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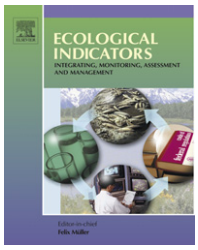

Letter to the Editor

On species–area and species accumulation curves: A comment on Chong and Stohlgren's index

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ABSTRACT

Chong and Stohlgren [Chong, G.W., Stohlgren, T.J., 2007. Species–area curves indicate the importance of habitats' contributions to regional biodiversity. Ecol. Indic. 7, 387–395] presented a combined ranking index to measure the habitats' contribution to regional biodiversity, in which the species–area curves perform poorly in the prediction of the species richness in multiple plots. After re-examination of the dataset (17 vegetation types of the Rocky Mountain National Park, CO, USA), I present the reason for this poor performance: (1) species–area curve is not identical with species accumulation curve; (2) the latter is steeper than the former due to: (a) rare species normally appearing at coarser spatial scales and (b) beta diversity being positively correlated to the distance between samples. This result implies that Chong and Stohlgren's ranking index is scale dependent. The total number of species in different habitats could serve as an intuitive indicator that is highly correlated with the Chong–Stohlgren index.

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Based on the ranking of mean number species, slopes of species–area curves, Jaccard's coefficients (beta diversity index) and mean unique species, Chong and Stohlgren (2007) presented an index (the sum of the rankings of above variables) to describe the contribution of different habitats (specifically vegetation types) to the regional biodiversity. Using a regional-scale dataset of 17 vegetation types in the Rocky Mountain National Park (CO, USA), the index gives a relatively stable result ($R^2 = 0.41$, $P < 0.001$; Fig. 2 in Chong and Stohlgren, 2007), that the types making the greatest contributions to regional biodiversity covered the smallest areas. Here I want to argue the problems of using species–area curves (Table 2 in Chong and Stohlgren, 2007) to predict the species richness in multiple plots of different vegetation types (Table 3 in Chong and Stohlgren, 2007).

Chong and Stohlgren (2007) adopted a typical hierarchical sample strategy (the standard modified-Whittaker plot design) to measure the species number in the 1, 10, 100 m^2 subplots and 1000 m^2 plots. Species–area curves (type IV in Scheiner, 2003) were constructed using the mean number of species within the plots, which should use species accumulation curves instead (type IIIB in Scheiner, 2003; also see Gray et al., 2004b). Chong and Stohlgren (2007) then use those curves to predict the total species richness in the multiple plots (e.g. four plots in the alpine tundra). Although the species–area curves have relatively high confidence (e.g. for the alpine tundra, species–log(area): $r^2 = 0.87$; log(species)–log(area): $r^2 = 0.89$), there is a large discrepancy between the predicted and observed results (Table 3 in Chong and Stohlgren, 2007). It is due to the general confusion about species–area curves and species accumulation curves (Scheiner, 2003, 2004; Gray et al., 2004a,b).

Based on the Jaccard's coefficient J and the mean number of species per plot S_1 (Tables 2 and 4 in Chong and Stohlgren, 2007), we can calculate the number of species in two plots $S_2 = 2S_1/(1 + J)$. Together with the total species observed S_N (observed column in Table 3; N is the number of plots listed in Table 2; both listed in Chong and Stohlgren, 2007), we can give the species accumulation curves (Table 1). Species accumulation curves (also called species discovery curves) describe the sampling results in a species pool with a total number of species S_T. Although using the traditional regression methods to describe species accumulative curves still have a high confidence ($R^2 > 0.95$ and $P < 0.001$ for all the S–A, S–log(A) and log(S)–log(A) in Table 1), a negative exponential distribution ($S_x = S_T(1 - \exp[-\lambda x])$) was normally used so that the total species richness S_T could be decided (Fisher et al., 1943).

Table 1 – Species accumulation curves for 17 vegetation types in Rocky Mountain National Park, CO, USA

Vegetation type	S_2	S–A		S–log(A)		log(S)–log(A)		Negative exponential distribution			
		Slope	C	Slope	C	Slope	C	S_T	S.E.	λ	S.E.
Alpine tundra	79	0.02	40.26	84.71	−201.12	0.49	0.27	113.43	3.64	0.61	0.05
Aspen	112	0.01	67.52	316.85	−906.09	0.59	0.09	538.44	8.32	0.12	0.01
Douglas fir	68	0.01	34.69	93.32	−237.63	0.54	0.04	127.62	5.83	0.39	0.04
DF/lodgepole	48	0.01	20.61	53.93	−129.17	0.53	−0.07	68.75	5.19	0.63	0.10
Dry meadow	78	0.01	42.00	127.18	−335.92	0.55	0.06	181.97	8.03	0.29	0.03
Limber pine	48	0.01	17.48	60.47	−150.63	0.61	−0.32	75.76	2.51	0.52	0.03
Lodgepole (LP)	53	0.01	29.18	146.06	−416.80	0.62	−0.34	234.35	3.67	0.13	0.01
LP/LIM	47	0.02	15.50	62.01	−156.62	0.63	−0.42	80.15	7.88	0.45	0.08
LP/ponderosa	80	0.02	28.11	102.13	−255.78	0.62	−0.14	128.34	4.27	0.50	0.03
LP/spruce/fir	36	0.01	14.64	34.41	−78.22	0.50	−0.10	42.68	1.60	0.88	0.08
Mixed conifer	54	0.02	14.74	110.11	−302.29	0.76	−0.76	176.64	18.45	0.19	0.03
Ponderosa pine	76	0.01	43.82	140.18	−379.22	0.55	0.05	212.50	5.59	0.23	0.02
PP/DF	79	0.02	29.80	97.70	−241.64	0.59	−0.05	123.04	7.23	0.54	0.06
Spruce/fir	66	0.02	25.21	122.75	−333.25	0.67	−0.41	172.77	9.67	0.25	0.03
Subalpine	52	0.01	24.98	102.27	−278.61	0.61	−0.32	146.32	8.05	0.23	0.03
Wet meadow	82	0.02	33.60	230.57	−659.74	0.71	−0.46	358.43	6.88	0.13	0.01
Willow	93	0.02	41.24	192.08	−529.21	0.65	−0.20	274.64	7.91	0.21	0.01

S_2, The mean number species of two plots; S, species; A, area (the unit is m^2 for S–A, S–log(A) and log(S)–log(A)) and is plot, i.e. 1000 m^2 for the negative exponential distribution; S_T, predicted total species richness; λ, the parameter of NED; S.E., standard error. Slope and C have the same meaning as in Chong and Stohlgren (2007).

Species–area curves are related to, but not identical with the species accumulative curves (Barbour et al., 1980).

The reason that Chong and Stohlgren (2007) underestimate most species richness (species–log(area) and log(species)–log(area) models) in the multiple plots is now clear: they should use species accumulation (discovery) curves, instead of species–area curves, to predict the species richness (Gray et al., 2004a). Comparing their results with Table 1, we found that species accumulation curves have a significantly steeper slopes than species–area curves (*t*-test of the slope of log(*S*)–log(*A*) model; $t = 10.83$, $P < 0.001$. The difference in steepness reflects that the turn over rate of species (differentiation diversity; Scheiner, 2003) in samples at coarse/large scales (from 2000 to 36,000 m^2 in the species accumulation curves) will be much higher that those at small scales (<1000 m^2 in the Whittaker's sample design; Chong and Stohlgren, 2007). This is the real reason for the low accuracy of Chong and Stohlgren (2007) prediction. Two factors lead to this discrepancy. First, the occurrence of rare or uncommon species is more likely to be encountered at coarser spatial scales. The same kind of difference has also been found in California shrubland (including four vegetation types; Keeley, 2003). Second, beta diversity between plots is higher (lower Jaccard's coefficients) than between subplots within the plot. That beta diversity increases with the distance between samples is the reason that the species accumulation curve has a steeper slope than the species–area curve. An excellent discussion on species accumulation and species–area curves can also be found between Scheiner (2003, 2004) and Gray et al. (2004a,b).

If we use the species number in two plots instead of in one plot and use the slope of the species accumulation curves instead of those of species–area curves, the contribution of different vegetation types to regional diversity calculated by Chong and Stohlgren (2007) index will also be changed. This suggests that Chong and Stohlgren's index is scale-dependent. Intuitively, the contribution of a specific vegetation types to

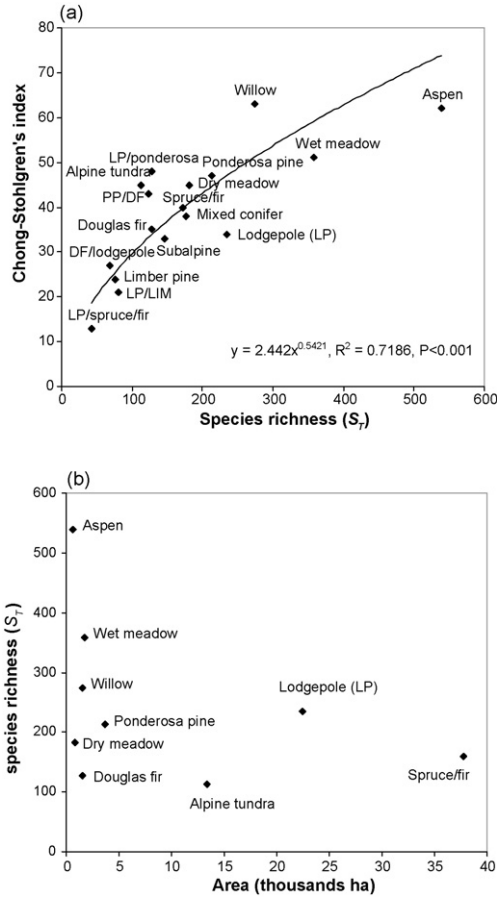

Fig. 1 – (a) The relationship between species richness, S_T, in different vegetation types and Chong and Stohlgren (2007) index. (b) The relationship between vegetation covers in Rocky Mountain National Park (CO, USA) and species richness.

the regional biodiversity should be the total species richness of this vegetation types, i.e. S_T. Chong and Stohlgren's index shows a high correlation with S_T (Fig. 1a). Moreover, the total species richness S_T appears a negative correlation with the vegetation covers (Fig. 1b), which is consistent with the result shown in Fig. 2 of Chong and Stohlgren (2007). This scale-independent S_T could be an improvement of Chong and Stohlgren's index. A better index of habitats' contributions to regional biodiversity could be a combination of Chong and Stohlgren's index and the adjusted result S_T from species accumulation curves.

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REFERENCES

Barbour, M.G., Burk, J.H., Pitts, W.D., 1980. Terrestrial Plant Ecology. Benjamin/Cummings, Menlo Park, CA, pp. 158–160.
Chong, G.W., Stohlgren, T.J., 2007. Species–area curves indicate the importance of habitats' contributions to regional biodiversity. Ecol. Indic. 7, 387–395.
Fisher, R.A., Corbet, A.S., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 12, 42–58.
Gray, J.S., Ugland, K.I., Lambshead, J., 2004a. Species accumulation and species area curves—a comment on Scheiner (2003). Global Ecol. Biogeogr. 13, 473–476.
Gray, J.S., Ugland, K.I., Lambshead, J., 2004b. On species accumulation and species–area curves. Global Ecol. Biogeogr. 13, 567–568.
Keeley, J.E., 2003. Relating species abundance distributions to species–area curves in two Mediterranean-type shrublands. Diver. Distr. 9, 253–259.
Scheiner, S.M., 2003. Six types of species–area curves. Global Ecol. Biogeogr. 12, 441–447.
Scheiner, S.M., 2004. A mélange of curves—further dialogue about species–area relationships. Global Ecol. Biogeogr. 13, 479–484.

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