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Spatial Autocorrelation Patterns of Understory Plant Species in a Subtropical Rainforest at Lanjenchi, Southern Taiwan

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ABSTRACT: Many studies described relationships between plant species and intrinsic or exogenous factors, but few quantified spatial scales of species patterns. In this study, quantitative methods were used to explore the spatial scale of understory species (including resident and transient species), in order to identify the influential factors of species distribution. Resident species (including herbaceous species, climbers and tree ferns < 1 m high) were investigated on seven transects, each 5-meter wide and 300-meter long, at Lanjenchi plot in Nanjenshan Reserve, southern Taiwan. Transient species (seedling of canopy, subcanopy and shrub species < 1 cm diameter at breast height) were censused in three of the seven transects. The herb coverage and seedling abundance were calculated for each 5 × 5 m quadrat along the transects, and Moran's *I* and Galiano's new local variance (NLV) indices were then used to identify the spatial scale of autocorrelation for each species. Patterns of species abundance of understory layer varied among species at fine scale within 50 meters. Resident species showed a higher proportion of significant autocorrelation than the transient species. Species with large size or prolonged fronds or stems tended to show larger scales in autocorrelation. However, dispersal syndromes and fruit types did not relate to any species' spatial patterns. Several species showed a significant autocorrelation at a 180-meter class which happened to correspond to the local replicates of topographical features in hilltops. The spatial patterns of understory species at Lanjenchi plot are mainly influenced by species' intrinsic traits and topographical characteristics.

KEY WORDS: Spatial autocorrelation, Moran's *I*, new local variance (NLV), herbaceous species, seedlings and functional traits.

INTRODUCTION

Understanding spatial patterns provides vital clues to the influential factors of species distribution and helps to generate hypotheses about their relationships (Ford and Renshaw, 1984). Therefore, simultaneously quantifying spatial scales for both of species' intrinsic and external factors can provide both biological and environmental information in controlling factors (Dale, 2000). Many studies revealed that the variability of environmental factors can directly influence the spatial pattern of plants. For example, Pool (1914) was the first scientist who recognized the association between topography and species in a Nebraska Sandhills; later, the distribution of grass species were proved to be controlled by spatial distribution of available water along a topographic gradient in the same area (Barnes and Harrison, 1982). Spatial association patterns between plants and topography in tropical areas are also shown at various scales, including local (He et al., 1997; Condit et al., 2000), meso- (Clark et al., 1998) and regional scales (Newbery et al., 1986; Tuomisto and Ruokolainen, 1994). Those spatial scales and distribution patterns may reflect niche requirements of a species and availability of environmental resources (Dale, 2000).

The forest understory (including resident species and transient species) is an important component of biodiversity with both intrinsic and functional values (Whitney and Foster, 1988; Poulsen and Balsley, 1991; Scheiner and Istock, 1994; Tchouto et al., 2006). Resident species, such as herbs and small shrubs, are those with life-history characteristics that confine them to above-ground height of ca. 1-1.5 meter (Gilliam and Roberts, 2003). Transient species comprise plants whose existence in understory layer is temporary because they have potential to develop and emerge into higher strata (*e.g.*, subscanopy and canopy strata) (Gilliam and Roberts, 2003). The stratum of forest vegetation containing resident species often called the herbaceous layer. The herbaceous layer can serve as a "filter" for future canopy trees (Royo and Carson, 2008), and provides both food and habitat for a wide array of animal species (Martin et al., 1951; Pough et al., 1987). However, the studies of understory vegetation were relatively few comparing to overstory investigation (Hart and Chen, 2006). Here we examine the spatial patterns of understory vegetation in a subtropical forest with the intention for revealing determining factors of this stratum.

The emergence of understory species is influenced by both extrinsic and intrinsic processes that occur over small areas. Abundance pattern of an understory species may reflect on the spatial characteristic of an external factor such as micro-topography (Bratton, 1976; Beatty, 1984). For example, in neotropical forests, understory fern and palm cover appear positive relatedness to soil fertility and moisture (Wright, 1992) and seedling density was negatively correlated with palm cover (Harms et al., 2004). Intrinsic traits of species such as dispersal ability and reproduction traits can also influence species distribution patterns. For example, wind-dispersal syndromes are fairly evenly distributed at all elevations and distance from river banks, comparing with plants dispersed by animals (Drezner et al., 2001; Miller et al., 2002). Plant with vigorous vegetative growth and large individual size are autocorrelated in a broader scale than species without vegetative propagules and show a patched distribution pattern in local scale (Verburg et al., 1996). Relationships between the spatial pattern and intrinsic traits of plants or between plant and spatial heterogeneity can be detected using quantitative methods. For example, Kershaw (1964) found that in *Eriophorum angustifolium* and *Trifolium repens*, the first three scales of distribution patterns are related to their length of branch growth and to their stolon or rhizome system.

Nanjenshan forests, on the southern tip of Taiwan, harbor some of best examples of lowland forests in subtropical region. The overstory vegetation of Nanjenshan forests were attracted much attention and well-investigated (Chao et al., in press) because of their mixture of holarctic and tropical plant elements (Li and Keng, 1950; Huang et al., 1980). However, the study of understory vegetation is still limited. In this study, quantitative methods (*i.e.*, autocorrelations and new local variance) were used to explore the patterns of species distribution and species abundance in understory layer. We ask the following questions (1) what are the autocorrelation scales of understory species distributions, and (2) what are the major determining factors for the autocorrelation patterns of understory species. Specifically, we ask that if there are any intrinsic traits of understory species (*e.g.*, reproduction traits, individual size, and life forms) or exogenous factor (*i.e.*, topography) showing correlations with the spatial scales of understory species.

MATERIALS AND METHODS

Study site

Lanjenchi Forest Dynamics Plot (22°3’N, 120°51’E), in the Nanjenshan Reserve of the Kenting National Park is located on the eastern slope of the Central Mountain Range near the coast of the Pacific Ocean in southern Taiwan (Fig. 1). The climate is coastal and tropical with a mean annual temperature of 22.3°C (recorded from 1994 to 1998) and monthly mean temperature ranging 18°C in January to 26.1°C in July. The average annual precipitation is 3,793 mm and 72 percent of it occurred between June and October mainly by typhoons. The forest in the Nanjenshan reserve was classified as a monsoon forest (Su and Su, 1988). Although the elevation is low (about 300 to 350 m above sea level), forests here were classified as a *Machilus-Castanopsis* forest by the vegetation classification system of Taiwan (Su, 1984) and the oerstory is constituted of evergreen oak-laurel species, due to the influence of monsoon (Liu and Liu, 1977).

The 3 ha Lanjenchi Forest Dynamics Plot (100 m by 300 m) was established in 1989 (Fig. 1). The plot has moderate relief with slopes mostly between 10 and 30% and elevation ranging from 300 to 350 m above sea level. The plot is crossed by a small north-south oriented creek and separated the plot into hills (Fig. 1). The exposed geological strata consist of interbedded sandstones and shales of Miocene age (Chen et al., 1997).

Field sampling

Field work for understory vegetation was carried out from July to October in 1991. For resident species (*i.e.*, herbaceous species, including climbers and tree ferns < 1 m in height), 420 contiguous quadrats, each five meter by five meter, on seven transects in the Lanjenchi Forest Dynamics Plot were established (Fig. 1), and the resident plants sampled within each quadrat were identified and recorded. The coverage of each species was measured by line intercept method along two transect lines within each quadrat, which were set one meter from the northern and from the southern borders of each quadrat. Among the seven transects, three of them were selected to census transient species (*i.e.*, seedlings of canopy, subcanopy and large shrub species < 1 cm diameter at breast height). A total of 180 contiguous quadrats on three transects were established (Fig. 1) and all seedlings within each quadrat were identified and recorded. Nomenclature, life forms, individual heights, dispersal syndromes and vegetative tissues of understory species followed the definition in the *Flora of Taiwan* (Huang, 1993-2000).

Analysis

Coverage for each herbaceous species in each quadrat was calculated as the sum of the intercept lengths divided by the total sampled length (10 m in each quadrat). Abundance of seedling species in each quadrat was evaluated as the number of individuals within the sample area. The herb coverage and seedling abundance were used to quantify spatial scale for each species. Two indices, Moran’s *I* (1950) and Galiano’s new local variance (Galiano, 1982) were computed in spatial analysis.

Moran’s *I*, a spatial autocorrelation coefficient, estimates the similarity of sampled values within a certain distance class. The Moran’s *I* is calculated as:

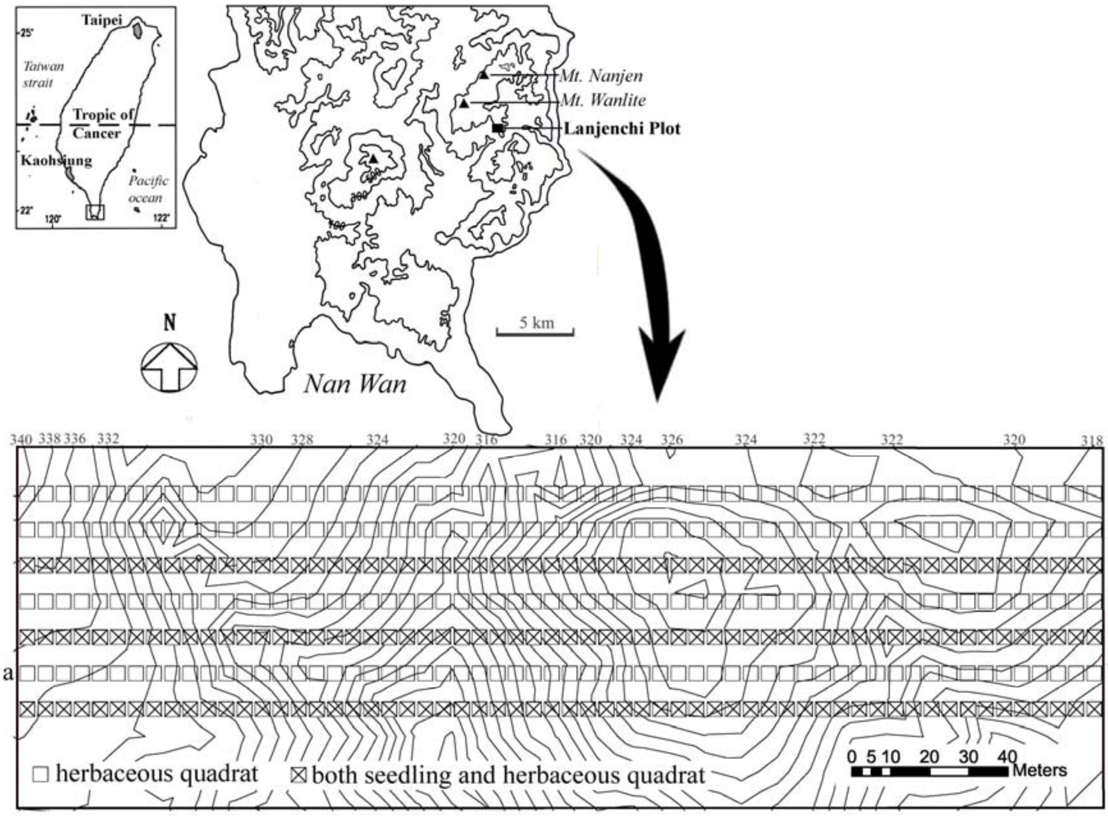

Fig. 1. Locations of the study site, Lanjenchi Plot in Nanjenshan Reserve of the southernmost part of Taiwan (22°3'N and 120°51'E) and contiguous quadrats for sampling seedling abundance and herbaceous coverage. (The second last transect (a-b) in the study plot was used for constructing the correlogram shown in Fig. 2).

$$I(d) = \frac{\frac{1}{w}\Sigma_{h=1}^{n}\Sigma_{i=1}^{n} w_{hi}(y_h-\bar{y})(y_i-\bar{y})}{\frac{1}{n}\Sigma_{i=1}^{n}(y_i-\bar{y})^2} \quad for \quad h \neq i \quad \ldots (1)$$

The y_h and y_i are the values of the observed variables at quadrats h and i; d is a distance class and n is the number of sampled quadrats. The weights $w_{hi} = 1$ when sites h and i at distance d and $w_{hi}=0$ otherwise; w is the number of quadrat pairs at d distance. For the autocorrelation pattern, in the beginning the similarity values (in Moran's I) of samples decreases with the increase of distances, and becomes level and not significantly different from 0 when the autocorrelation cannot be detected. However, the value of Moran's I could be significantly larger than 0 again if there are some replicates of environmental conditions. Under these circumstances, the scale of autocorrelation pattern is defined as the distance at which similarity values (in Moran's I) becomes level and not significantly different from 0. A correlogram is a graph in which autocorrelation values (Moran's I) are plotted against distance classes (Legendre and Legendre, 1998). For example, Fig. 2 is a correlogram of quadrat slope along the second last transect (a-b) in the study plot (Fig. 1) and the similarities of topographical slopes between sampled quadrats decline with the increasing distance in the Lanjenchi plot. The scale of spatial pattern for the topographical index (slope) was ca. 50 meters (Fig. 2). Randomization test of significance was used for each individual autocorrelation coefficient and the 95% upper limits against distance classes can be plotted as dashed line on Fig. 2. The autocorrelation values above dashed line mean that the samples at this distance were significantly positively correlated. For example, the spatial autocorrelation pattern became significant again in ca. 180 meters distance class (Fig. 2), which reflected the distance between the two replicates of hilltops within the study plot.

Galiano 's new local variance (NLV) is a quadrat variance method for detecting the size of distributed patches rather than as a method for estimating scales of spatial pattern (Dale, 2000). However, it can only be used in contiguous sampling. The variance is calculated as:

$$V_N(b) = \Sigma_{i=1}^{n-2b}\left|(\Sigma_{j=1}^{i+b-1} y_j - \Sigma_{j=i+b}^{i+2b-1} y_j)^2 - (\Sigma_{j=i+1}^{i+b} y_j - \Sigma_{j=i+b+1}^{i+2b} y_j)^2\right| / 2b(n-2b) \quad \ldots(2)$$

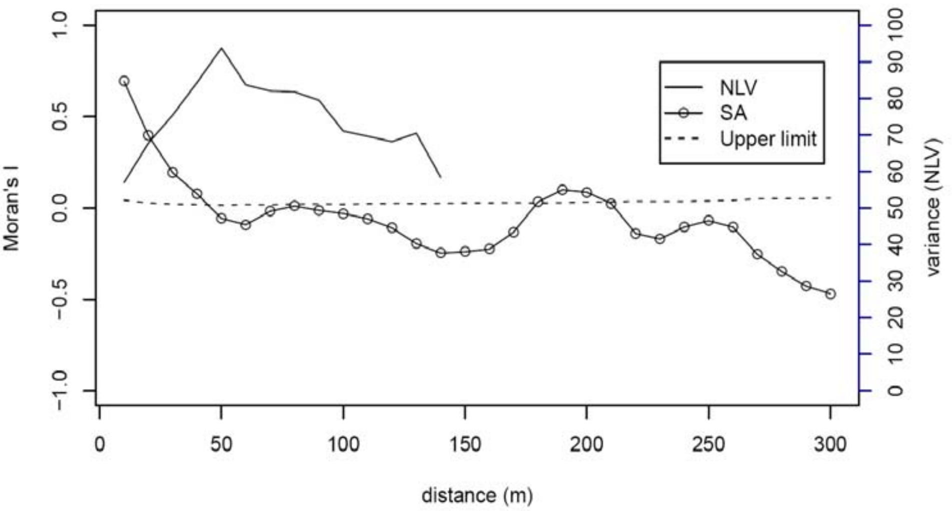

Fig. 2. Construction of a correlogram and a variogram, using Moran's *I* (SA) and new local variance (NLV), respectively. The correlogram was generated using slopes values of 420 herbaceous quadrats and the variogarm was generated using contiguous quadarts of transect a-b (indicated in Fig. 1). The upper limits of Moran's I estimated by randomization method were also plotted in dahed lines.

The y_i is the value of the observed variable at quadrat i; n is the number of quadrats in a transect. NLV examines the average of squared differences between duos of adjacent blocks of size b. The peak in a variogram of NLV values (as a function of distance) is interpreted as the average patch size of the pattern. For example, Fig. 2 showed that in Nanjenshan, the average patch size of slope changed in 50 meters, which is similar to the results by the Moran's *I* correlogram.

In this study we examined the spatial scale and patch size for understory species were estimated by Moran's *I* and NLV respectively. Species was strongly aggregated and patchily distributed in Lanjenchi plot, thus there would be some absent data in part of the sampled quadrats. When using data with absent values, all the species would be significant in autocorrelation calculations. Therefore, those quadrats with an absent (zero) were eliminated from computing Moran's *I* in order to emphasize the correlation within a finer environmental scale for species in Lanjenchi plot. Because NLV uses only contiguous sampling, the absent value cannot be eliminated. Coverage or abundance data of resident and transient species scattered in seven and three transects respectively; there were seven replicates of NLV calculation for resident species and three replicates for seedling species. Patch size was defined as the minimal distance of spatial scale class with maximal variance among replicates.

In terms of external (environmental) factors, we compared the results of Moran's *I* spatial scale for available data between resident species and transient species. We assume that if there is a similar proportion of species showed significant spatial scale for both resident species and transient species, this would indicate that there are similar external (environmental) factors can influence both types of species. Otherwise, the two types of species were controlled by different external factors.

In terms of intrinsic (biological) factors, we compared the results of Moran's *I* spatial scale for available data within resident species for their vegetative growth types, including with and without rhizomes, and with prolonged tissue (fronds or stems). We assume that if with rhizome or prolonged tissues is contributing factor for spatial patterns, then the proportion of species has significant autocorrelation scales would be in broader distances (*i.e.*, larger spatial scale) than species without rhizomes or prolonged tissue, due to with rhizomes or with prolonged tissue can help extend the distribution range of species (Verburg et al., 1996).

As for the intrinsic factors (sexual reproductive traits), we compared the results of Moran's *I* spatial scale for their life forms (*i.e.*, "canopy" or "subcanopy and shrub" in transient species), dispersal syndromes (wind-dispersed or not), and fruit types (*i.e.*, berry, capsule, drupe and fruits). We assume that a canopy life form, a "wind-dispersed" species, or berry fruit type would have a broader spatial scale than other species, due to a larger individual size (Verburg et al., 1996; Kuuluvainen et al., 1998) or longer-distance dispersal of winds and birds (Drezner et al., 2001; Miller et al., 2002).

RESULTS

A total of 150 understory species, consisting of 45 resident herbaceous species and 60 transient woody species, could be used in spatial analysis because of sufficient presence data in more than 30 quadrats. The results showed larger phase sizes (in NLV) than spatial

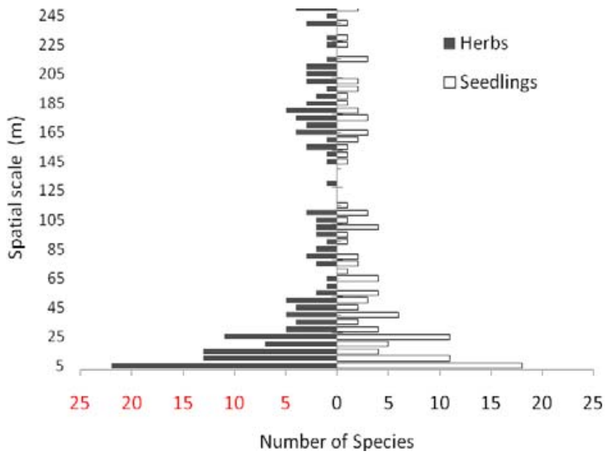

Fig. 3. Numbers of resident and transient species showing significant autocorrelations in each distance spatial scale class.

Fig. 4. Proportions of species (with and without rhizomes) showing significant autocorrelations in each distance spatial scale class.

scales (in Moran's *I*) of most species especially in trnsient species. However, separating resident and transient species, the estimated spatial scale and phase size showed a roughly consistent trend among species (Appendix).

Values of spatial autocorrelation generally decreased with distance for most species. Also, with the increase of spatial scale, there was a decline of species number with significant autocorrelation results (Fig. 3). The peaks on variogram of NLV values against distance were located at various distance classes among species. Therefore, understory species had varied spatial scales and patch sizes (Appendix).

Most species (> 98% of species) showed patch size and spatial scale at distance class less than 50 meters by Galiano's NLV and Moran's *I*. Comparing spatial patterns between resident and transient species at fine scale within 50 meters, larger number of resident species showed significant autocorrelation in various distance classes which indicated that resident species generally had large spatial scale than transient species (Fig. 3). There was a peak at 180 meter spatial scale on Fig. 3, due to several species showed significant autocorrelations at broader scales. Therefore, in Lenjenchi plot, the spatial pattern of species might be influenced by both fine- and broad-scale factors.

In terms of vegetative growth types, all resident species were perennial and more than half resident species (53 %) were with rhizomes in Lanjenchi plot (Appendix). A high proportion of significant autocorrelation among rhizomed species were showed only at five meter spatial scale, but were not differedat other broader spatial scale (Fig. 4). This indicated that the possession of rhizomes did not significantly contribute to the spatial scale of species. However, seven of ten species with prolonged fronds or stems in vegetative growth types (*e.g.*, *Dicranopteris linearis*, *Liriope spicata*, *Schizostachyum diffusum*) tended to show significant autocorrelation at more than five meter distance classes (Table 1). The spatial scale of resident species correlated with their individual height (Pearson correlation: 0.473, $p < 0.05$); this showed a relationship between spatial scale and individual size.

In terms of life form, seedlings of shrub and subcanopy species showed high proportions of significant autocorrelation at fine scales within 50 meters (Fig. 5), which is not as expected. Comparing spatial pattern among different dispersal syndromes, we did not find larger scale of significant autocorrelation for wind-dispersed species than for species with other dispersal syndromes, which is also not as expected (Table 1). Species among different fruit types (*i.e.*, berry, capsule, drupe and nut fruits) did not showed a particular pattern of autocorrelations, but species with berries showed a large number of species with significant autocorrelation at ten meter spatial scale (Table 1).

DISCUSSION

Species had different spatial autocorrelation scales ranging from five to 40 meters. This information of spatial scales among species can help us to understand the crucial factors contributing to species occurrences and also a basic criterion of sampling design. Spatial autocorrelation may also causes misinterpretation in statistical tests than the data can actually justify because the number of truly independent observations may be less than what were used in the tests (Legendre, 1993; Thomson et al., 1996). For example, spatial scale of herbaceous species (*e.g.*, *Schizostachyum diffusum*) can be larger than 40 meters. This indicates a unique prolonged growth pattern for this climbing species. Moreover, when examining the

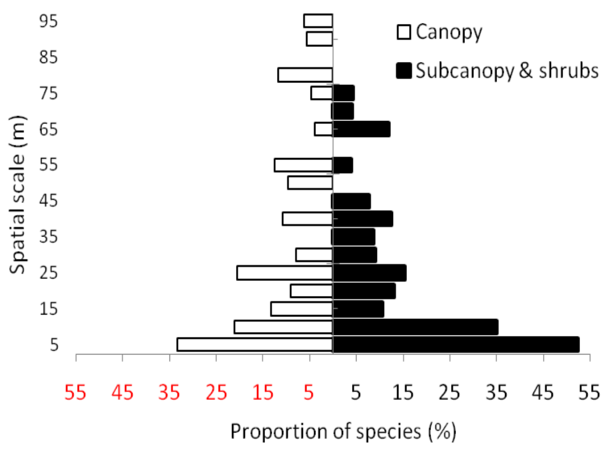

Fig. 5. Proportions of species (”canopy” or “subcanopy and shrubs”) showing significant autocorrelations in each distance spatial scale class.

relationship between abundance of *Schizostachyum diffusum* and the density of woody seedling under a herbaceous layer using a quadrat-based method, each quadrat should be at least apart from each other for more than 40 meters. The sample quadrats in a smaller spatial scale than autocorrelation spatial scale would result in pseudo-replication and dependent of data.

Understory species had different spatial scales between resident and transient species; this showed that characteristic of species may affect their spatial scales. Resident species with large individual size are easy to form a larger size of distribution patch than those with small individual size in spatial patterns (Verburg et al., 1996; Miller et al., 2002). Therefore, in Nanjenshan forest, a single herb (*e.g.*, tree ferns and palms) with relatively big individual size (large individual height) might occupy a large area over several quadrats, causing spatial autocorrelation between neighboring quadrats.

The well adaptation to changes of environmental conditions of understory species may increase their abundance and form a large patch size in spatial patterns (Einsmann et al., 1999). Herbaceous species was considered to own a quick development of root systems and could quickly reflect on environmental fluctuations; they also showed a greater scale of response to external conditions (Einsmann et al., 1999). Therefor, several herbaceous species (*e.g.*, *Pleocnemia rufinervis*, *carex makinoensis* and *Alpinia oblongifolia*) showed large spatial scale in our results. Shrub and subcanopy seedlings (e.g. *Psychotria rubra*, *Lasianthus* spp.) rather than most canopy species also showed a large spatial scale in our study. The seedlings of shrubs defined in our study (1 meter high) might be mature enough to be in adult phase rather than in seedling phase and well adapted to understory condition, showing a large spatial scale.

Except for size-related spatial pattern, vegetative growth of species also influenced the spatial pattern (Kershaw, 1964; Dale and Macisaac, 1989). For example, herbs with prolonged stems and fronds tended to have large spatial scales (Table 1) and patch sizes (Appendix) of distribution patterns. Rhizome is one of the common vegetative organs of perennial herbs (Buell and Wilbur, 1948; Cain, 1950). Herbaceous species in Lanjenchi plot were all perennial and half of them with rhizomes. However, the existence of rhizomes in a plant did not always indicate large spatial scale (11 of 24 species with rhizomes showing small spatial scale within five meters). Comparing to prolonging stems, rhizomes may express different functions such as storage and generation of

Table. 1. Summary of spatial scales (minimal distance with non-significant autocorrelation by Moran’s *I*) among different life forms, vegetative growth types for resident species, dispersal syndromes and dispersed fruit types (excluded the wind-dispersed diaspore).

Number of species	Spatial scale (m)							
	5	10	15	20	25	30	35	40
Life form								
Canopy tree (N=34)	28	3	3	0	0	0	0	0
Subcanopy tree (N=11)	7	3	1	0	0	0	0	0
Shrub (N=15)	10	2	1	1	0	0	1	0
Tree-like fern (N= 1)	0	0	0	1	0	0	0	0
Herb (N=36)	21	8	2	2	1	1	1	0
Climber (N=8)	3	2	0	1	0	1	0	1
Vegetative growth types								
With rhizomes (N=24)	11	7	2	0	1	1	1	1
With prolonged tissue (N=10)	3	2	0	3	0	1	0	1
Dispersal syndrome								
Wind-dispersed (N=27)	17	6	2	2	0	0	0	0
Others (N=78)	52	12	5	3	1	2	2	1
Dispersed fruit types								
Berry (N=22)	13	6	1	1	0	0	1	0
Capsule (N=11)	8	2	1	0	0	0	0	0
Drupe (N=26)	18	2	3	1	0	1	1	0
Nut (N= 6)	6	0	0	0	0	0	0	0
Others (N=13)	6	2	1	1	1	1	0	1

ramets as substitutes for old ones. Therefore, a dormant rhizome with function of storage may not expand population size; small vegetative growth organs may only create small patches barely to detect in spatial analysis. As the quadrat size of our study was 5 by 5 meter, we cannot detect any spatial autocorrelation smaller than a five-meter scale.

The sexual reproduction traits of species (*i.e.*, dispersal syndromes and fruit types for all understory species) did not relate to spatial scale. Diaspores with different dispersal syndromes and fruit types might show different dispersal distance, for example, wind-dispersed type > aminal-dispersed type and ingested type (berry) > adhesive type (others) (Drezner et al., 2001; Miller et al., 2002). Dispersal ability can influence the spatial scale (Miller et al., 2002). However, the relationship between spatial scale and dispersal abilities could not be revealed among species in our results. The dispersal limitation among different fruit types might exist in a broad scale larger than 300 meters. As for the experimental design, the longest distance interval between quadrats was 300 meters, it not allowed to detect spatial autocorrelation large than 300 meters.

Spatial patterns of species in Lanjenchi were related to life traits at fine scale within 50 meters and were simultaneously affected by topographical position in broad scale. Previous studies pointed out that vegetation types and plant distributions in Lanjenchi plot were strongly affected by the interaction of topography and northeast monsoon (Chen et al., 1997; Sun et al., 1998; Chao et al., 2007). Hence the vegetation varied according to topographical positions and was classified into windward and leeward types. Most of the species could be classified as windward-, leeward- and widely distributed types (Cheng, 1992; Sun, 1993; Chao et al., in press). These all showed the different response of plant species to exogenous factors. Two hilltops ca. 180 meters apart in the study plot provided similar micro-habitats and several herbaceous species corresponded to this broader scale replication of habitats, especially for the resident species (Fig. 3).

In conclusion, our study indicated that the spatial patterns of species were influenced by both intrinsic (life form) and exogenous factors (topographic features). The vegetative growth patterns (prolonged tissue) for resident species and were much important than the sexual reproductive traits (dispersal syndromes) for a local spatial scales within 50 meters. The topographical spatial characteristic was also one of the major exogenous factors to influence spatial patterns for both resident and transient understory species at Lanjenchi Plot, southern Taiwan.

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Appendix. Summary of biological characteristics of 105 understory species of Lenjenchi plot in Nanjenshan Reserve, Taiwan. N = the number of quadrats containing this species; SA= the minimal distance class showing non-significant spatial autocorrelation (Moran's I) within 50-meter scale; NLV= the distance class at which large variance occurred. IV= importance values of species, calculated as percent coverage for resident species and relative basal area of large trees (≥ 1 cm DBH) for transient species.

Scientific name	N	Max. Cover (%)	Spatial scale (m)		IV (%)	Ind. height (m)	Life form	diaspore size (cm^3)	diaspore	vegetative growth
			SA	NLV						
Understory resident species										
Pteridophyte										
Aspidiaceae										
Hemigramma decurrens	62	25	5	5	0.66	0.3	herb	<0.001	wind-dispersed spore	rhizomes
Pleocnemia rufinervis	173	62	15	25	4.99	0.5	herb	<0.001	wind-dispersed spore	rhizomes
Athyriaceae										
Diplazium dilatatum	166	55	10	10	3.13	0.4	herb	<0.001	wind-dispersed spore	rhizomes
Diplazium donianum	208	88	10	10	8.61	0.4	herb	<0.001	wind-dispersed spore	rhizomes
Blechnaceae										
Blechnum orientale	39	28	5	5	0.63	0.8	herb	<0.001	wind-dispersed spore	underground storage tissue
Cyatheaceae										
Alsophila podophylla	239	91.5	20	20	11.66	1.5	tree-like	<0.001	wind-dispersed spore	
Dryopteridaceae										
Dryopteris sordidipes	153	35	5	5	0.94	0.3	herb	<0.001	wind-dispersed spore	rhizomes
Gleicheniaceae										
Dicranopteris linearis.	75	100	20	5	4.14	0.5	herb	<0.001	wind-dispersed spore	prolonged frond
Hymenophyllaceae										
Cephalomanes laciniatum	31	4	5	5	0.05	0.2	herb	<0.001	wind-dispersed spore	rhizomes
Lindsaeaceae										
Lindsaea merrillii ssp. *yaeyamensis*	133	12	10	5	0.50	0.2	herb	<0.001	wind-dispersed spore	rhizomes
Lindsaea orbiculata var. *deltoidea*	206	14	10	5	0.80	0.5	herb	<0.001	wind-dispersed spore	rhizomes
Tapeinidium pinnatum	106	41.5	15	10	1.27	0.3	herb	<0.001	wind-dispersed spore	rhizomes
Pteridaceae										
Pteris grevilleana	34	5	5	5	0.05	0.5	herb	<0.001	wind-dispersed spore	rhizomes
Pteris plumbea	33	4	5	5	0.04	0.3	herb	<0.001	wind-dispersed spore	rhizomes
Selaginellaceae										
Selaginella doederleinii	58	9	10	5	0.10	0.15	herb	<0.001	wind-dispersed spore	rhizomes
Thelypteridaceae										
Pronephrium cuspidatum.	45	16	5	5	0.42	0.3	herb	<0.001	wind-dispersed spore	rhizomes
Pronephrium triphyllum	65	20	5	5	0.57	0.2	herb	<0.001	wind-dispersed spore	rhizomes
Dicotyledon										
Acanthaceae										
Codonacanthus pauciflorus	39	0.2	5	5	0.01	0.15	herb	0.002	capsule	
Asteraceae										
Farfugium japonicum var. *formosanum*	99	10	10	5	0.26	0.3	herb	0.085	wind-dispersed achenes	rhizomes
Piperaceae										
Piper kawakamii	197	9	5	5	0.20	0.15	climber	0.019	berry	prolonged stem
Rubiaceae										
Psychotria serpens	319	19	10	5	0.70	0.1	climber	0.206	drupe	prolonged stem
Urticaceae										
Elatostema lineolatum var. *major.*	35	38.5	5	5	0.81	0.4	herb	<0.001	wind-dispersed achenes	
Monocotyledon										
Araceae										
Pothos chinensis	115	7.5	5	5	0.17	0.15	climber	0.520	animal-dispersed berry	
Arecaceae										
Calamus formosanus	266	78	20	10	10.79	1.2	climber	0.520	fruit	prolonged stem

Appendix. Continued.

Scientific name	N	Max. Cover (%)	Spatial scale (m)		IV (%)	Ind. height (m)	Life form	diaspore size (cm^3)	diaspore	vegetative growth
			SA	NLV						
Calamus quiquesetinervius	252	60	10	10	6.79	1	climber	3.062	fruit	prolonged stem
Cyperaceae										
Carex makinoensis	217	100	30	15	13.50	0.4	herb	0.002	achenes	rhizomes
Scleria terrestris	164	18	5	5	0.65	0.8	herb	0.006	achenes	rhizomes
Dioscoreaceae										
Dioscorea japonica var. *pseudojaponica*	86	5	5	5	0.03	0.2	climber	3.033	capsule	prolonged stem
Liliaceae										
Aspidistra elatior var. *attenuata*	48	46	10	5	0.71	0.5	herb	0.520	berry	rhizomes
Dianella ensifolia	83	19	5	5	0.51	0.5	herb	0.520	berry	rhizomes
Liriope spicata	327	44.5	20	10	3.37	0.2	herb	0.127	berry-like fruit	prolonged stem
Orchidaceae										
Calanthe speciosa	34	10	5	5	0.14	0.5	herb	<0.001	wind-dispersed seed	rhizomes
Calanthe triplicata	42	5	5	5	0.06	0.4	herb	<0.001	wind-dispersed seed	underground storage tissue
Cephalantheropsis gracilis	111	12	5	5	0.34	0.2	herb	<0.001	wind-dispersed seed	
Liparis henryi	116	10	5	5	0.19	0.15	herb	<0.001	wind-dispersed seed	
Malaxis latifolia	49	3.5	5	5	0.06	0.2	herb	<0.001	wind-dispersed seed	
Tropidia somai	34	5	5	5	0.06	0.11	herb	<0.001	wind-dispersed seed	
Pandanaceae										
Freycinetia formosana	305	100	30	15	10.53	0.5	climber	0.666	drupe	prolonged stem aerial rooting
Poaceae										
Isachne nipponensis	39	8	5	5	0.17	0.1	herb	0.022	caryopsis	prolonged stem
Lophatherum gracile	220	21.5	25	5	1.25	0.15	herb	0.022	animal-dispersed caryopsis	rhizomes with storage tissue
Oplismenus compositus	94	31.5	10	5	0.26	0.2	herb	0.033	animal-dispersed caryopsis	aerial rooting
Oplismenus hirtellus	54	5	5	5	0.10	0.2	herb	0.022	caryopsis	aerial rooting
Schizostachyum diffusum	363	100	40	20	19.32	1.5	climber	0.008	caryopsis	rhizomes, prolonged stem
Zingiberaceae										
Alpinia oblongifolia	342	39	35	10	4.96	0.8	herb	0.421	berry-like	rhizomes with storage tissue
Alpinia pricei	121	12	5	5	0.37	1	herb	0.421	capsule	rhizomes
Understory transient species										
Gymnosperm										
Podocarpaceae										
Nageia nagi	36	15	5	5	0.44	10.2	canopy	0.899	seed	
Podocarpus macrophyllus	45	12	5	5	0.93	8	canopy	0.399	seed	
Dicotyledon										
Aquifoliaceae										
Ilex cochinchinensis	120	38	10	10	4.21	11	subcanopy	0.204	berry like drupe	
Ilex lonicerifolia var. *matsudai*	62	13	5	5	2.56	11	canopy	0.333	drupe	
Ilex maximowicziana	55	16	5	10	1.14	9	canopy	0.520	drupe	
Ilex uraiensis	77	4	5	10	2.50	15	canopy	0.692	drupe	
Araliaceae										
Schefflera octophylla	83	13	10	5	2.85	17	canopy	0.065	capsule-like fruit	
Celastraceae										
Euonymus pallidifolia	79	11	5	10	0.33	2	shrub	0.819	capsule	

Appendix. Continued.

Scientific name	N	Max. Cover (%)	Spatial scale (m)		IV (%)	Ind. height (m)	Life form	diaspore size (cm^3)	diaspore	vegetative growth
			SA	NLV						
Microtropis japonica	136	12	10	5	2.02	7.9	canopy	8.125	capsule	
Chloranthaceae										
Sarcandra glabra	40	5	5	10	na.	1.5	shrub	0.266	berry	aerial rooting
Clusiaceae										
Garcinia multiflora	78	19	5	30	0.71	8.9	canopy	14.040	berry	
Daphniphyllaceae										
Daphniphyllum glaucescens ssp. *oldhamii*	143	40	15	15	3.92	15	canopy	0.674	drupe	
Ebenaceae										
Diospyros eriantha	46	6	5	20	0.58	8.4	subcanopy	0.599	berry	
Elaeocarpaceae										
Elaeocarpus sylvestris	56	3	5	5	1.42	15	canopy	0.599	drupe	
Euphorbiaceae										
Antidesma hiiranense	115	35	5	15	2.08	1.8	shrub	0.078	drape	
Glochidion rubrum	44	7	5	15	0.52	13	canopy	0.266	capsule	
Mallotus paniculatus	41	9	5	20	0.59	11	canopy	0.104	capsule	
Sapium discolor	32	4	5	15	1.13	14	canopy	4.576	capsule	
Fabaceae										
Archidendron lucidum	31	20	5	10	0.39	9	canopy	0.150	Seed from legume	
Fagaceae										
Castanopsis carlesii	109	20	5	10	8.72	16	canopy	0.832	nut	
Cyclobalanopsis longinux	56	14	5	60	4.08	15	canopy	5.068	nut	
Cyclobalanopsis pachyloma	39	7	5	20	1.16	13	canopy	14.040	nut	
Lithocarpus amygdalifolius	63	7	5	10	2.14	12	canopy	6.327	nut	
Pasania harlandii	33	5	5	10	0.85	14	canopy	5.616	nut	
Illiciaceae										
Illicium arborescens	151	90	15	75	8.85	11	subcanopy	4.160	follicle (capsule-like)	
Lauraceae										
Beilschmiedia erythrophloia	75	8	5	20	0.90	14	canopy	1.582	drupe	
Beilschmiedia tsangii	148	16	15	15	1.42	12	canopy	1.647	drupe	
Cinnamomum rigidissimum	41	10	5	10	0.37	10	canopy	0.676	berry	
Litsea acutivena	109	52	10	10	1.07	13	subcanopy	0.225	berry	
Machilus obovatifolia	43	5	5	10	0.67	9.1	canopy	1.142	drupe	
Machilus thunbergii	77	9	5	10	0.79	16	canopy	0.520	drupe	
Machilus zuihoensis	39	5	5	10	0.29	13	canopy	0.266	drupe	
Neolitsea buisanensis	60	12	5	5	0.52	4	subcanopy	0.178	drupe	
Neolitsea hiiranensis	101	10	5	5	0.82	12	subcanopy	0.187	drupe	
Melastomataceae										
Melastoma candidum	82	42	5	10	1.05	2	shrub	1.755	capsule	
Moraceae										
Ficus formosana	58	8	5	10	0.03	1.8	shrub	0.780	fig (berry-like)	
Ficus caulocarpa	38	4	5	35	0.01	15	shrub	1.755	fig (berry-like)	
Myrsinaceae										
Ardisia cornudentata	106	24	15	15	0.46	1.8	shrub	0.520	berry	aerial rooting
Ardisia quinquegona	81	13	10	10	0.33	12.7	subcanopy	0.520	berry	
Myrsine seguinii	43	25	10	10	0.73	10	canopy	0.112	drupe	
Myrtaceae										
Decaspermum gracilentum	38	3	5	10	0.88	11	canopy	0.112	berry	
Syzygium buxifolium	55	30	5	5	2.15	8	canopy	0.520	drupe	
Syzygium euphlebium	38	10	5	10	1.02	14	canopy	0.632	drupe	
Oleaceae										
Osmanthus marginatus	146	116	15	15	3.51	10	canopy	0.758	animal-dispersed drupe	
Proteaceae										
Helicia formosana	52	18	5	10	0.35	9.5	subcanopy	14.040	nut-like fruit	
Rosaceae										
Prunus phaeosticta	64	6	5	5	0.41	10	canopy	0.333	drupe	
Rubiaceae										

Appendix. Continued.

Scientific name	N	Max. Cover (%)	Spatial scale (m)		IV (%)	Ind. height (m)	Life form	diaspore size (cm^3)	diaspore	vegetative growth
			SA	NLV						
Lasianthus bunzanensis	37	4	5	5	na.	1.8	shrub	0.065	drupe	
Lasianthus cyanocarpus	97	7	5	10	0.11	1.8	shrub	0.078	drupe	
Lasianthus fordii	79	9	20	25	0.01	1.8	shrub	0.065	drupe	
Lasianthus wallichii	108	17	35	5	0.00	1.8	shrub	0.780	drupe	
Psychotria rubra	172	49	10	5	3.08	2.5	shrub	0.204	berry	
Tarenna gracilipes	70	12	5	15	0.21	2	shrub	0.333	berry	
Tricalysia dubia	51	5	5	10	0.90	8.6	subcanopy	0.094	berry	
Symplocaceae										
Symplocos congesta	62	7	5	5	0.89	7.6	subcanopy	0.255	drupe	
Symplocos theophrastaefolia	67	8	5	5	1.22	13	canopy	0.153	drupe	
Theaceae										
Eurya nitida var. *nanjenshanensis*	59	30	5	15	3.12	10	subcanopy	0.065	berry	
Gordonia axillaris	48	5	5	10	1.69	11	canopy	0.058	wind-dispersed seed	
Schima superba var. *kankoensis*	35	5	5	5	1.90	14	canopy	0.006	wind-dispersed seed	
Thymelaeaceae										
Wikstroemia taiwanensis	47	12	10	35	0.18	1.8	shrub	0.599	berry	
Verbenaceae										
Callicarpa remotiflora	87	10	5	35	0.08	1.8	shrub	0.112	drupe	

臺灣南部南仁山亞熱帶雨林林下物種的空間自相關格局

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摘要：許多研究描述外在環境及內部因子與植物種類分布的關連，但鮮少定量物種的空間尺度。本文章使用定量的方法，如：空間自相關及軌跡方差法，來估計物種的空間尺度；並以其反映的尺度來探討影響物種分布的可能因子。我們於台灣南部南仁山保護區欖仁溪樣區進行林下小苗(即胸高直徑小於 1 公分的灌木、冠層及次冠層樹種)及草本植物(即高度小於 1 公尺的草本植物、小型灌木和樹蕨)的帶狀取樣。共建立樣七條樣線並選取其中三條進行小苗普查，央 5 公尺×300 公尺樣線分為 60 個 5 公尺×5 公尺樣方進行調查。利用相連樣方中草本植物覆蓋度及小苗數量來計算各物種的空間尺度。各物種呈現不同的空間尺度及相尺寸。草本植物較木本植物的小苗有較大的空間尺度。個體大及具有延伸性莖葉的物種傾向擁有較大的空間尺度。然而，在我們的研究尺度中種子傳播方式與果實種類並未能呈現與空間尺度的相關。在約 180 公尺的尺度下，物種呈現顯著的空間自相關，剛好反應欖仁溪樣區兩個山頭的距離，顯示物種豐富度反映地形的重複。由上總結，欖仁樣區林下層物種的空間尺度反映出地形變化及物種本身的特性。

關鍵詞：空間自相關、軌跡方差法、草本物種、苗木及功能特性。