houlahan et al. 2007; Korňan & Kropil 2014). The results of pairwise analyses of Bismarck and Solomon archipelagos (Sanderson, Diamond, & Pimm 2009) and of extensive meta-analyses of 272 published spatial presence/absence matrices (Gotelli & Ulrich 2010) showed a greater predominance of segregated than aggregated species pairs; even the most conservative tests in the meta-analyses indicated a four-fold increase in the frequency of perfectly segregated species pairs in comparison to the null model expectations. By contrast, Pitta, Giokas, and Sfenthourakis (2012) found only a very small proportion of significant species pairs (8–9 species pairs), with negative pairs prevailing, in a dataset of 269 published spatial data matrices. It seems that negative species associations prevail more frequently in spatial datasets compared to temporal datasets.

In our previous studies (Korňan & Kropil 2014; Korňan, Svitok, & Krištín 2016), we analysed species association patterns in 18 and 19 published temporal datasets of breeding bird assemblage dynamics by binary and quantitative null models at the community and guild levels. We detected a strong prevalence of random or positive species associations at both community and guild levels. Thus, our results did not confirm the predictions of competition theory. In this study, we used the same dataset with the aim of subjecting matrices to pairwise analyses with the same types of null binary models to prove or disprove the general conclusions from our community and guild studies. Here, we analysed compensatory dynamics patterns and tested for species pair associations in 19 long-term time series of breeding bird assemblages. In particular, we (1) examined the number and proportion of significantly aggregated, segregated and random species pairs revealed by null model simulations based on the traditional confidence limit criterion, empirical Bayes mean based criterion and empirical Bayes confidence limit based criterion; (2) assessed the relationships between the results of the null model simulations and species association indices; and (3) tested the effect of various dataset characteristics (e.g., matrix size, duration of study, matrix fill, etc.) on the outcomes of the null model simulations.

If the competitive interactions are important drivers of bird assemblage structure, then long-term datasets should reveal segregated patterns in species distributions. If the results are robust, then we hypothesize that different combinations of null model and species association indices should yield similar results.

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