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Species Abundance Distribution Pattern of Microarthropod Communities in SW Canada

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Abstract.- It is still unclear whether simple niche-derived or neutrality-derived statistical models is better to quantify the experimental species-abundance distribution pattern (SAD) for microarthropod communities. In the present study, by utilizing the sampling diversity data of three microarthropod taxonomic groups (oribatids, collembolans and mesostigmatids), my objectives are to test and compare five alternative statistical models for fitting empirical microarthropod SAD curves, including neutral, Zipf, broken stick, niche preemption and geometric models. Fitting power of the models were evaluated using χ^2 test, Kolmogorov-Smirnov (KS) test and Akaike Information Criterion (AIC). my results showed that, for the SAD of the whole microarthropod community and mesostigmatid group, Zipf model is the best model identified by AIC criteria. For oribatid and collembolan SAD curves, geometric model is the most favored one. However, all the models yielded significant difference between the expected and observed SAD patterns over different taxonomic groups, as indicated by both χ^2 and K-S tests. Thus, either neutral and niche models could explain SAD patterns of microarthropod communities perfectly. In summary, the synergy of different mechanisms and the development of hybrid models and the proper transformation might be of some helps to remove the observed significant difference for microarthropod communities.

Keywords: Dominance-rank relationship, neutral theory, least-square minimization, microcosm model system

INTRODUCTION

Over the past ten years, there was a hot debate on the deterministic role of niche and neutrality processes on influencing biological communities (Hubbell, 2001; Nee and Stone, 2003; Rosindell *et al.*, 2011, 2012; Munoz *et al.*, 2012; Ricklefs and Renner, 2012). Neutrality theory assumed no differentiation between species, thus each species is functionally and physiologically equivalent (Hubbell, 2001, 2006). Species under neutral theory have identical birth, death and mutation rates. Moreover, neutral theory emphasizes the importance of stochasticity, which has been usually overlooked in niche theory (Cheng *et al.*, 2011).

The most striking support for neutral theory is the fitting of species abundance curve (SAD), which might yield the highest fit for the neutral model (Volkov *et al.*, 2003, 2007). However, other simple models, whether they were directly derived from niche theory or not, also have remarabkly high fitting powers. Also, even when neutral theory could predict empirical SAD perfectly, the underpinning mechanisms driving species assemblages are still niche-based (Cheng *et al.*, 2011). SAD could not fully reflect the mechanisms structuring species communities.

The comparison of different statistical models on their powers for fitting SAD has been well quantified in recent studies (Walker and Cyr, 2007; Du and Zhou, 2008; Gao *et al.*, 2011; Yan *et al.*, 2012). In most cases, simple statistical models are powerful enough to quantify SAD (Cheng *et al.*, 2011), and the neutral model didn’t have a remarkably better fit.

It is still not fully clear whether a simple niche model, a sophisticated neutral model or none could be applied to the SAD of microarthropod communities, although the universality of some common SAD statistical models is expected to prevail across species assemblage and sampling spatial scales. There are indeed some historic literature describing the species-abundance rank relationship (Cepeda-Pizarro and Whitford, 1989; Coulson *et al.*, 2003; Hoyle and Harborne, 2005; Perdomo *et al.*, 2012). However, up to date, there is no literature being found to compare the SAD patterns for different taxonomic groups of microarthropod and fit alternative statistical SAD theoretical modelsIn the present study, by utilizing

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the sampling data of microarthropod communities in SW Canada, I evaluated the most suitable SAD models for major microarthropod taxonomic groups, including oribatids, collembolans and mesostigmatids and all species as a whole.

Dispersal ability is one of the major important mechanisms structuring the distribution and diversity, and biogeographic patterns of species (Morrone and Crisci, 1995; Potthoff *et al.*, 2006; Gove *et al.*, 2009; Chen, 2013a,b,c). Thus, if some species have long-distance dispersal ability, then the resultant species abundance and presence will be expected to be high because they can occur over different areas with high likelihood. Accordingly, long-distance dispersers can escape the influence of environmental filtering stresses and thus the corresponding SAD pattern should be neutrality-favored (Chen, 2013a). In contrast, when species assemblage has very restricted dispersal ability, it is expected that these species are subjected to strong environmental influence, and correspondingly the niche-related SAD models might better fit the observed SAD pattern for short-distance dispersers.

Based on the above arguments, I thus set up the following hypotheses to be tested in the study: oribatids are soil-dwelled and wingless, therefore their abundances are presumed to be largely influenced by dispersal limitation (Lindo and Winchester, 2007, 2009; Chen, 2013c). As such, I predict that neutral model should be of highest power among the models to fit SAD for oribatids. In contrast, collembolans could disperse actively and passively via different vectors (Binns, 1982; Szymkowiak *et al.*, 2007; Lindo and Winchester, 2009). I predicted this taxonomic group should be environmentally structured, and therefore, nice-based models might be better to fit the SAD. At last, the corresponding model for the SAD of mesostigmatids is undetermined given that they have intermediate dispersal abilities.

MATERIALS AND METHODS

Sampling locations

32 moss field plots were surveyed across SW Canada based on the following standards of site selection: (1) they should be contiguous with the mainland (islands excluded); (2) they should be flattened large rocky outcrops with >4m^2 of moss carpets; (3) they should be accessed easily, being adjacent to highway roads. 353 morphospecies were identified and a total number of 13260 individuals were counted. The abundance of each species was calculated and utilized in the subsequent analyses.

SAD statistical models

Zipf model

The existence of a new species in the community is influenced by the species arrived earlier (Cheng *et al.*, 2011), thus, the Zipf model (Frontier, 1985) has the formula as,

$$N_i = Nqi^{-r} \quad (1)$$

Where N_i denoted the predicted abundance for the i-th species in the SAD, N is the total individual number in the community, q is the predicted relative abundance of the species with highest abundance in the community, γ indicated the influence of priority effect.

Broken stick model (BSM)

BSM model (MacArthur, 1957) has the expected abundance for the i-th species based as below,

$$N_i = \alpha \sum_{k=i}^{S} 1/k \quad (2)$$

Where α is the estimated scale parameter, S is the total species number in the community.

Niche preemption model (NPM)

NPM (Motomura, 1932) assumed that the percentage of the total niche occupied by the first species is α , the second one occupied a percentage α of the reminder, being α(1- α), and so on… As such, the expected abundance for the i-th species is,

$$N_i = N\alpha(1-\alpha)^{i-1} \quad (3)$$

Geometric model (GEOM)

GEOM (Bastow, 1991) is another form of niche preemption model, but the formula is different since it has two independent parameters,

$$N_i = \alpha\beta^{i-1} \quad (4)$$

Neutral model (NM)

NM sampling formula is complex (Etienne, 2005), for simplicity, it is not present here. Two important parameters, fundamental biodiversity index θ and migration rate m, are fitted using the program Tetame version 2.1 (Jabot *et al.*, 2008). Expected abundance of species were estimated by taking the means of 1000 simulations of neutral communities using the estimated θ, m and total individual number J (for the whole dataset, J=13260) as the input in "urn.gp" program (Etienne, 2005) under PARI computational algebra system (http://pari.math.u-bordeaux.fr/).

Model evaluation

I implemented both χ^2 test and Kolmogorov-Smirnov (KS) test for comparing the discrepancy of the fitted and observed SAD patterns. The Akaike Information Criterion (AIC) method is used as well to compare the models and identify the bets model by using log-likelihoods (log$L$) of the fitted models as the input. The calculation of AIC formula is given by,

$$AIC = -2\log L + 2k \quad (5)$$

Where k is the parameter number in the fitted model.

Most of the computations (except for the NM model) were done using ad-hoc scripts under R computing environment (R Development Core Team, 2013), the codes are available upon request.

RESULTS

SAD for microarthropod species as a whole

As showed in Figure 1 and Table I, all the models could fit the whole-microarthropod SAD quite well, but the difference between the expected and observed SAD still have a large significant discrepancy (indicated by χ^2 and K-S tests). Among the models, Zipf model has the lowest AIC value, indicating the most favored model for whole-microarthropod SAD pattern.

SAD for oribatids

As showed in Figure 2 and Table I, all the models could fit the oribatid SAD quite well, but the difference between the expected and observed SAD still have a large significant discrepancy (indicated by Chi-square and K-S tests). Among the models, geometric model has the lowest AIC value, indicating the most favored model for oribatid SAD pattern.

SAD for mesostigmatids

As showed in Figure 3 and Table I, all the models could fit the mesostigmatid SAD quite well, but the difference between the expected and observed SAD still have a large significant discrepancy (indicated by Chi-square and K-S tests). Among the models, Zipf model has the lowest AIC value, indicating the most favored model for mesostigmatid SAD pattern.

SAD for collembolans

As showed in Figure 4 and Table I, all the models could fit the collembolan SAD quite well, but the difference between the expected and observed SAD still have a large significant discrepancy (indicated by Chi-square and K-S tests). Among the models, geometric model has the lowest AIC value, indicating the most favored model for collembolan SAD pattern.

DISCUSSION

Previous studies have showed the importance of spatial scales (Cheng *et al.*, 2011) on influencing the selection of the best-fit model. At local scales, typically niche-derived models were found to have highest powers for plant communities (Cheng *et al.*, 2011; Gao *et al.*, 2011; Yan *et al.*, 2012). In contrast, at large spatial scales, Hubbell's neutral model was found to be of highest power in many cases (Cheng *et al.*, 2011).

For microarthropod communities, I would originally expect that sampling area of my study (130km × 60km) is large enough for microarthropod species. As a consequence, neutrality might be prevailing to influence SAD patterns. However, based on the results (Table I), it is broadly supported that niche-based Zipf and geometric models are the best models over different taxonomic groups based on AIC standard. Thus, my hypotheses were falsified.

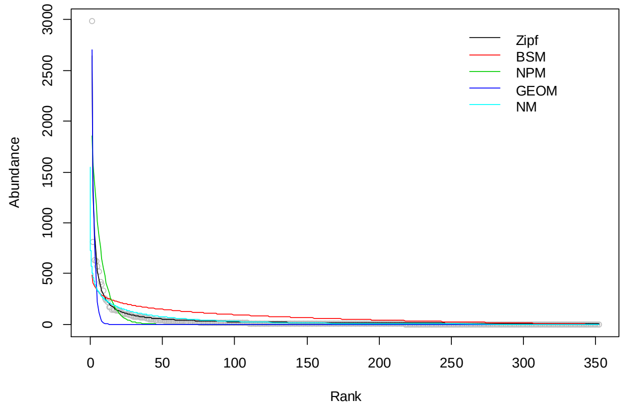

Fig. 1. SAD for the whole microarthropod community and fitting of five statistical models. Codes: Zipf-Zipf model; BSM-broken stick model; NPM-niche preemption model; GEOM-geometric model; NM-neutral model.

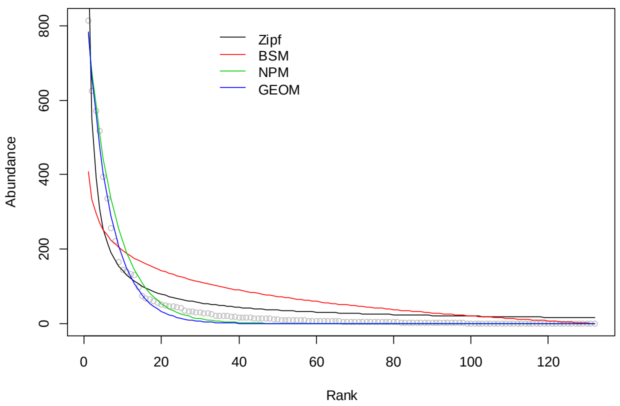

Fig. 2. SAD for the orbatid community and fitting of four statistical models (neutral model (NM) failed to fit the data with odd parameter value θ =1.79855e+10, thus not being presented here). Codes: Zipf-Zipf model; BSM-broken stick model; NPM-niche preemption model; GEOM-geometric model.

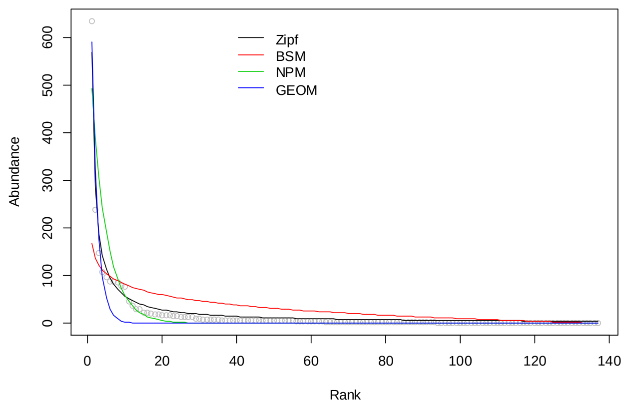

Fig. 3. SAD for the mesostigmatid community and fitting of four statistical models (neutral model (NM) failed to fit the data with odd parameter value θ=2.47436e+10, thus not being presented here). Codes: Zipf-Zipf model; BSM-broken stick model; NPM-niche preemption model; GEOM-geometric model.

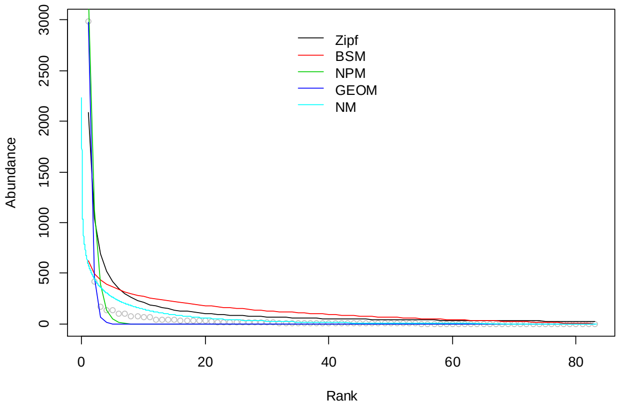

Fig. 4. SAD for the collembolan community and fitting of five statistical models. Codes: Zipf-Zipf model; BSM-broken stick model; NPM-niche preemption model; GEOM-geometric model; NM-neutral model.

One important reason for the contradictory predicted and fitted patterns above should be related to the mechanisms structuring SAD. Many studies have showed that it is not safe to draw relevant conclusions on the importance of niche and neutrality processes based on the fitting ability of exclusive models on SAD patterns. As mentioned earlier in the introduction, different mechanisms could result into similar SAD patterns (Harpole and Tilman, 2006; Cheng *et al.*, 2011), and therefore the corresponding mechanisms could be not inferred.

My results are remarkably different from any previous empirical comparisons of different methods for fitting plant SADs (Du and Zhou, 2008; Cheng *et al.*, 2011; Yan *et al.*, 2012) because I found either neutral or niche-relevant models could fit the microarthropod SADs models satisfying the requirement of statistical significance based on χ^2 and K-S tests. A key possible reason of the present observations might be because I fitted different

Table I.- **Evaluation of different models for fitting SADs of various microarthropod taxonomic groups. Codes: Zipf-Zipf model; BSM-broken stick model; NPM-niche preemption model; GEOM-geometric model; NM-neutral model. The best AIC model for each taxonomic group is marked in boldface. Asterisk denotes significant difference between expected and observed SAD with P<0.05. NA depicts non-applicable results without numeric information.**

Models	Evaluation methods	Oribatids	Mesostigmatids	Collembolans	Whole community
Zipf	AIC	424673.018	**32225.320**	4206503.747	**987957.109**
	χ^2 test	1543.139*	249.54*	2664.335*	1497.454*
	K-S test	0.689*	0.599*	0.759*	0.634*
BSM	AIC	1501178.146	595071.245	13403249.460	15965443.975
	χ^2 test	3198.674*	1496.289*	6070.837*	11212.600*
	K-S test	0.508*	0.569*	0.627*	0.577*
NPM	AIC	94857.987	205574.169	1387780.160	7052598.293
	χ^2 test	559.878*	617.622*	1551.823*	4535.233*
	K-S test	0.636*	0.803*	0.904*	0.858*
GEOM	AIC	**46259.356**	95267.384	**203697.032**	3427744.618
	χ^2 test	622.263*	758.575*	1210.223*	5314.049*
	K-S test	0.689*	0.92*	0.94*	0.963*
NM	AIC	NA	NA	11724160	12601528
	χ^2 test	NA	NA	2274.287*	3076.281*
	K-S test	NA	NA	0.169	0.176*

SAD models on the raw data without any transformation. Typically, log-transformation is a common practice before fitting SAD models (McGill *et al.*, 2007). Thus, the present results might be altered to some extents if log-transformation of the raw abundance data of species is utilized.

Conflict of interests

The author declares that there is no conflict of interests regarding the publication of this article.

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