Co-occurrence Patterns of Above-ground and Below-ground Mite Communities in Farmland of Sanjiang Plain, Northeast China

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Abstract: One of the fundamental questions in community ecology is whether communities are random or formed by deterministic mechanisms. Although many efforts have been made to verify non-randomness in community structure, little is known with regard to co-occurrence patterns in above-ground and below-ground communities. In this paper, we used a null model to test non-randomness in the structure of the above-ground and below-ground mite communities in farmland of the Sanjiang Plain, Northeast China. Then, we used four tests for non-randomness to recognize species pairs that would be demonstrated as significantly aggregated or segregated co-occurrences of the above-ground and below-ground mite communities. The co-occurrence pattern of the above-ground mite community was significantly non-random in October, suggesting species segregation and hence interspecific competition. Additionally, species co-occurrence patterns did not differ from randomness in the above-ground mite community in August or in below-ground mite communities in August and October. Only one significant species pair was detected in the above-ground mite community in August, while no significant species pairs were recognized in the above-ground mite community in October or in the below-ground mite communities in August and October. The results indicate that non-randomness and significant species pairs may not be the general rule in the above-ground and below-ground mite communities in farmland of the Sanjiang Plain at the fine scale.

Keywords: above-ground mite; below-ground mite; mite communities; co-occurrence patterns; interspecific competition; species pair associations

1 Introduction

Species co-occurrence analyses are increasingly applied to evaluate whether communities are random assemblages of species or the results of deterministic mechanisms, such as competition (Diamond, 1975), nestedness (Patterson and Atmar, 1986), core-satellite structure (Hanski, 1982), favored and unfavored species combinations (Fox and Brown, 1993) and compartmentation (Leibold and Mikkelson, 2002). Diamond (1975) first suggested that the composition of the avifauna is governed by assembly rules mediated by interspecific competition. Most notably, he suggested that interspecific competition would prevent species that are ecologically

similar from co-occurring within communities in the Bismark Archipelago. That study caused a heated controversy in which the significance, or even existence, of assembly rules was questioned (Gotelli and Graves, 1996; Adams, 2007). Despite this controversy, species assembly rules based on competition received further support from the study of Graves and Gotelli (1993), in which it was reliably applied to Amazonian bird guilds. Later on, these rules were applied to other taxa, including plants (Wilson and Whittaker, 1995), ants (Gotelli and Ellison, 2002), ectoparasites (Gotelli and Rohde, 2002), earthworms (Jiménez *et al.*, 2012) and springtails (Fiera and Ulrich, 2012).

When considering the patterns of species co-occurrence using a null model, a crucial question is whether, in a given community, there are species combinations (usually, but not necessarily, pairs) that exhibit significant association (Pitta *et al.*, 2012). Associations of species may be either positive or negative. Positive associations are those in which species pairs occur at the same sites more often than expected by chance, and these associations are sometimes are called 'aggregations' or simply 'co-occurrences' (Pitta *et al.*, 2012). Negative associations are those in which species tend to avoid one-another, in the sense that they occur at the same sites less often than expected by chance. Such associations have been called 'segregations' or 'mutual exclusions' (Pitta *et al.*, 2012). If associations of the majority of species are predominantly positive, the community is an aggregation structure, while if the associations are predominantly negative, the community is segregation structure (Krasnov *et al.*, 2011). A statistical challenge in community ecology is to identify segregated and aggregated pairs of species from a presence-absence matrix, which often contains hundreds or thousands of such potential

pairs (Gotelli and Ulrich, 2010). Many of these pairs may not be biological or statistically independent of each other. Gotelli and Ulrich (2010) used four methods to assess the significance of associations between species pairs, proposing two versions of the 'Bayes approach' and Bonferroni corrections. These methods have been applied in several studies based on many databases (Gotelli and Ulrich, 2010; Krasnov *et al.*, 2011; Escoriza and Boix, 2012).

The spatial patterns of soil animals are generally found to be clumped, with alternation of high-density and low-density population patches, ranging from small to large scales, i.e., several centimeters to hundreds of meters (Albrecht and Gotelli, 2001; Jiménez *et al.*, 2001; Ettema and Yeates, 2003; Rossi and Nuutinen, 2004; Gutiérrez-López *et al.*, 2010). It is difficult to identify the factors that cause and control these discrete patches and their spatial segregation. Some studies investigated the co-occurrence patterns of soil animal communities by using null model analysis. Through this method, ant (Gotelli and Ellison, 2002), earthworm (Jiménez *et al.*, 2012), oribatid mite (Ingimarsdóttir *et al.*, 2012) and collembola (Fiera and Ulrich, 2012) communities exhibit non-random or random co-occurrence patterns (Ward and Beggs, 2007). Interspecific competition as a driver of community structuring has been detected in soil animal community assembly (Jiménez and Rossi, 2006; Decaëns *et al.*, 2008; Ingimarsdóttir *et al.*, 2012; Caruso *et al.*, 2013).

However, none of these studies clearly examined the patterns of coexistence in above-ground and below-ground soil animal communities. Above-ground and below-ground interactions drive ecosystem properties at the local scale (Deyna and Putten, 2005; Bardgett and Wardle, 2010). A combined above-ground/below-ground approach to community assembly will enhance our understanding of the regulation and functional significance of biodiversity (Wardle *et al.*, 2004). Therefore, a comparison of the co-occurrence patterns between above-ground and below-ground soil animal communities will promotes our understanding of the assembly rule in community ecology. The scale should be taken into account during the co-occurrence pattern analysis, because the co-occurrence pattern might be different at different scales. Researches have revealed the community structuring of arboreal and terrestrial oribatid mite communities across a large scale (Lindo and Winchester, 2009),

but seldom at the fine scale. Soil mite communities provide a potential case for investigating co-occurrence pattern of communities (Caruso *et al.*, 2012; Ingimarsdóttir *et al.*, 2012). Soil mites are small, wingless, that serve important functions in soil ecology (Lindo and Winchester, 2009). Thus, in this study, the very diverse mites (Acari) were selected for co-occurrence pattern analysis in above-ground and below-ground communities at the fine scale.

In this study, we used null-model analysis to compare the frequencies of co-occurrences of mite species at 100 sites with those expected by chance and to examine the above-ground and below-ground mite community co-occurrence patterns of farmland in the Sanjiang Plain, Heilongjiang Province, Northeast China. We hypothesized that 1) non-randomness co-occurrences pattern is a general rule in above-ground and below-ground mite communities; and 2) there are many significant non-random species pairs in the mite communities.

2 Materials and Methods

2.1 Study area

The study area is located at the Sanjiang Plain, Northeast China, which is one of the largest marshy regions in the Heilong River Basin. There are three main rivers, comprising the Heilong River, the Wusuli River and the Songhua River. Sampling was carried out in farmland of the integrated experimental field of wetland, the Sanjiang Mire Wetland Experimental Station, Chinese Academy of Sciences (47°35′N, 133°31′E), in August and October 2011. The study area belongs to the temperate zone, with a continental monsoon climate that shows clear seasonal periods: long and cold in winter, warm and humid in summer. Annual precipitation ranges from 550 mm to 600 mm, of which 65% occurs on July and August. Average elevation ranges from 55 m to 58 m. The mean annual temperature is about 1.9℃, and the frost-free period about 125 d. The soil type is albic. The crop on the farmland was soybean, which was planted in 2011.

2.2 Soil mite sampling

The size of the experimental plot were 50 m × 50 m. It was divided into 100 squares of 5 m × 5 m by using bamboo poles with a height of 80 cm. Samples were taken from the bottom left-hand region of each square.

For the below-ground mite community, four soil samples replicates (diameter 7 cm, height 10 cm) were collected from each point for the extraction of mite in the laboratory. The below-ground mite community was extracted from samples with a Berlese-Tullgren apparatus (self-made equipment). Pitfall traps (diameter 33 mm, height 54 mm) filled with vinegar and sugar (attractant) and alcohol (preservative) were used to capture the above-ground mite community. At each point, three traps were set and left open for three days. The extracted mites were preserved in 95% alcohol, identified and counted. Soil mites were determined to species, genus or family level (Krantz, 1978; Balogh and Balogh, 1992; Yin *et al.*, 1998; Walter and Proctor, 2001; Krantz and Walter, 2009).

2.3 Data analysis

Differences between the species richness and density of soil mite communities were tested by repeated measures ANOVA after logarithmic transformation of the data. The analyses were performed using the statistical software SPSS 19.0.

2.3.1 Co-occurrence pattern analysis

Data of mite abundance were converted into a presence-absence matrix, which is the fundamental unit of analysis in community ecology. The advent of co-occurrence analysis and other statistical techniques has provided ecologists with more precise tools to explore non-random patterns in natural communities (Jiménez *et al.*, 2012). In the presence-absence matrix, each row of the matrix represents a different species, and each column represents a different sample ($n = 100$). In such a matrix, the entries represent the absence (0) or presence (1) of a particular mite species at a particular point.

In this study, two indices were used to quantify the co-occurrence patterns of the mite community structures: the *C*-score and the *V*-ratio. Each index is a single number that calculates the pattern for a presence-absence matrix.

(1) The *C*-score. Stone and Roberts (1990) introduced the *C*-score as an index, which quantifies the average number of checkerboard units that can be found for each species pair. The number of checkerboard units (CU) for any species pair can be calculated as:

$$CU = (R_i - S)(R_j - S) \tag{1}$$

where R_i is the number of occurrences for the *i*th species, R_j is the number of occurrences for the *j*th species,

and *S* is the number of sites at which both species occur. The *C*-score is the average number of CU calculated for all unique pairs of species. The *C*-score measures the degree to which species pairs segregate across a set of samples, but it does not require complete segregation. The *C*-score index was used because of its statistical power and non-proclivity to type I error (Gotelli, 2000). It is one of the most commonly used metrics of community structure (Ellwood *et al.*, 2009; Jiménez *et al.*, 2012).

(2) The *V*-ratio. Schluter (1984) popularized the *V*-ratio (variance ratio) as a measure of community structure. The ratio is the variance of the column sum to the sum of the row variances. Unlike the *C*-score index, the *V*-ratio does not measure patterns of co-occurrence within the matrix, but instead is determined exclusively by the row and column sums of the matrix (Gotelli, 2000). Therefore, this index is not valid for the fixed-fixed null model (described below) and was therefore not tested with this null model. The *V*-ratio measures the variability in the number of species at each site. If species richness is regulated by biological interactions, communities should converge on a relatively constant number of species at each site (Gotelli, 2000).

The observed index value was calculated and compared to 50 000 null communities that were randomly assembled (Fayle and Manica, 2010). Because the co-occurrence tests are very sensitive to variation in species occurrence frequencies, row totals should be preserved as a constraint in the null model (Gotelli, 2000). We selected three algorithms to compute the *C*-score (fixed-equiprobable, fixed-fixed and fixed-proportional) and two algorithms to compute the *V*-ratio (fixed-equiprobable and fixed-proportional).

(1) Fixed-equiprobable is where species occurrence totals (rows) are fixed and all sites (columns) are equiprobable. This is recommended for analyzing ′sample lists′ (Gotelli, 2000), as it has good statistical properties (Haukisalmi and Henttonen, 1998; Gotelli, 2000).

(2) Fixed-fixed is where both the row and column sums of the original matrix are fixed, so that differences in the frequency of the occurrence of each mite species (row sums) and differences in the number of mite species per site (column sums) are preserved (Connor and Simberloff, 1979). This model has greater statistical power than the equiprobable model (Ulrich and Gotelli, 2007).

(3) Fixed-proportional is where species occurrence

totals (rows) are fixed and the sites differ in suitability. This algorithm is a hybrid of the first two, and it may cause the null hypothesis to be incorrectly rejected when using the *C*-score (Gotelli, 2000).

To compare the results of this study, we calculated the standardized effect size (SES) for the matrix. The SES measures the number of standard deviations that the observed index is above or below the mean index of the simulated communities. This is a *Z*-transformed score:

$$Z = (x - \mu) / \delta \qquad (2)$$

where *x* is observed index value, μ is the mean, and δ is the standard deviation of the 100 index values from the simulated matrices compared to the observed index. Assuming a normal distribution of the SES, a 95% confidence interval of the SES values should range from –2.0 to 2.0. For the *C*-score, values higher than 2.0 indicate non-random species segregation, and values lower than –2.0 indicate non-random species aggregation. In contrast, for the *V*-ratio, values higher than 2.0 indicate non-random species aggregation, and values lower than –2.0 indicate non-random species segregation.

2.3.2 Significant species pairs identification
The particular pairs of species that co-occurred significantly were thus identified as either aggregated or segregated. The identification of particular pairs of species that co-occurred significantly was performed by calculating the *C*-score for each pair of species, and by identifying its significance using the four methods proposed by Gotelli and Ulrich (2010). The simplest and the most liberal method is the confidence limit criterion (CL). In this method, the observed co-occurrence metric for each pair of species is related to the confidence limits of a simulated random distribution, and species pairs with scores outside the 95% confidence limits are considered significantly segregated or aggregated (depending on whether the observed *C*-score is higher or lower than the mean of the simulated *C*-scores for a given pair of species). The main problem with the CL criterion is that if the number of species pairs in a matrix is high, 5% of them will fall outside the 95% confidence limits merely by chance (Gotelli and Ulrich, 2010; Krasnov *et al.*, 2011). To resolve this problem, the Benjamini and Yekutieli (BY) criterion, which is a sequential Bonferroni correction of the probability benchmark (Benjamini and Yekutieli, 2001; Gotelli and Ulrich, 2010; Krasnov *et al.*, 2011), can be used. Gotelli and Ulrich (2010) intro-

duced two more conservative criteria for the identification of significantly co-occurring pairs of species. In these methods, instead of comparing the observed and expected scores of each species pair, the observed frequency distribution of the scores is compared with the frequency distribution of the scores generated by the null model.

The steps in the implementation of these methods include the following: 1) calculation of the observed *C*-score for each species pair and rescaling of these *C*-scores to a range from 0 to 1; 2) calculation of the rescaled *C*-score index for all $n(n - 1) / 2$ species pairs and grouping of them into a number of evenly spaced classes (22 classes in Gotelli and Ulrich, 2010); 3) assembly of 1000 null matrices (using the fixed-fixed and fixed-equiprobable randomization algorithm), and the mean and confidence limits of the expected number of species pairs within each class are calculated from these null matrices; 4) ordering of each species pairs within each class according to their observed *C*-scores, and pairs that fall above the mean (Bayes Mean-based criterion) or confidence interval (Bayes CL criterion) for the expected number of species are considered significant; 5) reducing this set by retaining only those species pairs that are significant in an individual test (simple CL criterion); and 6) classifying each non-random species pair as segregated or aggregated. During this process, segregated pairs are those for which the observed *C*-score was higher than the average simulated *C*-score (negative associations), and aggregated pairs are those for which the observed *C*-score was lower than the average simulated *C*-score (positive associations). These pairs represent cases of very strong segregation (perfect or near perfect checkerboard distributions) or very strong aggregation (complete or nearly complete overlap). Although none of the three conservative methods (BY, Bayes M and Bayes CL criteria) appeared to be ideal in the reliable detection of non-random pairs in both the simulated and empirical presence-absence matrices, they nevertheless reduce the false detection error rate and, therefore, may be useful in the analyses of community structure.

The analyses of the *C*-score and the *V*-ratio were conducted with Ecosim 7.72 software (Gotelli and Entsminger, 2009). Pairwise co-occurrences were calculated using PAIRS (Ulrich, 2008).

3 Results

3.1 Species richness and density in above-ground and below-ground mite communities

There were 12 species being recorded in this study. Species richness and density showed significant differences between communities in August and in October ($p <$ 0.001), and there were significant difference between above-ground and below-ground communities ($p <$ 0.001) according to repeated measures ANOVA (Table 1).

Table 1 Species richness (number of mite species) and density (individuals/m^2) of soil mite communities in August and October, 2011

		Above-ground		Below-ground	
		August	October	August	October
1	*Punctoribates* sp.	7 292±4983	24±114	2 327±1476	6 804±5456
2	*Suctobelbella* sp.	890±1638	12±91	2 936±2367	9 335±5716
3	*Tectocepheus* sp.	98±299	NF	6 579±4909	11 186±8475
4	*Areozetes* sp.	82±356	16±100	597±2264	676±3718
5	*Acrotritia sinensis* Jocat	NF	NF	2±20	1±6
6	*Epilohmannia* sp.	NF	NF	1±12	NF
7	Laelapidae sp.	123±359	29±120	2 666±1731	2 182±2486
8	Sejidae sp.	36±132	NF	252±243	219±291
9	*Kampinodromus* sp.	8±58	NF	5±18	NF
10	Mesostigmata sp.1	45±175	207±207	176±205	54±327
11	Mesostigmata sp. 2	4±41	NF	NF	29±55
12	Prostigmata sp. 1	12±91	NF	NF	NF
	Richness	10	5	10	9
	Density	8590	288	15541	30486

Note: NF indicates not found

3.2   Spatial co-occurrence patterns of mite communities

3.2.1   C-score

For the above-ground mite community in October, with the fixed-proportional null model algorithm, the C-score was significantly more than that expected by chance, indicating that the mite community showed non-random species segregation. With the fixed-fixed and fixed-equiprobable null model algorithms, the C-scores did not differ significantly from random (Table 2).

For the above-ground mite community in August and the below-ground mite communities in August and October, using all null model algorithms, the C-scores did not differ significantly from random (Table 2).

3.2.2   V-ratio

For the above-ground mite community in October, with the fixed-proportional null model algorithm, the V-ratio was significantly lower than the expected by chance, suggesting that mite community was species segregation. And with the fixed-equiprobable null model algo-rithm, the V-ratio did not significantly different from the randomness (Table 2).

For the above-ground mite community in August and the below-ground mite communities in August and October, with the fixed-equiprobable and fixed-proportional null model algorithms, the V-ratios did not significantly different from randomness (Table 2).

3.3   Species pairs associations

There were 45 unique species pairs in the matrix of the above-ground mite community in August. With the fixed-equiprobable null model, only one species pair (2.2% of total species pairs) was considered as a candidate pair for significant co-occurrence. Comparison of observed and simulated pairwise, C-score demonstrated that the single segregated species pair was *Punctoribates* sp.-Laelapidae sp., and the negative association of the pair was supported by simple CL, Bayes M and BY criteria. With the fixed-fixed null model, no significant species pairs were detected.

Table 2   Observed and expected by chance (mean null-model indices of 50 000 simulated matrices) values of null-model indices for presence-absence matrices of above-ground and below-ground mite communities

Community	Month	Null index	Null model	Observed index	Mean of simulated index	Average SES	p
Above-ground	August	C-score	FE	52.71	54.26	−0.28	NS
			FF	52.71	50.10	1.26	NS
			FP	52.71	48.03	0.86	NS
		V-ratio	FE	1.14	1.00	1.08	NS
			FP	1.14	1.15	−0.08	NS
	October	C-score	FE	40.60	38.75	0.36	NS
			FF	40.60	41.67	−0.70	NS
			FP	40.60	18.59	4.78	$p < 0.001$
		V-ratio	FE	0.93	1.00	−0.62	NS
			FP	0.93	1.49	−4.25	$p < 0.001$
Below-ground	August	C-score	FE	32.51	30.83	0.38	NS
			FF	32.51	32.65	-0.12	NS
			FP	32.51	30.27	0.50	NS
		V-ratio	FE	0.93	1.00	−0.56	NS
			FP	0.93	1.02	−0.71	NS
	October	C-score	FE	50.89	56.21	−0.79	NS
			FF	50.89	52.07	−0.92	NS
			FP	50.89	54.80	−0.58	NS
		V-ratio	FE	1.07	1.00	0.61	NS
			FP	1.07	1.03	0.38	NS

Notes: SES is standardized effects size. The p value is the tail probability that is related to the difference between observed and expected values of the null-model indices. FE is fixed row and equiprobable column null model. FF is fixed row and fixed column null model. FP is fixed row and proportional column null model. NS indicates not significant

There were 10, 45 and 36 unique species pairs of the above-ground mite community in October, and the below-ground mite communities in August and October, respectively. For both null models (fixed-equiprobable and fixed-fixed), no significant co-occurrence were found in those communities.

4   Discussion

One of the most fundamental questions in the ecology of soil animals is whether communities are composed of random species assemblages or whether there are processes that influence the composition of species within communities. Null model analyses have generally been used in soil animal community studies (Ingimarsdóttir *et al.*, 2012; Caruso *et al.*, 2013). Thus, the utilization of null model analysis from spatially delimited sampling seems appropriate for revealing competitive interactions in soil mite communities at the small scale. However, we should consider the potential shortcomings related to our sampling efficiency in the above-ground mite communities. Pitfall traps may give biased abundance estimates, and there is the possibility that our methods may have missed some species at some points. Nevertheless, our methods certainly minimized these potential biases by intensive sampling in the experiment plot, and pitfall trapping has been used in other null model analyses of mite community in the field (Pitzalis *et al.*, 2010; Ingimarsdóttir *et al.*, 2012).

There was clear evidence of non-randomness of the above-ground mite community in October, as shown by the null model results, by the *C*-score and by *V*-ratio analyses, which is consistent with the predictions of Diamond (1975). In this study, strong interspecific competition only exists for the above-ground mite community in October, suggesting that interspecific competition represents a driver of mite community structuring. Caruso *et al.* (2013) also demonstrated that negative biotic interactions are a structuring force in soil communities. On the other hand, we did not find any evidence of non-randomness in the above-ground mite community in August or in the below-ground mite communities in August and October, according to both *C*-score and *V*-ratio analyses. The observed random co-occurrence patterns may arise from a ′stochastic checkerboard′ (Chave, 2004; Ulrich, 2004). Overall, many studies have detected random co-occurrence patterns in below-ground soil animal communities. For

example, Sanders *et al.* (2007) found that ant species co-occurrence patterns did not differ from randomness. Ehouman *et al.* (2012) revealed that the distribution of earthworm species was random in forest and wooded savanna. Overall, the co-occurrence patterns were distinctly different in August and October for above-ground communities. Gotelli and Ellison (2002) suggested that harsh environments (habitats) were the primary filter for assembly rules. Environmental filtering might also be the most important driver in soil animal community structuring (Lindo and Winchester, 2009; Ingimarsdóttir *et al.*, 2012). The relatively harsh physical conditions faced by the above-ground community in the Sanjiang Plain in October (low temperature, high diurnal range of temperature, high wind-speed and frost) may act as strong habitat filters, restricting the pool of potential colonists and therefore altering co-occurrence patterns. Therefore, the first hypotheses of this study can not be supported.

The results of this study also showed that significant species pairs were not a general rule in the mite community. In this study, only one significantly associated pair of species was found in the above-ground mite community in August. This species pair showed negative association. Significant species pairs were not detected in any other mite communities, indicating that the associations between all other species were random. Pitta *et al.* (2012) demonstrated that significant pairwise co-occurrence patterns are not the rule in the majority of biotic communities. Caruso *et al.* (2013) found only two significant pairs in collembolan and mite communities. Actually, not every species in a community is positively or negatively associated with other species, but rather, some pairs of species contribute to a general pattern of non-randomness, while other species are randomly associated (Sfenthourakis *et al.*, 2006; Veech, 2006; Gotelli and Ulrich, 2010). In other words, non-random structure may result from non-random associations of only a subset of species (Krasnov *et al.*, 2011). The species associations were random for the above-ground mite community in August and for the below-ground mite communities in August and October, which might give rise to random co-occurrence patterns in these mite communities.

5   Conclusions

In this study, we used null-model analysis to evaluate

the above-ground and below-ground mite community co-occurrence patterns of farmland in the Sanjiang Plain, Heilongjiang Province, Northeast China. The co-occurrence patterns of above-ground and below-ground mite communities are different in different seasons. There is only a single significant species pair recognized in the above-ground mite community in August. The study demonstrates that non-randomness and significant species pairs are difficult general rules in the above-ground and below-ground mite communities at the small scale. However, this study did not analyze the roles of environmental variables and geographical distances. The relative roles of environmental filtering, geographical distances and interspecific competition in species co-occurrence patterns are important topics for further research.

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