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Negative spatial and coexistence patterns and species associations are uncommon for carrion beetles (Coleoptera: Silphidae) at a small scale

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A R T I C L E I N F O

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A B S T R A C T

Biotic interactions are an important factor in determining community composition. However, spatial and coexistence patterns and species associations within a trophic group remain unclear, particularly for belowground ecosystems. We tested the hypothesis that the spatial patterns, coexistence patterns and species associations would be negative for ground carrion beetles (Coleoptera: Silphidae) at a small scale and that negative species associations would be stronger within a subfamily than between different subfamilies. To test this hypothesis, ground carrion beetles were collected from two permanent plots (each 300 × 300 m) within a mixed broad-leaved Korean pine forest in northeastern China and separated into the subfamilies Nicrophorinae and Silphinae. Geostatistical methods were used to evaluate the spatial patterns and spatial species associations. Null model analyses were performed to examine the coexistence patterns and coexisting species associations. Overall, most communities and species populations were positively spatially autocorrelated at multiple scales. Moreover, spatial patterns of all communities and most species populations were non-randomly aggregated, and most coexisting patterns of communities were also non-random. Furthermore, most spatial species associations were positive, with only a small number of nonsignificant negative spatial species associations observed between Nicrophorinae species. All coexisting species associations that were significant occurred only within the same subfamily. Notably, all significant spatial and coexisting species associations were positive. Based on this study, negative spatial and coexistence patterns and species associations are uncommon for carrion beetles at a small scale, and the only significant positive associations were within the same subfamily.

1. Introduction

One of the primary tasks of belowground ecology is to understand the mechanisms that regulate the spatial distribution of species and the assembly of communities. Dispersal ability, life history strategy, geological history, biotic and abiotic variables are all factors that can determine the composition and distribution of communities [1]. Biotic interactions are recognized as one of the most important processes that controls spatial patterns and compositions of communities.

As one of the most important forms of biotic interaction, interspecific competition within the same trophic group is a key factor in the regulation of communities [2]. Because species within the same trophic group typically have similar feeding preferences and behaviors, competing for space or food is most likely to contribute to the structuring of a community [2]. In belowground ecosystems, interspecific competition is an important regulator of detrivorous, saprophagous and necrophagous groups [3,4]. However, interspecific interactions within a trophic group are not necessarily negative [2]. Positive interactions between species within the same trophic group, such as facilitation, have also been proposed as an important driver of the composition of belowground communities [5]. However, the contributions of interspecific interactions to the regulation of community composition within a trophic group remain controversial.

Soil animal communities usually appear to be spatially structured at multiple scales based on spatial autocorrelation. Because field samples collected close to one another are often more similar than those collected farther away, soil animals are usually spatially dependent at less than 100 m [6]. When spatial autocorrelation is ignored during ecological and spatial analyses, misleading results can be produced [7]. Additionally, determining coexisting relationships between species

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within a trophic group is essential because the coexistence of species is fundamental to the examination of different theories. Coexisting relationship analysis focuses on detecting inter-specific patterns that result from either positive (aggregated), negative (segregated) or random relationship [8]. Traditionally, spatial and coexisting associations between species have been evaluated in field investigations or manipulation experiments. However, few studies simultaneously evaluate both spatial and coexisting associations within a trophic group.

Silphidae beetles (Coleoptera), usually called carrion beetles, are one of the totally necrophagous beetle groups recognized for the richness and abundance in which they can appear on carcasses [9]. Practically, carrion beetles are useful as environmental and forensic indicators [10]. Theoretically, carrion beetles are important for accelerating material decomposition. However, little is known about the spatial and co-occurrence patterns of Silphidae. Adult carrion beetles are classified into two subfamilies. Adults from Nicrophorinae search for and then bury carcasses that serve as food resources for themselves and their offspring [11]. By contrast, adults of Silphinae arrive and use a carcass during the early- or mid-stages of decomposition [12], while their larvae eat developing blowfly maggots. These two subfamilies provide an ideal system in which to test the patterns and species associations within a trophic group.

A fierce competition begins for the carcass when a terrestrial vertebrate dies, and strong interspecific competition often occurs among adult carrion beetles [13]. Fighting for a breeding opportunity and preventing other individuals from access to carrion are relatively normal behaviors [14]. Interspecific competition may be an important regulator for generating ecological feature displacement [15], which occurs in the body size of offspring [16] and in the preparation of a discrete and useful resource for offspring through biparental cooperation [17]. In carrion beetles, interspecific competition likely determined the elevation distributions of two species of *Nicrophorus* [18]. Recently, based on stable isotope analysis, niche differentiation was detected among *Nicrophorus* species using a carcass resource [19]. For the two subfamilies of carrion beetles, less is currently known about the Silphinae than about the Nicrophorinae beetles. Carcass use by Silphinae and Nicrophorinae beetles is differentiated to some extent. Silphinae beetles prefer relatively larger carcasses, but they also sometimes compete with *Nicrophorus* species for relatively smaller carcasses [20]. However, most studies of interspecific competition in carrion beetles focus on species within the same subfamily at a fine scale [17]. The spatial distribution, coexistence patterns and species associations for these two subfamilies of carrion beetles remain unknown.

In this study, we investigated carrion beetles in two permanent plots (9 ha each) within a mixed broad-leaved Korean pine forest in northeastern China. We examined the spatial and co-existence patterns and associations of carrion beetles. We hypothesized that 1) spatial autocorrelations of each 'Total' (Nicrophorinae and Silphinae communities together), Nicrophorinae and Silphinae communities and each species population are mostly negative, 2) spatial and coexistence patterns of each community and each population within a specific community are mostly segregated, 3) spatial and coexisting species associations are mostly negative, and 4) observed negative associations are more common within a subfamily than between different subfamilies. Therefore, we expected that negative spatial distributions, coexisting patterns and species associations would be more common at a small scale.

2. Materials and methods

2.1. Study site

The studies were conducted in the Liangshui National Nature Reserve (LS; 47°7′15″ - 47°14′38″ N, 128°48′8" - 128°55′46″ E) and Fenglin National Nature Reserve (FL; 48°02′ - 48°12′N, 128°58′ - 129°15′E). Both reserves are in the southern region of the Xiaoxing'a Mountains in northeastern China. The climate of LS is temperate continental monsoon. The annual mean air temperature and the annual mean rainfall are approximately −0.3 °C and 676 mm, respectively. The area is snow-covered for 130–150 days, and the frost-free period is approximately 100–120 days. The topography is relative complex with an average elevation of 280–707 m. The soil type is humaquepts or cryoboralfs [21]. The typical vegetation is mixed broad-leaved Korean pine forest. The species included *Pinus koraiensis*, *Abies nephrolepis*, *Picea* spp, *Acer mono*, *Betula costata*, and *Fraxinus mandshurica*. The climate of FL is also temperate continental monsoon. The annual mean air temperature is approximately −0.5 °C, and the annual mean precipitation is approximately 640.5 mm. The topography consists of low mountains and hills with an average elevation of approximately 285–688 m. The soil type is similar to that in LS. The primary tree species included *P. koraiensis*, *Quercus mongolica*, *B. costata*, *T. amurensis*, and *Picea* sp.

2.2. Sampling carrion beetles

The field study in the LS site was conducted in a permanent plot of 9 ha (300 × 300 m) that was established in 2005. The field study in the FL site was conducted in a permanent plot of 30 ha (500 × 600 m) that was established in 2009. To standardize the spatial areas, a 9 ha (300 × 300 m) plot was set in the northwest part of the FL plot. The LS and FL plots were equally divided into 225 subplots with 20 m intervals; thus, both plots had 256 intersect nodes. Pitfall trapping with a saturated sodium chloride solution was used to collect beetles. A 14-cm deep pitfall trap with a 7-cm inner-diameter was set near each intersect node within a circle with a radius of 50 cm. A circular disposable plate, with a 15 cm diameter, was placed approximately 10 cm above the trap to exclude litter fall and precipitation. Pitfall traps were active for 7 days in each investigation. The field collections in the LS plot were conducted in July (July 4 to 11), August (August 25 to September 2), and October (October 2 to 9) in 2015, and in the FL plot, beetles were collected in August and October during the same periods. Carrion beetles were sorted into taxa and stored in 90% alcohol, and the beetles were then identified by species [22,23]. Only adults were included in the subsequent analyses.

2.3. Data analyses

A Shapiro-Wilk test (with the *shapiro.test* function in 'stats' package) for evaluating the data normality and Bartlett's test (with the *bartlett.test* function in 'stats' package) for examining homogeneity of variance were performed before the analysis. Data at the community and species levels were non-normally distribution and did not have homogeneity of variance. Thus, differences in richness and abundances were tested using a Kruskal-Wallis test (with the *kruskal.test* function in 'vegan' package), and then a multiple test (with the *kruskalmc* function in 'pgirmess') was conducted. Species rarefaction curves (with the *specaccum* function in 'vegan' package) were performed for each community. All analyses were performed in R 3.2.2 (for references please see References S1). Communities and species populations with low abundances (less than 5) were removed for the spatial and null model analyses, because those communities and species populations did not form significant spatial patterns at such a small scale.

2.3.1. Spatial patterns and spatial species associations

Geostatistical methods were used to reveal the spatial patterns and spatial species associations of carrion beetles. Because variograms are sensitive to extreme values [24], abundance data were square-root transformed for approximate normalization before performing spatial analysis. Moran's I coefficient was used to evaluate the significance of spatial autocorrelations for each community and species population. Values of the Moran's I coefficient are plotted in a correlogram to show the changes in the autocorrelation coefficient with increasing distance classes and their significance [25]. In this study, data were allocated to