Biodiversity shapes tree species aggregations in tropical forests

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Spatial patterns of conspecific trees are considered as the consequences of biological interactions and environmental influences. They also reflect species interactions in plant communities [1, 2]. However, biological attributes are often neglected while deliberating the factors shaping species distributions. As rising attentions are paid to spatial patterns of tropical forest trees, we noticed that seven Center of Tropical Forest Sites and four Forest Dynamic Plots in Asia and America have presented analogously high proportions of species with aggregated conspecific individuals coincidently [3-6]. This phenomenon is distinctive and repudiates fundamental ecology hypotheses which suggested dispersed distributions of conspecific tropical trees due to intensive density and natural enemy pressures in tropical forests. We believe that similar aggregation patterns shared by these tropical forests implies the existence of structuring forces in biogeographical scale instead of habitat heterogeneity in local community scales as scientists have considered [7-9]. To approach the factors contributing to this cross-continent spatial pattern of trees, we obtained and reviewed ecosystem attributes, including topography, temperature, precipitation, biodiversity, density, and biomass, of these forests. Here we show that the proportions of aggregated species are actually constants independent of any ecosystem attributes regardless the nature of these tropical forests. However, local biodiversity are the major factor determining the number of aggregated species and the aggregation of large individuals of these forests. Aggregation of large trees declines along rising biodiversity, while the numbers of aggregated species increase permanently along lifting biodiversity. We propose a possible equilibrium and saturated status of the tropical forests in accommodating aggregated species. Furthermore, the tight correlations of biodiversity and species

aggregation strongly imply the importance of overlooked biological interactions in shaping the spatial patterns in the tropical forests.

In the past decades, the most profound findings have been reported from a dry tropical forest in Costa Rica that most of the conspecific individuals, including large congeners, were spatially aggregated[3]. However, whether this pattern is common remains unknown. Factors contributing to species aggregations are yet revealed as well. Many studies have been implemented in the major tropical forests over the world afterwards to examine the universality of species aggregations [4, 5, 10] for better understanding of species coexistence and distribution in endangered tropical ecosystems. Surprisingly, we found that the most important tropical forest research sites coincidently possessed analogously high proportions of aggregated species, including six plots of Center of Tropical Forest Site (CTFS) and four Forest Dynamic Plots (FDP) (Table 1) [4, 5, 10]. The aggregation pattern challenged essential ecological hypotheses in spatial patterns, such as hyperdispersion[11] and Janzen-Connell hypotheses[12, 13], which addressed that mature tropical trees should be less aggregated due to mortality of young trees resulted from natural enemy attacks and intraspecific competition caused by neighboring congeners. As rising attentions have been paid to probe into the factors shaping species aggregation, environmental factors, such as topography and soil, have been overwhelmingly concluded as the major causes at local community scale[7, 8, 14, 15]. Few studies have confirmed that heterogeneous habitats constructed by topographic variations and climatic features were significantly contributive to species aggregation by providing varied niche spaces and copious resources to the tropical forests. Nevertheless, habitat heterogeneity is relatively localized and insufficient to explain the analogous patterns of species aggregation in the tropical forests located across biogeographical regions with various floras, habitat heterogeneity, and disturbance regimes. Furthermore, biological factors, such as delicate species interactions, which function in species coexistence and niche differentiations as well[16], are often forgotten in deliberating the factors shaping aggregated distributions of tropical forest species. The aggregation of conspecific individuals usually implies inconspicuous intraspecific competition and adult-juvenile allelopathy in these forests[1]. On the other hand, it also suggests vital interspecific competitions, since aggregations of congeners may reduce the front facing interspecific interferences.

Unfortunately, these mechanisms were seldom discussed for the tropical forests, probably because it is arduous to examine complicated interspecific interactions in highly diversified tropical forests. However, we suggest that easily accessible biological factors, such as density and diversity are capable of providing preliminary insights to these biological interactions shaping species aggregations in the tropics.

To reveal the factors contributing to the inter-continental phenomenon of species aggregations, we employed and analyzed the metadata of these ten forests featured with noticeable species aggregations and archived with comprehensive data of ecosystem attributes, including Hui Kha Khaeng (HKK) Wildlife Sanctuary (Thailand), Lambir Hills National Park (Sarawas, Malaysia), Pasoh Forest Reserve (Peninsular, Malaysia); Barro Colorado Island (BCI) (Panama), Sinharaja (Sri Lanka), and Mudumalai Wildlife Sanctuary (India), and four our lowland rain forests (FDP) in southern Taiwan: Lanjenchi, Nanjen Lake, Nanjenshan I and Nanjenshan II.

According to our results, the importance of biodiversity is evident in shaping species aggregations in these tropical forests. Significantly tight linear regression of fisher's alpha, a diversity index, to the number of aggregated species suggests that the size of species pools determined the amount of aggregated species (Fig. 1). As the biodiversity of plant communities ascends, the forests are capable of accommodating more species with aggregated conspecific individuals. Furthermore, the function of the linear regression indicates a consistent relationship between the local biodiversity and the numbers of aggregated species: the number of aggregated species equals four point five times the value of fisher's alpha, the biodiversity index. This fixed relationship, nevertheless, suggests that the proportions of aggregated species in these forests are actually constants independent of any ecosystem attributes, including biological and environmental factors (see supplementary information). These surprising results not only infer to a possible "equilibrium" of species aggregations in tropical forests which is similar to the idea of carrying capacity, and these forests all reached this saturated proportions of species aggregation a tropical plant community can possibly support.

Furthermore, biodiversity weighted on the number of aggregated large individuals and the tendency of species aggregation in these forests as well. Evident and significant correlations were found between the number of species with significantly aggregated large individuals and all of the factors representing local biodiversities, including fisher's alpha, family number and genus number (Fig. 2a, 2b, 2c). However, the best fitted logarithmic curve suggests a relatively saturated status, resembling the species-area relationship, of aggregated large individuals is reached regardless of rising biodiversities, suggesting other limiting factors restricting the amount of aggregated large individuals. Similar pattern of restriction is also reflected on the exponentially decreasing trend of LA ratio (Species with aggregated large individuals/all aggregated species) along ascending biodiversity (Fig. 3). Presumably, intensified biological interactions caused by complicated neighborhoods under high biodiversity functioned as shaping forces regulating the amount of aggregated species, especially on large individuals.

Although the fisher's alpha, family number and genus number simultaneously confirmed the importance of biodiversity and biological related mechanisms, insights of the existing publications and studies are, unfortunately, not able to approach why the size of species mixture is crucial in determining number of aggregated species. It is also unknown why aggregation of big trees is limited in these forests after reaching a biodiversity threshold. More importantly, we know nothing about the mechanisms resulting in the constant proportions of species aggregations across the globe. Our conjecture is that the aggregation of most tropical species is driven by mechanisms of species coexistence, especially biological interactions. The core of this conjecture inherits the lottery and neutral hypothesis of amazingly high biodiversity in the tropical forests[17, 18] that the presence of every individual of any species in the tropical forests should be stochastic or neutral initially. Mechanisms, such as seed dispersal, inter- and intra- specifc competition, and predation, function afterwards during long-term succession[19, 20]. The aggregations, consequently, form in the ecological processes toward a steady status of coexistence, equilibrium.

The effects of environmental factors on distribution of conspecific individuals, however, are relatively minor according to our results. For large trees, correlated environmental factors, such as elevations and disturbances suggest that topography and disturbances are critical restrictions to survival[21, 22] (see supplementary information). Stresses, such as space, water, and wind, may not be able to support clumped distribution of large individuals due to severe competition for resources.

Conclusion

According to our results, we would like to call for attentions on mechanisms shaping the consistent proportions of species aggregations across the tropics and on biological interactions resulted from magnificent biodiversity in these forests. However, the biodiversity here is not simply what have been defined in the past decades. It actually embraces family and genus, which were seldom considered as important indicators of biodiversity. We believe this will definitely contribute to better understanding of the shaping forces of species coexistence, biodiversity and spatial patterns of precious tropical forests over the world.

Methods

Ecosystem attributes

Accessible environmental factors of these forests obtained for the analyses included area (km^2), Log(area), topography(m), number of disturbance type, average elevation, highest elevation, lowest elevation, elevation difference, number of disturbance type, annual average temperature, highest monthly average temperature, lowest monthly average temperature, difference of highest and lowest monthly average temperature, annual average precipitation, highest monthly average precipitation, lowest monthly average precipitation, difference of highest and lowest monthly average precipitation, months with precipitation < 100 mm, and total precipitation in driest three months[6,10,14,15].

We obtained all of the available biological information published for these forests as the biological attributes, including the number of total species, number of family, number of genus, number of species /Log area, individual number per hectare, basal area per hectare, and fisher's alpha ($S=a*\ln(1+n/a)$ where S is number of taxa, n is number of individuals and a is the Fisher's alpha)[23].

Fisher's alpha is the only common biodiversity index published by these tropical forests, and number of species per Log area was utilized to present the biodiversity per area.

Parameters of species aggregation

Few parameters were selected as indicators of the spatial patterns of sampled forests. The number of significantly aggregated species indicated the overall aggregation patterns of these forests, while the percentage of significantly aggregated species to total analyzed species showed the proportions of aggregation. Number of species with significantly aggregated large individuals represents the aggregation pattern of large trees, while the percentage of these to total analyzed species showed the proportion of aggregated large trees. Furthermore, the ratio of species with significantly aggregated large individuals to total significantly aggregated species (LA Ratio) represented the aggregation tendency of large individuals in the forests.

Pearson's correlation was applied to assess the correlations among the factors and curve estimation of regression analysis (significance at 95% two tailed) was conducted to estimate the patterns of significant correlations by SPSS 15.0 for windows (SPSS Inc., Chicago, 2006).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions

Chao, W. C. and Hsieh, C. F. were in charge of data collecting and compiling. Wu, S. H. managed data analyses and manuscript preparations.

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number of individuals in a random sample of an animal population. *J. Ecol.* 12, 42-58 (1943).

Table 1. Numerical summary of the analyzed CTFS and FDP forest plots.

					DBH > 1[1]		Large trees[2]		
Plot	Location	Plot Size (ha)	Species number	No. of species analyzed	Species	%	Species	%	LA Ratio[3]
Barro Colorado	Panama	50	300	183	149	81.4	41	51.9	0.28
Huai Khae Khaeng	Thailand	50	231	95	77	81.1	34	68.0	0.44
Lambir	Malaysia	52	1174	772	653	84.6	72	46.5	0.11
Lanjenchi	Taiwan	5.88	136	88	86	97.7	51	78.5	0.59
Mudunalai	India	50	71	25	22	88.0	17	85.0	0.77
Nanjen Lake	Taiwan	1.61	120	91	87	95.6	28	63.6	0.32
Nanjenshan plot I	Taiwan	2.10	106	52	42	80.8	13	59.1	0.31
Nanjenshan plot II	Taiwan	0.64	67	25	15	60.0	3	17.6	0.20
Pasoh	Malaysia	50	817	535	433	80.9	46	28.0	0.11
Sinharaja	Sri Lanka	25	205	158	156	98.7	47	62.7	0.30

[1]: All species with individuals > 1 cm in DBH. [2]: Individuals with DBH > 10cm and 8 cm in CTFS and FDP plots respectively. [3]: Number of species with significantly aggregated large individuals/number of significantly aggregated species.

Legends

Figure 1. The regression and curve fitting analyses of the number of aggregated species and fisher's alpha diversity index. The equation and curve represent the most significant trend of the data. R^2 and P indicate the significance of regression and curve fitting at 95% confident interval with two tailed t-test.

Figure 2. The regression and curve fitting analyses of the number of species with aggregated large individuals and biodiversity indices, including (a) fisher's alpha, (b) family number, (c) genus number. The equation and curve represent the most significant trend of the data. R^2 and P indicate the significance of regression and curve fitting at 95% confident interval with two tailed t-test.

Figure 3. The regression and curve fitting analyses of the LA ratio and fisher's alpha diversity index. LA Ratio is determined by number of species with aggregated large individuals/number of aggregated species. The equation and curve represent the most significant trend of the data. R^2 and P indicate the significance of regression and curve fitting at 95% confident interval with two tailed t-test.

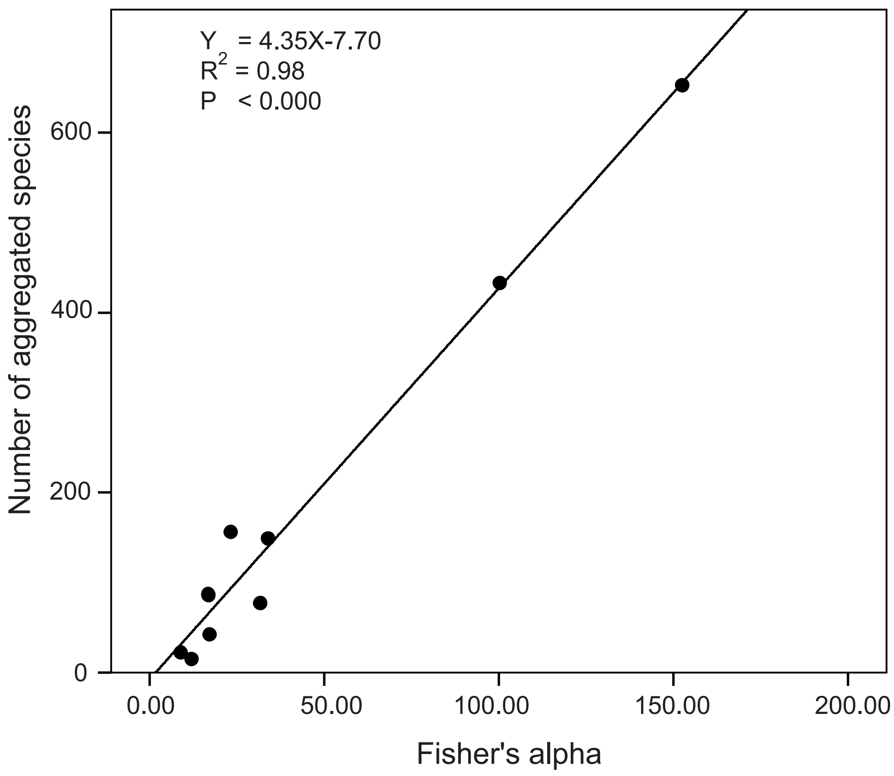
Supplementary information

Table 1. Pearson's correlations coefficients of species aggregations to the ecosystem attributes, including area factors, environmental factors, biomass and density factors, and biodiversity factors. Total significantly aggregated species are represented by "All" and "All (%)", while species with significantly aggregated large individuals are indicated by "Large" and "Large (%)". LA ratio shows the tendency of aggregation of large individuals. Negative mark indicates negative correlation between the parameters the ecosystem attributes.

	All	All (%)	Large	Large (%)	LA ratio
Area factor					
Area	0.522	-0.137	0.472	-0.071	-0.016
Log(area)	0.495	0.089	0.608	0.059	0.088
Environmental factor					
Disturbance1	0.066	0.087	0.266	0.525	0.527
Lowest elevation	-0.494	-0.259	-0.342	0819 **	0.846 **
Highest elevation	-0.408	-0.213	-0.251	0789 **	0.812 **
Elevation difference	0.213	0.119	0.341	0.317	0.310
Precipitation	-0.145	0.461	0.065	-0.132	-0.207
Highest precipitation	-0.422	0.139	-0.199	0.098	0.045
Lowest precipitation	0.613	0.663 *	0.651 *	-0.385	-0.465
Months w/prec. <100 m	-0.615	-0.647 *	-0.629 $^{+}$	0.336	0.426
Prec. of driest three months	0.560	0.704 *	0.644 *	-0.336	-0.421
Precipitation difference	-0.560	0.007	-0.339	0.180	0.143
Temperature	0.758 *	0.128	0.628	-0.495	-0.475
Highest Temperature	0.194	-0.632 *	-0.212	-0.354	-0.285
Lowest Temperature	0.708 *	0.095	0.499	-0.548	-0.536
Temperature difference	-0.657 *	-0.386	-0.621	0.416	0.435
Biomass and density					
Basal area(m^2)/ha	-0.008	0.235	-0.037	-0.367	-0.421
Number of total individuals	0.900 **	0.379	0.812 **	-0.588	-0.602 $^{+}$
Density	0.156	0.828 **	0.342	-0.154	-0.243
Biodiversity					
Total species number	0.933	0.334	0.832 **	-0.607 $^{+}$	-0.611 $^{+}$
Species/Log (area)	0.680 *	0.592	0.632 *	-0.297	-0.340
Fisher's alpha	0.988 **	0.169	0.727 *	-0.604 $^{+}$	-0.607 $^{+}$
Number of Family	0.889 **	0.290	0.759 *	-0.650 *	-0.648 *
Number of Genus	0.907 **	0.211	0.744 *	-0.626 $^{+}$	-0.616 $^{+}$

**Correlation is significant at the 0.01 level (2-tailed); *Correlation is significant at the 0.05 level (2-tailed); + : marginally significant with $P = 0.06$.

Figure 1



Y = 4.35X-7.70
R2 = 0.98
P < 0.000
Number of aggregated species
600
400
200
0
0.00
50.00
100.00
150.00
200.00
Fisher's alpha

Figure 2

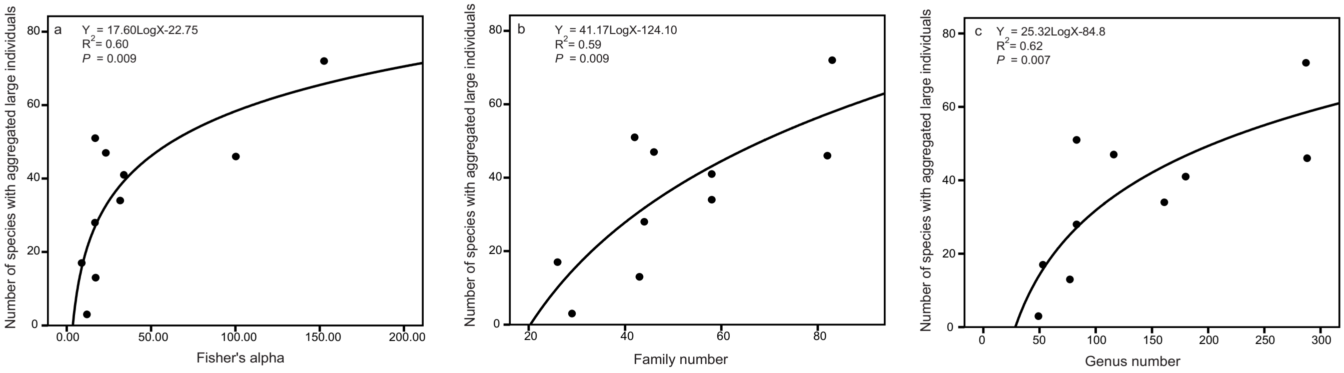
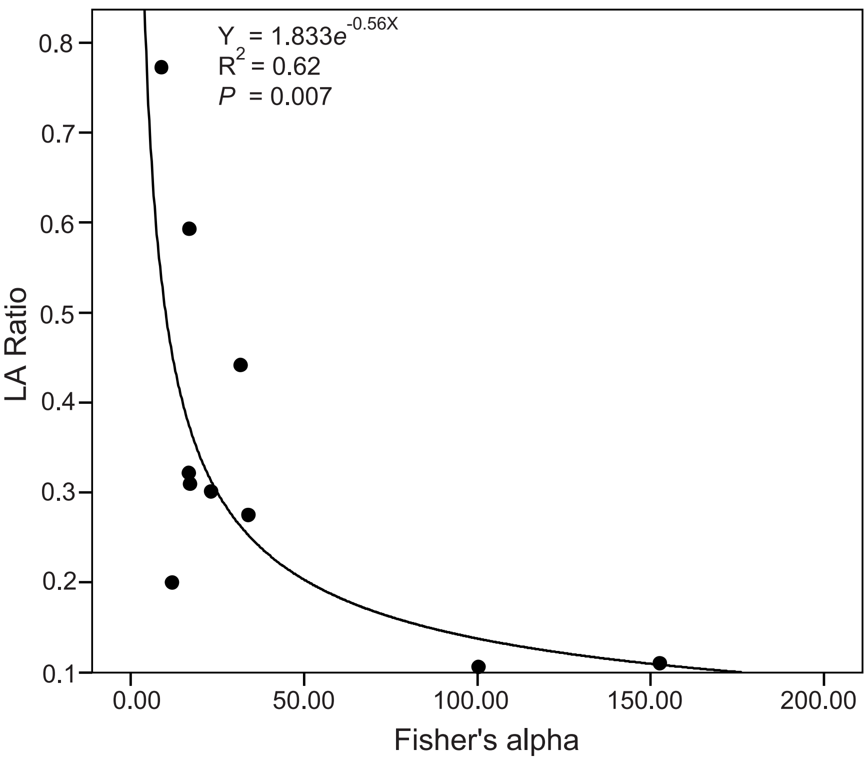

a
Y = 17.60LogX-22.75
R^2= 0.60
P = 0.009
Number of species with aggregated large individuals
0
20
40
60
80
0.00
50.00
100.00
150.00
200.00
Fisher's alpha
b
Y = 41.17LogX-124.10
R^2= 0.59
P = 0.009
Number of species with aggregated large individuals
0
20
40
60
80
20
40
60
80
Family number
c
Y = 25.32LogX-84.8
R^2= 0.62
P = 0.007
Number of species with aggregated large individuals
0
20
40
60
80
0
50
100
150
200
250
300
Genus number

Figure 3



Y = 1.833e^-0.56X
R² = 0.62
P = 0.007
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
LA Ratio
0.00
50.00
100.00
150.00
200.00
Fisher's alpha