

Plant Richness and β -Diversity of Small Coastal Islands in Wenzhou and Their Influencing Factors: Postprint

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Abstract

From 2012 to 2015, we investigated the plant composition of 20 small uninhabited islands along the Wenzhou coast, recording a total of 366 vascular plant species belonging to 95 families and 244 genera, including 226 herbaceous species and 140 woody species. Five species-area relationship models were fitted, and the Akaike Information Criterion (AIC) was used for model selection. The species-area-habitat type relationship model SAHnR exhibited the largest weight coefficient at 40.26%, while the two breakpoint regression species-area relationship models BR-SAR had weight coefficients of only 6.94% and 0.43%, respectively, indicating that the species-area relationship fitted based on these 20 islands showed no small island effect. Island plant species richness was primarily influenced by area A , whereas distance from mainland Im had no significant effect on richness. Partial correlation analysis revealed that, in addition to A , the perimeter/area ratio PAR and island habitat diversity index Hd significantly affected plant richness. The stepwise regression equations were as follows: total plant richness $S=76.714+1.696A-0.046PAR$, $R^2=0.839$; woody plant richness $S_{woody}=6.525+0.455A+24.544Hd$, $R^2=0.697$; herbaceous richness $S_{herbaceous}=66.899+1.285A-0.04PAR-23.434Hd$, $R^2=0.865$. In the partial least squares regression (PLS) analysis, the importance ranking of island spatial characteristic parameters for the island species similarity index was: $Im(0.61) > Ii(0.56) > PAR(0.49) > A(0.20) > shoreline\ length\ Per(0.14) > habitat\ type\ H(0.072) > island\ elevation\ E(0.065) > island\ shape\ index\ SI(0.05)$. Thus, plant richness in nearshore small islands is not always determined by island area; isolation has a relatively large influence on island plant β -diversity.

Full Text

Factors Affecting Species Richness and Beta Diversity of Vascular Plants on Small Islands in the Wenzhou Region of Eastern China

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Abstract

We conducted field surveys on 20 small, uninhabited islands off the coast of Wenzhou in the Pacific Ocean and recorded 366 vascular plant species belonging to 244 genera and 96 families. Of these, 140 were woody and 226 were herbaceous species. Five regression models were constructed to predict species richness (S) and selected based on the Akaike information criterion (AIC). The effects of island size (A), inter-island distance (I_i), shoreline length (Per), perimeter-to-area ratio (PAR), elevation (E), habitat diversity (H_d), and island shape index (SI) were examined. Model SAH_n had the highest Akaike weight (40.26%), with ratios of 1.19, 2.17, 5.80, and 94.08 over SAR, SAH_d, BR-SAR1, and BR-SAR2, respectively. Species richness increased with island size following the classic species-area relationship. However, the species similarity index decreased with increasing I_i ($r = 0.56$, $P < 0.05$), suggesting that isolation (i.e., I_m = 0.61, PAR = 0.49, I_i) played a major role. The importance of all explanatory variables on diversity was: I_m (0.61) > I_i (0.56) > PAR (0.49) > Per (0.14) > E (0.072) > SI (0.065) > H_n (0.05). Plant species richness was also significantly affected by PAR and habitat diversity. The best models to predict richness were: $S_{total} = 76.714 + 1.696A - 0.046PAR$ ($R^2 = 0.839$); $S_{woody} = 6.525 + 0.455A + 24.544H_n$ ($R^2 = 0.697$); and $S_{herbaceous} = 66.899 + 1.285A - 0.04PAR - 23.434H_n$ ($R^2 = 0.865$) for total, woody, and herbaceous species richness, respectively. This further indicated that species richness of different growth forms (i.e., woody and herbaceous) on these islands was not solely dependent on island size.

Keywords: island biogeography; species richness; species-area relationship; spatial characteristics; small island effect

Introduction

The species-area relationship (SAR) is one of the earliest established models in ecological theory and has received considerable attention in biogeography and conservation biology. Both niche and neutral theories have been used to explain the ecological mechanisms underlying SAR. Community assembly results from the combined effects of niche differentiation and stochastic ecological drift.

Environmental filtering and species' limiting similarity mean that sampling areas containing more heterogeneous habitat types lead to higher probabilities of encountering new species, while the random spatial distribution of individual species means that increased sampling area raises the probability of new species appearance. SAR quantitatively expresses the continuous increase in species richness with sampling area.

In island biogeography theory, changes in species composition cause dynamic fluctuations in island species richness, though richness remains relatively stable over time. Island species richness depends primarily on island area and isolation, though this theory may not apply to small islands. Logically, when island area becomes sufficiently small, it can only support very few species, or species may be absent at certain times due to dynamic fluctuations. This theory also suggests that SAR may not hold when island area falls below a certain threshold, a phenomenon known as the small island effect (SIE). Numerous biogeographical and biodiversity studies have demonstrated SIE across various taxa, including plants and birds. Lomolino and Weiser reviewed multiple studies using log-log and semi-log models. However, research results on SIE vary considerably due to differences in study regions and organisms, leading some scholars to question its existence. For example, Qie et al. found no effect of area on dung beetle richness in lake islands in Malaysia, while Zhao et al. found clear SIE for small mammals on peninsulas. In contrast, Wang et al. found no evidence of SIE for birds on lake islands.

Because island species richness is primarily influenced by area and isolation, SAR curves cannot clearly explain the roles of niche and species dispersal processes in determining richness. Beta diversity can more intuitively reflect changes in species composition across spatiotemporal scales and better explain isolation's role in affecting island species richness. The species similarity index, as a metric of β -diversity, is important for interpreting differences in species composition among communities. When islands are treated as patches, spatial characteristics such as patch area, isolation, and shape significantly affect species diversity. This study analyzes SAR and inter-island β -diversity to explore how island area, distance to mainland, and other spatial characteristics affect species richness.

The Wenzhou coastal region has numerous islands of varying sizes and isolation levels, providing an excellent setting for island biogeography and biodiversity research, though experimental studies are rarely reported. This study combines island geographic data with plant surveys of small uninhabited islands to address: (1) What island spatial characteristics primarily affect vascular plant richness, and does SIE exist? (2) How does β -diversity of vascular plants relate to island spatial characteristics?

1. Study Area

The study area spans Wenzhou' s jurisdiction, with islands distributed across 147.64 km north-south (27°05'54" N–28°22'26" N) and 79.59 km east-west (121°15'53" E–120°27'42" E). The region has a subtropical maritime monsoon climate with frequent sea fog in spring and typhoons with heavy rain in summer and autumn. Mean annual temperature is 15.4–17.7°C, mean annual precipitation is 1100–1400 mm, and mean annual evaporation is 1000–1300 mm. Most islands are concentrated in nearshore shallow waters within 15 m depth, with more distant islands relatively scattered.

With bridge construction projects, some islands have become connected. The islands are discontinuously distributed in groups along the southern Zhejiang coast, forming four major archipelagos: Dongtou, Nanji, Yueqing Bay, and Cangnan coastal islands. Wenzhou currently has 120 uninhabited islands, with those near the Oujiang River mouth (Dongtou archipelago) being most concentrated, accounting for about 55% of uninhabited islands. Cangnan eastern nearshore islands form a north-south chain and are relatively dispersed.

2. Methods

2.1 Survey Methods We conducted a census of islands smaller than 5 hm², recording all plant species encountered. For islands <1 hm², we used circumferential transects and central east-west or north-south transects. For islands of 1–20 hm², we set transects in lower and upper portions on both south and north slopes. For islands >20 hm², we used the same approach as for 1–20 hm² islands. We recorded plant species, habitat types (including broadleaf forest, grassland, and wetland), and habitat boundaries along transects. For islands <2 hm², we recorded all plant species and habitat types. For islands >2 hm², we recorded different habitat areas. Using GPS with <10 m error, we recorded boundary points of different habitats along transects, using the distance between two boundary points of the same habitat to represent its area [Figure 1: see original paper].

Collected plant specimens were identified in the laboratory, with questionable taxa verified by experts. Specimens are stored at the Zhejiang Institute of Subtropical Crops herbarium.

2.2 Data Processing Island Spatial Characteristics: Based on data from Wenzhou Marine and Fisheries Bureau, we described island spatial characteristics using area (A), distance to mainland (I_m), shoreline length (Per), perimeter-to-area ratio (PAR), maximum elevation (E), shape index (SI), and habitat type count (H_n). I_m represents the minimum straight-line distance from island edge to mainland. PAR is the relative edge length, representing boundary effects. SI reflects shape complexity, calculated as $SI = Per / [2 \times (\pi \times A)^{0.5}]$.

Species-Area Relationship Models and Selection: We used five models: SAR, SAH_n, SAH_d, and two breakpoint regression models (BR-SAR1, BR-SAR2) to detect SIE. The models were:

- SAR1 (log-log): $\log(S) = a + b \times \log(A)$
- SAR2 (semi-log): $\log(S) = a + b \times A$
- SAH_n: $\log(S) = a + b \times \log(A) + c \times \log(H_n)$
- SAH_d: $\log(S) = a + b \times \log(A) + c \times \log(H_d)$
- BR-SAR2: $\log(S) = a + b \times \log(A) + c \times \log(A) \times T$, where T is a breakpoint value (1 if true, 0 if false)

Habitat diversity index H_d was calculated using Shannon-Wiener formula: $H_d = -\sum(P_i \times \log(P_i))$, where P_i is the proportion of habitat i area on the island. Models were estimated using Quasi-Newton method in STATISTICA 10.0, with loss function = $(OBS - PRED)^2$. AIC was used to assess model complexity and fit. For small samples, $AIC_c = AIC + 2k(k+1)/(n-k-1)$, where k is parameter count and n is sample size. $\Delta AIC = AIC_i - AIC_{min}$, and model weights $W = \exp(-0.5 \times \Delta AIC) / \sum \exp(-0.5 \times \Delta AIC_i)$ were calculated to select the best model.

-Diversity Analysis: We calculated similarity coefficients (Jaccard index) between islands and analyzed relationships between C_j and island spatial characteristics using partial least squares regression (PLS) in STATISTICA 10.0, ranking parameter importance. Stepwise regression was used to build multivariate linear models for herbaceous and woody plant richness. Data analysis used Excel 2007, STATISTICA 10.0, and SPSS 13.0.

3. Results

3.1 Species Richness and Species-Area Relationship Fitting The 20 small islands recorded 366 vascular plant species (including subspecific taxa), comprising 140 woody species (38.3%) and 226 herbaceous species (61.7%). The number of islands in the 1-5 hm^2 range was highest (55%). Species richness varied greatly among islands, with the richest island having 140 species and the poorest having only 12.

Five species-area relationship models were fitted [Figure 2: see original paper]. The SAH_n model had the highest correlation coefficient ($R^2 = 0.891$), followed by SAH_d ($R^2 = 0.849$) and SAR ($R^2 = 0.825$). Both breakpoint regression models had lower R^2 values. No breakpoint appeared in the investigated area range for model BR-SAR1, while BR-SAR2 fitted a threshold of 1.26 hm^2 but with only 0.4% model weight. Based on minimum AIC_c , SAH_n, SAH_d, and SAR all had $\Delta AIC < 2$, while both breakpoint models had $\Delta AIC > 10$. The SAH_n model had the highest weight coefficient (40.26%), indicating no small island effect for plant richness on these 20 islands.

The SAH_n model explained 89.1% of variation in total species richness, 82.2%

for woody plants, and 86.6% for herbaceous plants. Woody plants had the highest z-value (0.251), while herbaceous plants had the lowest (0.208) .

3.2 Effects of Island Spatial Characteristics on Species Richness and -Diversity Correlation analysis showed that area, shoreline length, elevation, shape index, and habitat diversity significantly affected vascular plant richness. With increasing area, shoreline length, and elevation, islands with more complex shapes and higher habitat diversity had greater plant richness. PAR was significantly negatively correlated with species richness, representing island edge effects.

When using A as a control variable in partial correlation analysis, elevation and shape index showed no significant correlation with species richness, while PAR and habitat diversity still significantly affected total and herbaceous richness. Woody plants were significantly correlated with habitat diversity.

Stepwise regression models were: - Total richness: $S = 76.714 + 1.696A - 0.046PAR$ ($R^2 = 0.839$) - Woody richness: $S_{woody} = 6.525 + 0.455A + 24.544H_n$ ($R^2 = 0.697$) - Herbaceous richness: $S_{herbaceous} = 66.899 + 1.285A - 0.04PAR - 23.434H_n$ ($R^2 = 0.865$)

-diversity analysis showed that C_j was positively correlated with I_m ($r = 0.409$, $P < 0.05$) and negatively correlated with I_i ($r = -0.330$, $P < 0.05$). PLS analysis ranked parameter importance for species similarity as: I_m (0.61) > I_i (0.56) > PAR (0.49) > Per (0.14) > E (0.072) > SI (0.065) > H_n (0.05). The first principal component explained 33.52% of variation, with all six spatial characteristics collectively explaining only 36.08% of species similarity .

4. Discussion

4.1 Model Selection and Small Island Effect Detection Island biogeography theory predicts that species richness depends on the dynamic equilibrium between immigration and extinction rates, with immigration determined by isolation and extinction by area. When island area is sufficiently small (below a threshold), richness may become independent of area, with habitat type presence/absence becoming the main driver. Our breakpoint regression models found no threshold in the investigated area range, indicating no small island effect. The SAH_n model (40.26% weight) performed better than SAR (33.79%), suggesting habitat type number is more important than habitat diversity index in determining richness. This may be because H_d calculations used survey area rather than true habitat area, causing over- or underestimation of some habitats. Triantis et al. also noted that habitat type number alone can express the relationship between habitat diversity and species richness.

4.2 Spatial Determinants of Vascular Plant Richness and -Diversity In SAR models, the z-value represents the strength of area effects, typically

0.2–0.5 for islands. Our 20 islands had z -values of 0.208–0.251, with woody plants higher than herbaceous plants, possibly because woody species are more area-dependent. While species richness followed SAR and was primarily area-dependent, other spatial parameters also influenced richness, especially when considering growth forms. Habitat diversity significantly affected both woody and herbaceous richness, as species diversity depends on habitat heterogeneity, particularly in lower latitude regions.

PAR significantly affected total and herbaceous richness, representing edge effects. While edge effects typically increase biodiversity in habitat ecotones, on these small islands PAR reflects the proportion of exposed rocky coastal zones rather than true ecotones, explaining the negative relationship.

Isolation effects were complex. Using I_m and I_i as isolation measures, we found no significant correlation between richness and I_m , likely because most islands were within 10 km of mainland, insufficient to limit dispersal. However, β -diversity analysis showed I_m and I_i significantly affected species similarity, indicating isolation influences species composition rather than richness. This aligns with studies showing that near-mainland islands have higher similarity. The role of isolation in island plant richness requires further study, as assessing distance effects is difficult and results are often uncertain.

5. Conclusion

Herbaceous plants dominate the flora of small uninhabited islands in Wenzhou's coastal region. Island species richness follows the species-area relationship and is primarily area-dependent, with no small island effect detected. However, other spatial parameters, particularly habitat diversity index and island edge effects, significantly influence richness, especially when distinguishing plant growth forms. Comprehensive analysis of island spatial characteristics helps deepen understanding of SAR patterns and plant diversity drivers.

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References

- [1] Gleason H A. On the relation between species and area. *Ecology*, 1922, 3(2): 158-162. [2] Lomolino M V. Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography*, 2000, 27(1): 17-26. [3]

Desmet P, Cowling R. Using the species-area relationship to set baseline targets for conservation. *Ecology and Society*, 2004, 9(2): 301-303. [4] Murakami M, Hirao T, Loyola R. Lizard predation alters the effect of habitat area on the species richness of insect assemblages on Bahamian isles. *Diversity and Distributions*, 2010, 16(6): 952-958. [5] Rybicki J, Hanski I. Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters*, 2013, 16(S1): 27-38. [6] Gravel D, Canham C D, Beaudet M, Messier C. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters*, 2006, 9(4): 399-409. [7] Hubbell S P. Neutral theory and the evolution of ecological equivalence. *Ecology*, 2006, 87(6): 1387-1398. [8] Wilson J B, Gitay H. Limitations to species coexistence: evidence for competition from field observations, using a patch model. *Journal of Vegetation Science*, 1995, 6(3): 369-376. [9] Webb C O, Ackerly D D, McPeck M A, Donoghue M J. Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 2002, 33: 475-505. [10] MacArthur R H, Wilson E O. *The Theory of Island Biogeography*. Princeton: Princeton University Press, 1967: 8-18. [11] Morrison L W. Why do some small islands lack vegetation? Evidence from long-term introduction experiments. *Ecography*, 2011, 34(3): 384-391. [12] Triantis K A, Vardinoyannis K, Tsolaki E P, Botsaris I, Lika K, Mylonas M. Re-approaching the small island effect. *Journal of Biogeography*, 2006, 33(5): 914-923. [13] Lomolino M V, Weiser M D. Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography*, 2001, 28(4): 431-445. [14] Burns K C, McHardy R P, Pledger S. The small-island effect: fact or artifact? *Ecography*, 2009, 32(2): 269-276. [15] Qie L, Lee T M, Sodhi N S, Lim S L H. Dung beetle assemblages on tropical land-bridge islands: small island effect and vulnerable species. *Journal of Biogeography*, 2011, 38(4): 792-804. [16] Zhao Q Y, et al. Diversity of small mammal communities on lake islands in Qiandao Lake. *Acta Ecologica Sinica*, 2009, 29(4): 406-412. [17] Wang Y P, Zhang M, Wang S Y, Ding Z F, Zhang J C, Sun J J, Li P, Ding P. No evidence for the small-island effect in avian communities on islands of an inundated lake. *Oikos*, 2012, 121(12): 1945-1952. [18] Chave J. Neutral theory and community ecology. *Ecology Letters*, 2004, 7(3): 241-253. [19] Wang X G, Wiegand T, Wolf A, Howe R, Davies S J, Hao Z Q. Spatial patterns of tree species richness in two temperate forests. *Journal of Ecology*, 2011, 99(6): 1382-1393. [20] Qian H. Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. *Journal of Systematics and Evolution*, 2009, 47(5): 509-514. [21] Qian H, Ricklefs R E, White P S. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, 2005, 8(1): 15-22. [22] Honnay O, Endels P, Vereecke H, Hermy M. The role of patch area and habitat diversity in explaining native plant species richness in disturbed suburban forest patches in northern Belgium. *Diversity and Distributions*, 1999, 5(4): 129-141. [23] Morrison L W. Determinants of plant species richness on small Bahamian islands. *Journal of Biogeography*, 2002, 29(7): 931-941. [24] Wang Y, Liu J S. Effects of remnant wetland patch characteristics on species diversity in the Sanjiang Plain. *Acta Ecologica Sinica*, 2010, 30(24): 6683-6690. [25] Chen Q X. Disposal of historical

property rights issues on uninhabited islands: A case study of Wenzhou. *Journal of Zhejiang Provincial Party School*, 2013, (3): 10-15. [26] Wu J G. Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology*, 2004, 19(2): 125-138. [27] Hoffmeister T S, Vet L E M, Biere A, Holsinger K, Filser J. Ecological and evolutionary consequences of biological invasion and habitat fragmentation. *Ecosystems*, 2005, 8(6): 657-667. [28] Triantis K A, Mylonas M, Lika K, Vardinoyannis K. A model for the species-area-habitat relationship. *Journal of Biogeography*, 2003, 30(1): 19-27. [29] Gentile G, Argano R. Island biogeography of the Mediterranean sea: the species-area relationship for terrestrial isopods. *Journal of Biogeography*, 2005, 32(10): 1715-1726. [30] Burnham K P, Anderson D R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd ed. New York: Springer, 2002: 60-80. [31] Whittaker R H. Evolution and measurement of species diversity. *Taxon*, 1972, 21(2/3): 213-251. [32] Whitehead D R, Jones C E. Small islands and the equilibrium theory of insular biogeography. *Evolution*, 1969, 23(1): 171-179. [33] Drakare S, Lennon J J, Hillebrand H. The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology Letters*, 2006, 9(2): 215-227. [34] Kreft H, Jetz W, Mutke J, Kier G, Barthlott W. Global diversity of island floras from a macroecological perspective. *Ecology Letters*, 2008, 11(2): 116-127. [35] Fridley J D, Peet R K, Wentworth T R, White P S. Connecting fine- and broad-scale species-area relationships of southeastern U.S. flora. *Ecology*, 2005, 86(5): 1172-1177. [36] May R M, Stumpf M P H. Species-area relations in tropical forests. *Science*, 2000, 290(5499): 2084-2086. [37] Kerr J T, Packer L. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 1997, 385(6613): 252-254. [38] Hu Y H, et al. Edge effects on plant community structure of land-bridge islands in Qiandao Lake. *Chinese Journal of Applied Ecology*, 2014, 25(1): 77-84. [39] Alignier A, Alard D, Chevallier R, Corcket E. Can contrast between forest and adjacent open habitat explain the edge effects on plant diversity? *Acta Botanica Gallica: Botany Letters*, 2014, 161(3): 253-259. [40] He F L, Legendre P. Species diversity patterns derived from species-area models. *Ecology*, 2002, 83(5): 1185-1198. [41] Galanes I T, Thomlinson J R. Relationships between spatial configuration of tropical forest patches and woody plant diversity in northeastern Puerto Rico. *Plant Ecology*, 2009, 201(1): 101-113. [42] Qian H, et al. Beta diversity of vascular plants on islands in Qiandao Lake and its influencing factors. *Acta Ecologica Sinica*, 2014, 34(14): 3866-3872. [43] Whittaker R J, Fernández-Palacios J M. *Island Biogeography: Ecology, Evolution, and Conservation*. 2nd ed. Oxford, New York: Oxford University Press, 2007: 83-87.

Appendices

Attached Table 1. Pearson correlation coefficients among island spatial characteristics of the 20 investigated islands

Parameter	Area	Distance to mainland (I_m)	Perimeter (Per)	Maximum elevation (E)	Shape index (SI)	PAR
Area	1	0.016	0.945**	0.906**	-0.629**	-
Distance to mainland (I_m)		1	0.002	0.019	0.921**	0.775**
Perimeter (Per)			1	0.533*	-0.719**	-
Maximum elevation (E)				1	-0.622**	-
Shape index (SI)					1	0.622**
PAR						1

*P < 0.05; **P < 0.01

Attached Table 2. Similarity index between the 20 investigated islands

[Species similarity matrix table would be reproduced here with island codes]

Note: Island codes: DW, WSD, etc. [Full list of island names corresponding to codes would be included]

Figure Captions

FIGURE:1. Distribution of investigated islands; base map from Mapworld Zhejiang (Chart number S(2010)280)

FIGURE:2. The five regression models of species-area relationships for vascular plants on 20 investigated islands

FIGURE:3. Species-area-habitat relationship (SAH_n) of herbaceous and woody plants

FIGURE:4. Scatter plot of the relationship between island characteristics and C_j

Note: Figure translations are in progress. See original paper for figures.

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