

Analyzing patterns of species diversity as departures from random expectations

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Insight into the factors that influence patterns of species diversity can be obtained by comparing real patterns to their counterparts derived under a model of randomness or a null model. For example, intraspecific aggregation is very common among a wide variety of protozoan, plant, and animal taxa. Despite this, ecologists do not yet fully appreciate the potential effect of intraspecific aggregation on patterns of species diversity. Intraspecific aggregation is predicted to limit alpha-diversity (mean species richness of a set of ecological communities) to a level less than that expected based on random distributions of individuals. Conversely, intraspecific aggregation should enhance beta-diversity (differences in species composition among communities). These effects on alpha- and beta-diversity should be related to the mean amount of intraspecific aggregation within a species assemblage (group of taxonomically similar species distributed among a set of communities). I tested these predictions by applying additive diversity partitioning and a randomization routine to 28 arthropod assemblages. Intraspecific aggregation was very common. It significantly limited alpha-diversity to less than that expected under the random model. At the same time, intraspecific aggregation enhanced beta-diversity. These effects were greatest in assemblages where intraspecific aggregation was greatest. The next step for ecologists is to identify those factors that cause conspecifics to aggregate and thus also influence patterns of species diversity.

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The importance of intraspecific aggregation to spatial patterns of species diversity has recently been examined in the context of species–area relationships (He and Legendre 2002, Storch et al. 2003) and the effect of aggregation on the sampling of biodiversity (Plotkin and Muller-Landau 2002). Such studies are long overdue. Intraspecific aggregation is very common among a wide variety of protozoa, plant, and animal taxa (Taylor et al. 1978, Colwell and Landrum 1993, Bosco et al. 1997, O’Connell and Bolger 1998, Blome et al. 1999, Inouye 1999, Condit et al. 2000, Richard et al. 2000, Finlay et al. 2001) and yet the effect of aggregation on diversity has not been thoroughly examined (Plotkin and Muller-Landau 2002). The sole exceptions are the large amounts

of research that have been directed at developing and testing the aggregation model of coexistence in a few insect taxa (Shorrocks et al. 1979, Ives 1988, 1991, Krijger and Sevenster 2001, Hartley and Shorrocks 2002) and the research on intraspecific aggregation in tropical trees (Hubbell 1979, Condit et al. 2000, He and Legendre 2002). Given that intraspecific aggregation describes a non-random pattern, it is also worthwhile to examine the effect of aggregation on species diversity in the context of a random or null model. That is, to what extent does intraspecific aggregation cause patterns of species diversity to depart from the patterns expected if all individuals of every species were randomly distributed among communities?

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In the simplest terms, intraspecific aggregation means that individuals are aggregated with members of their own species, present in some ecological communities and absent in others. This fundamental ecological pattern should affect the diversity of species within and among communities (alpha- and beta-diversity, respectively), given that these types of species diversity derive from the spatial locations of individuals. For instance, consider a group of taxonomically similar species (i.e. a regional species “pool”) distributed among a set of communities, hereafter referred to as a “species assemblage”. Intraspecific aggregation should limit the mean alpha-diversity (species richness) of the communities to a level less than what it would be if individuals were randomly distributed among the communities. This is because intraspecific aggregation entails that a species is found in fewer communities than if it were randomly distributed. Furthermore, the limiting effect of intraspecific aggregation on alpha-diversity should be greatest for those species assemblages where intraspecific aggregation is greatest.

Opposite of this prediction, intraspecific aggregation should enhance beta-diversity (Plotkin and Muller-Landau 2002). That is, communities should differ in composition (and perhaps, richness) to a greater extent when species exhibit intraspecific aggregation as compared to when they are randomly distributed. Furthermore, the enhancement of beta-diversity by intraspecific aggregation should be greatest for those assemblages where intraspecific aggregation is greatest. The recent development of additive diversity partitioning allows measurement of alpha- and beta-diversity in the same units (Lande 1996, Veech et al. 2002, Crist et al. 2003) and rigorous tests of these predictions. I tested for these predicted effects of intraspecific aggregation on the alpha- and beta-diversity of arthropods.

Methods

I compiled 28 data sets of the distribution of arthropod species among 10 or more sampling sites (communities); hereafter the “data sets” are referred to as species assemblages (Table 1). For each species assemblage, I determined the mean amount of intraspecific aggregation using the standardized Morisita index. I also calculated the observed amount of alpha- and beta-diversity as additive components of the total diversity of the entire assemblage (Lande 1996, Loreau 2000, Veech et al. 2002). A robust non-parametric randomization routine was used to derive the alpha- and beta-diversity of each species assemblage that would be expected if individuals of each species were randomly distributed among the sampling sites (Crist et al. 2003). This randomization routine also permitted testing the significance of the observed alpha- and beta-diversity

(Crist et al. 2003, Gering et al. 2003, Summerville et al. 2003) as well as the significance of intraspecific aggregation. That is, I tested whether observed alpha- and beta-diversity and intraspecific aggregation were significantly different from the expected values based on random distributions of individuals. Finally, the ratios of observed to expected alpha-diversity and observed to expected beta-diversity were each regressed against the mean standardized Morisita indices of the assemblages to test the prediction that an increase in intraspecific aggregation should be related to a decrease in the ratio of observed to expected alpha-diversity and an increase in the ratio of observed to expected beta-diversity. I also tested for a relationship between the ratio of observed to expected variation in alpha-diversity and intraspecific aggregation.

Compilation of species assemblages

I obtained arthropod data sets by searching ecological and entomological journals. Half of the 28 data sets were published in full; the other 14 were obtained by contacting the authors. For inclusion in this study, the data sets had to have 10 or more sampling sites in which each site was separated from all others by at least 2 km but no more than 100 km distant from another site. The separation of the sampling sites was great enough that the sampling sites could be considered distinct, though not isolated, ecological “communities”. Likewise, the separation was small enough that the communities likely contained arthropod species belonging to the same regional fauna. Before analyses, all singleton species were removed from the data sets, given that aggregation cannot be assessed for species represented by only one individual.

Measurement of alpha- and beta-diversity

The total diversity in a species assemblage (e.g. total number of species) can be partitioned into the additive components of alpha- and beta-diversity (Lande 1996, Loreau 2000). Alpha-diversity is the mean diversity within a sample (e.g. sampling site or ecological community) and beta-diversity is the diversity among samples. Alpha-diversity is calculated as a weighted average such that $\alpha = \sum d_j q_j$, where d_j = the number of species in sample j and q_j = the weight or number of individuals (of all species) in sample j as a proportion of the total number of individuals in all samples (Lande 1996, Veech et al. 2002). Note that the weights are relative sample sizes measured in numbers of individuals.

Beta-diversity is calculated as $\beta = \text{total} - \alpha$ (Veech et al. 2002), which is simply an algebraic rearrangement of $\text{total} = \alpha + \beta$. An important distinction between this

Table 1. Species assemblages used in the study. Variables of each assemblage are given.

Assemblage*	Type of organisms	Sampling sites	Total individuals	Total species	Alpha diversity	Beta diversity	CV _z [†]	Intraspecific aggregation [‡]	Proportion of species with intraspecific aggregation [§]
1*	ants	11	1537	49	13.1	35.9	0.23	0.632	0.82
2*	beetles	17	34046	426	61.1	364.9	0.22	0.869	0.94
3*	beetles	10	1468	34	15.7	18.3	0.43	0.505	0.74
4*	grasshoppers	27	1631	30	13.0	17.0	0.32 [†]	0.555	0.47
5	spiders	12	7356	74	38.4	35.6	0.14 [†]	0.270	0.58
6	beetles	24	9426	278	99.5	178.5	0.39	0.427	0.62
7*	grasshoppers	12	2997	31	15.7	15.3	0.30	0.477	0.71
8*	beetles	10	21444	65	43.6	21.4	0.14	0.430	0.63
9	true bugs	24	5469	65	18.7	46.3	0.33	0.291	0.51
10	beetles	36	15061	195	41.6	153.4	0.31 [†]	0.434	0.68
11	beetles	24	16478	327	91.4	235.6	0.32	0.426	0.69
12	beetles	47	20972	305	54.9	250.1	0.33	0.450	0.73
13	beetles	47	36755	438	89.4	348.6	0.33	0.440	0.71
14*	beetles	16	684	13	6.4	6.6	0.30	0.298	0.62
15*	spiders	21	1082	45	15.2	29.8	0.33	0.160	0.44
16	beetles	15	10887	50	16.8	33.2	0.27	0.732	0.90
17	ants	10	4754	65	23.9	41.1	0.46	0.710	0.86
18	beetles	30	43154	418	149.4	268.6	0.15 [†]	0.174	0.42
19*	beetles	14	4822	48	19.1	28.9	0.26	0.618	0.67
20	beetles	71	80685	87	24.2	62.8	0.25	0.590	0.87
21	spiders	71	72092	141	27.2	113.8	0.40	0.516	0.75
22*	beetles	10	1310	24	13.8	10.2	0.23 [†]	0.557	0.50
23*	beetles	19	2028	37	13.9	23.1	0.30	0.358	0.51
24*	spiders	19	7992	51	20.8	30.2	0.37	0.399	0.71
25*	butterflies	10	2109	92	45.1	46.9	0.19	0.225	0.58
26*	moths	18	16081	187	96.2	90.8	0.14	0.234	0.57
27*	grasshoppers	11	2853	23	9.8	13.2	0.22	0.746	0.83
28*	butterflies	16	1337	39	21.9	17.1	0.13 [†]	0.374	0.72

*Sources of published data available from JAV.

[†]Value is not statistically greater than the random expectation ($P > 0.01$, rand. test).

[‡]Intraspecific aggregation is the mean standardized Morisita index for all species in the assemblage.

[§]Proportion of species exhibiting intraspecific aggregation is based on the number of species with a statistically significant ($P < 0.05$, rand. test) standardized Morisita index.

concept of beta-diversity and all previous concepts is that the additive partition of total diversity allows alpha- and beta-diversity to be expressed in the same units and thus to be compared (Veech et al. 2002). Beta-diversity is the average diversity not found in a sample, or the average diversity missing from a community but present in the total diversity of all other communities of the assemblage (Veech et al. 2002). Beta-diversity is not the variation in species richness among the communities of an assemblage; the variance in alpha-diversity (recall that α is a mean) measures the variation in species richness. As with the more traditional concepts of beta-diversity, β measured as total diversity minus alpha-diversity does assess “species turnover” or the differences among communities with regard to species composition. Obviously, turnover can be affected by differences in species richness, hence β is not completely independent of variation in richness. For each species assemblage, I determined alpha- and beta-diversity as additive components of the total number of species in the assemblage. Variation in alpha-diversity was determined by calculating the coefficient of variation for the α of each assemblage, CV_α .

Measurement of intraspecific aggregation

I used a standardized version of the Morisita index (Morisita 1962, Smith-Gill 1975, Krebs 1999) to measure intraspecific aggregation of each non-singleton species in each dataset. The standardized Morisita index is robust to variation in sample number (i.e. the number of sites over which a species is potentially distributed) and sample size (i.e. the number of individuals of a species; Myers 1978, Krebs 1999). It is obtained by first calculating the raw Morisita index as follows:

$$I_M = N \times \left[\frac{\sum x_j^2 - \sum x_j}{(\sum x_j)^2 - \sum x_j} \right]$$

where N = the number of samples or sites and x_j = the number of individuals in sample j for each sample $j = 1$ to N . This index is then standardized (I_{MS}) to a scale of -1 to 1 using either of two critical values derived from a chi-square distribution with $N - 1$ degrees of freedom (see Krebs 1999, p. 217 for details). Values of $I_{MS} < 0$ indicate intraspecific repulsion whereas $I_{MS} > 0$ indicates intraspecific aggregation (Krebs 1999). In cases where all the individuals of a species were found at only one site, I_{MS} was set to 1.0 . The mean I_{MS} over all species was obtained for each species assemblage. This variable represented a measure of assemblage-wide average intraspecific aggregation. Mean I_{MS} was not significantly correlated with the number of sampling sites or the number of species in an assemblage.

Randomization routine

I used a randomization routine to test whether the observed alpha- and beta-diversity of each species assemblage was significantly different from the random expectation. The routine randomly reassigns individuals to samples such that the total number of individuals in a sample is conserved and the number of individuals per species is conserved (Crist et al. 2003). Each time the randomization routine is applied to a given data set (i.e. species assemblage) a random data set is created. All the variables previously described (α , β , CV_α , I_{MS} for individual species, and mean I_{MS}) can be calculated for the random data sets. In such a way, a null distribution is created for each variable. The null distribution represents values of the variable that could be obtained by chance alone. The statistical significance of the observed value of the variable can be determined as the proportion of null values greater than the observed value (i.e. a test for a significantly large observed value) or less than the observed value (i.e. a test for a significantly small observed value). For instance, if only 15 of 10,000 random data sets had an alpha-diversity greater than the observed value of alpha-diversity for the real data set, then that observed value is significantly large ($P = 0.0015$). Furthermore, the means of the null distributions can be taken as the values expected when individuals of all species in the assemblage are randomly distributed among the sampling sites or communities (Crist et al. 2003). Thus, the ratios of observed to expected alpha- and beta-diversity were obtained for each species assemblage, abbreviated as $obs:exp(\alpha)$ and $obs:exp(\beta)$. Each of the 28 data sets were randomized 10,000 times; all reported P-values are based on these randomizations.

Results

As expected, most species exhibited significant intraspecific aggregation (I_{MS}). On average, 67% of the species in an assemblage were aggregated and one assemblage had as many as 94% of its species aggregated (Table 1). The lowest percentage of aggregated species in an assemblage was 42%. Furthermore, the mean amount of intraspecific aggregation was highly significant ($P < 0.0001$, rand. test) for all assemblages (Table 1). Alpha-diversity was significantly low ($P < 0.0001$, rand. test) and beta-diversity was significantly high ($P < 0.0001$, rand. test) for all species assemblages (Table 1). Given that a large number of species assemblages (28) were examined, a Bonferroni correction of the significance level might be warranted. If the original significance level is taken as 0.05 then a Bonferroni correction using $0.05/28 = 0.0018$ as the significance level still does not change the results.

Intraspecific aggregation significantly limited alpha-diversity within communities and enhanced beta-diversity among communities (Fig. 1). However, because beta-diversity was calculated as total diversity minus alpha-diversity, the separate correlations of alpha- and beta-diversity with intraspecific aggregation are not independent. Thus, the two correlations should be taken together as one significant result. Lastly, there was no significant relationship between intraspecific aggregation and variation in species richness among the communities of an assemblage (Fig. 2), even though the observed amount of variation was significantly large in most assemblages ($P < 0.01$, rand. test; Table 1).

Discussion

With this study, one of the most fundamental observations of species in nature, intraspecific aggregation, is seen to limit the number of arthropod species in ecological communities while also maintaining differences among communities. The mean alpha-diversities of all 28 arthropod assemblages were substantially less than what they would be in the absence of intraspecific aggregation. Conversely, beta-diversities, were substantially greater because of intraspecific aggregation. Moreover, the enhancement of beta-diversity mostly exists because increasing intraspecific aggregation increases differences among communities in species composition (i.e. species turnover) not differences in species richness. For most assemblages the observed variation in species richness was greater than the amount expected if individuals were randomly distributed, but the difference was not related to the strength of intraspecific aggregation. The ratio of observed to expected CV_x did not increase with increasing intraspecific aggregation (Fig. 2).

By using a single randomization routine to test for statistical significance, alpha- and beta-diversity can be linked statistically to intraspecific aggregation. However, this statistical link does not predetermine that assemblages with relatively low alpha-diversity and high beta-diversity must have many species that are highly aggregated (i.e. large mean I_{MS}). Between the extremes of maximal intraspecific aggregation (each species in only one community, mean $I_{MS} = 1$) and overdispersion (every species in every community, mean $I_{MS} = -1$) alpha- and beta-diversity are free to vary. That is, there are many possible values of alpha- and beta-diversity for a given mean value of I_{MS} . Mathematically, they can be either greater than or less than the alpha- and beta-diversity expected based on random distributions. The relationship between intraspecific aggregation and species diversity is not a mathematical or statistical inevitability, but rather a consequence of the fact that both

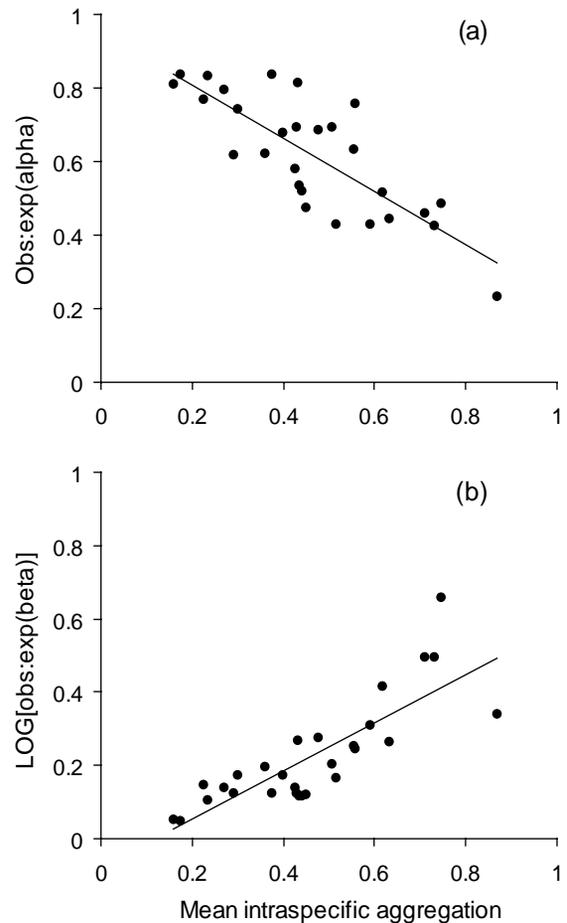


Fig. 1. The effect of intraspecific aggregation in (a) limiting alpha-diversity and (b) enhancing beta-diversity. As intraspecific aggregation increases, the observed amount of alpha-diversity decreases as a proportion of the expected amount ($R^2 = 0.65$, $P < 0.0001$) while the observed amount of beta-diversity increases as a proportion of the expected amount ($R^2 = 0.67$, $P < 0.0001$). The expected values for alpha- and beta-diversity represent the amount of diversity expected when individuals are randomly distributed among communities; the values derive from the randomization routine. Note that obs:exp(beta) was log-transformed so as to normalize the variable and put it on a scale (0 to 1) identical to that for obs:exp(alpha) . Intraspecific aggregation is measured as the mean standardized Morisita index of all species in an assemblage.

ecological patterns emanate from the spatial locations of individuals.

Previous researchers have recognized the importance of intraspecific aggregation to species diversity in different ways. The "aggregation model of species coexistence" (Ives 1988, 1991, Krijger and Sevenster 2001) explains the number of species in a community as a consequence of positive population growth for species that avoid one another by aggregating with conspecifics at a limited number of resource patches (Shorrocks et al. 1979, Ives 1988, Sevenster 1996, Hartley and Shorrocks

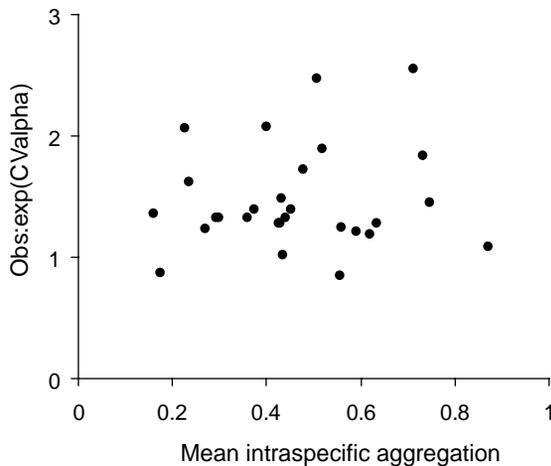


Fig. 2. The lack of an effect of intraspecific aggregation on the variation in species richness among communities (CV_{α}). For 26 of 28 arthropod assemblages, the observed amount of variation is greater than the expected amount but the ratio of observed to expected is not affected by intraspecific aggregation ($r=0.11$, $P=0.57$).

2002). Since individuals choose among resource patches within an ecological community, the aggregation model is focused on explaining alpha-diversity. The “species-aggregation relationship” describes a decrease in alpha-diversity within a sample plot as intraspecific aggregation increases within a larger geographic area containing the plot (He and Legendre 2002, Veech et al. 2003); again the focus is on alpha-diversity. Lastly, the effect of intraspecific aggregation on community similarity indices (i.e. pairwise estimates of beta-diversity between two communities) has been addressed from the perspective of improving the inventorying of biodiversity (Plotkin and Muller-Landau 2002).

The present study adds to these previous studies by introducing a conceptual and statistical unification of the effect of intraspecific aggregation on alpha- and beta-diversity. That is, both alpha- and beta-diversity are viewed as a direct consequence of the way in which individuals are distributed among communities. Moreover, the important feature of alpha- and beta-diversity is the extent to which each is “displaced” (limited or enhanced) from the values that are expected if individuals of each species are randomly distributed. Typically, there will be substantial displacement because individuals of most species are not randomly distributed in nature. However, if the observed distributions are random then the observed to expected ratios of alpha- and beta-diversity should both equal 1.0. Extrapolation of the regression line of $obs:exp(\alpha)$ and $obs:exp(\beta)$ illustrates this point (Fig. 3). Alpha- and beta-diversity are statistically and conceptually linked to intraspecific aggregation when both are viewed as additive components of total diversity and as “displacements” from

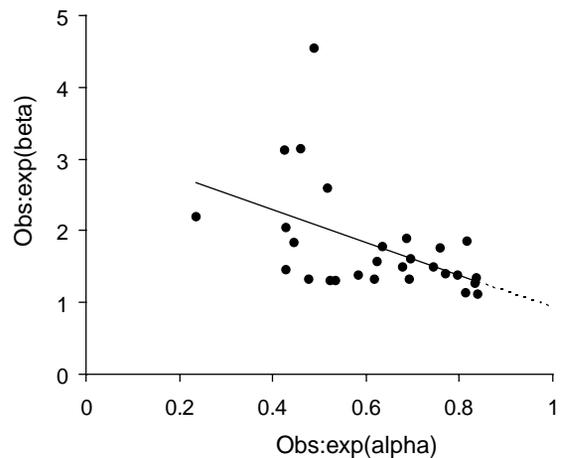


Fig. 3. The relationship between the ratios of observed to expected beta-diversity and observed to expected alpha-diversity of the 28 arthropod assemblages. The regression ($y = -2.28x + 3.2$, solid line) is statistically significant ($R^2 = 0.24$, $P = 0.009$). As predicted, when the regression line is extrapolated to $obs:exp(\alpha) = 1.0$, then $obs:exp(\beta)$ is approximately 1.0 (actually, 0.924). If the observed intraspecific distributions of species were random then both $obs:exp(\alpha)$ and $obs:exp(\beta)$ would equal 1.0.

random expectations. Indeed, the partition of total diversity into the additive components of alpha and beta diversity necessitates that if one component is displaced (enhanced or limited) so will be the other component in the other direction. In a similar way, Loreau (2000) used additive diversity partitioning to show that the relationship between local and regional species diversity (i.e. community saturation vs proportional sampling) is determined by the way total diversity is partitioned into alpha- and beta-diversity.

The displacement of alpha- and beta-diversity (from random expectations) arises from processes that can be studied. Environmental, ecological, evolutionary, and behavioral factors produce intraspecific aggregation and hence limit alpha- and enhance beta-diversity. For instance, differences in abiotic conditions among the geographic locations of communities, existence of predators and competitors, differences in species adaptations, and dispersal ability might all influence the distributions of species among communities. A useful first step in the study of these factors is the application of diversity partitioning and the multipurpose randomization routine to simultaneously test for significant intraspecific aggregation and significant displacement of alpha- and beta-diversity.

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