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Designing cluster plots for sampling local plant species composition for biodiversity management

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Abstract

Aim of the study: Cluster plot designs are widely used in national forest inventory systems to assess current forest resources. By spreading subplots apart, a cluster plot could potentially capture a large variety of local plant species. This aspect has rarely been examined in the past. This study is conducted to understand how design factors of a cluster plot affect estimates of local plant species composition.

Area of study: Two large census forest plots in Taiwan and Peninsular Malaysia over 25 ha with different species richness were used.

Materials and methods: Design factors of a cluster plot were plot configuration (PCONFIG), plot area (PAREA), cluster layout (CLAYOUT), and extent of ground area covered by a cluster (CEXTENT). Jaccard and Sørensen similarity indices were used to compare species compositional similarity between two cluster plot designs. A simulation study was carried out.

Main results: Results were consistent among the study sites and similarity indices. PAREA, CLAYOUT, and CEXTENT notably influenced how species composition was sampled. Larger PAREA increased similarity in species composition between two cluster plot designs. Square and rectangle CLAYOUT had the most dissimilar species composition between them. Larger CEXTENT decreased similarity in species composition.

Research highlights: We recommend that for $CEXTENT \leq 1000 \text{ m}^2$ and $PAREA \leq 500 \text{ m}^2$, a cluster plot of rectangle CLAYOUT is preferred for information gain. The study could potentially benefit forest managers designing cluster plots for plant diversity assessment.

Key words: Biodiversity assessment; composition similarity; national forest inventory; species diversity; sampling design; sampling efficiency.

Abbreviations used: extent of ground area covered by a cluster (CEXTENT); cluster layout (CLAYOUT); Jaccard similarity index (JAC); plot area (PAREA); plot configuration (PCONFIG); Sørensen similarity index (SOR).

Authors' contributions: Original idea and study design: TYL. Simulation program: HTL; Data analysis: CQ, HTL and TYL. Manuscript preparation and revision: CQ and TYL.

Supplementary material: Tables S1 to S3 and Figures S1 to S6 accompany the paper on FS website.

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Introduction

Plant diversity provides multifaceted benefits to human society. The loss of it will have important consequences on our economies, food security, and livelihoods (FAO & PAR, 2011; IPBES, 2018). To address this, national and/or regional policies require robust data to report on biodiversity trends (Geijzen-dorffer *et al.*, 2016). In many countries, National

Forest Inventories (NFIs) provide such data, which is useful for decision-makers to shape policy instruments to halt the loss of plant diversity (Winter *et al.*, 2008; Geijzen-dorffer *et al.*, 2016). However, NFIs provide only sample-based estimates of plant diversity because it is difficult to fully enumerate all plant individuals (Lam & Kleinn, 2008). Uncertainty in these estimates could hamper understanding and conservation of valuable natural resources (Costello *et al.*, 2013).

Thus, there is a need to develop an efficient forest inventory design to accurately gather information on plant diversity (Burley & Gauld, 1995).

Ground plots are the primary source of information on plant diversity. Understanding the effects of a plot design on sampling plant diversity is necessary (Yang *et al.*, 2019b). A review of the common plot designs used in NFIs could provide insights into how biodiversity information is gathered on the national level. In 36 countries with a NFI system, Tomppo *et al.* (2010) found that half of the countries applied systematic sampling with cluster plots. A cluster plot is a group of subplots organized at a specific distance and a configuration at a sample location (Kershaw *et al.*, 2016). Thompson (2012) suggested that a cluster plot ideally represents the full diversity of a plant population at a local scale. By spreading subplots far apart within practical constraints, subplots should capture largely different plant species between them. A high similarity in species composition between subplots suggests an ineffective cluster plot design. However, plant species tend to aggregate at the local scale as a result of ecological processes such as limited dispersal (Seidler & Plotkin, 2006) and interspecific competition (Fowler, 1986). If this spatial autocorrelation is known, an optimal cluster plot design could be constructed for sampling plant species composition (Korhonen & Maltamo, 1991). But, spatial autocorrelation is generally unknown *a priori* for a forest, as it is site specific due to its underlying ecological processes, and is scale-dependent (Malanson, 1985; Schetter *et al.*, 2013). Perhaps, certain configurations of cluster plot could intrinsically take the spatial autocorrelation into account without the need to specifically quantify it, e.g. some particular distance between subplots or geometrical arrangement of subplots. If so, they could be applicable across forest types and would appeal to practices that assess plant species composition with only presence/absence data. This aspect of cluster plot has not been explicitly examined in the past.

Past studies on optimum cluster plot design focus on stem volume (Tokola & Shrestha, 1999), woody debris (Scheuber & Köhl, 2003), and stand density and basal area (Yim *et al.*, 2015). To our knowledge, none has examined cluster plot designs on sampling species composition. There are, however, studies of other plot designs on sampling plant species richness (number of species) and biodiversity indices. For example, Potts *et al.* (2001) compared single plots of various plot sizes (0.01 to 1.0 ha), plot shapes (L- and rectangular shape), and plot width-to-length ratio (1:1 to 1:32) in sampling species richness in two Malaysian tropical forests. Motz *et al.* (2010) compared angle count sampling to fixed area plots in estimating biodiversity indices. Many other studies also used species richness as a measure for evaluation of

optimum plot designs (e.g. Phillips *et al.*, 2003; Grussu *et al.*, 2016) because it is a metric widely used to detect biodiversity trends (Hillebrand *et al.*, 2018). However, Feeley *et al.* (2011) argued that attention should also be paid to species composition because a composition change could signal ecosystem responses to global climate change. For instance, compositional changes in keystone plants could affect the production of seasonally critical tropics (Peres, 2000). Yang *et al.* (2019b) is the only study to our knowledge that compares various single plot designs on sampling species composition. As many NFIs are designed around cluster plots (Tomppo *et al.*, 2010), there is a need to study performances of cluster plots in assessing plant species composition.

The overall goal of this study was to evaluate cluster plot designs in capturing local plant species composition. Three specific objectives were established to compare similarity in species composition: (1) between a single plot and a cluster plot, (2) between two cluster plots with different spatial arrangement of subplots, and (3) between two cluster plots of different ground coverage. Species composition similarity is expressed as the Jaccard and Sørensen similarity indices, which account for number of shared species between two plot designs (Chao *et al.*, 2005). The first objective examines whether a single large plot would perform better than a group of smaller sized subplots in capturing local plant species composition. Green & Young (1993) argued that many small plots would be better than a few large ones in sampling plant species that showed spatial aggregation. A geometrical arrangement of subplot would characterize the compactness of a cluster. Thus, the second objective examines how cluster compactness affects sampling of local plant composition. Ground enclosed by a cluster (ground coverage) determines distance between subplots. Larger ground coverage should theoretically lower similarity in species composition between subplots. Hence, the third objective examines this proposition. Lastly, this study does not intend to find an optimum sample size for sampling species composition similarity with cluster plot designs. Instead, its motivation is to assist decision makers in choosing a cluster plot design, which is a key factor in a forest inventory program, that adequately samples local species composition given available financial and capital resources at the selected sample locations.

Materials and methods

Data

Two datasets that differed in forest ecosystems and plant diversity were used in this study. The first cen-

sus dataset was the 50-ha Pasoh Forest Dynamics Plot (Pasoh), which measured 1000×500 m and was classified as tropical lowland mixed dipterocarp forests. Data from 1986-1989 were used in this study and consisted of 335,343 tree records and 820 species (Manokaran & LaFrankie, 1990). The second census dataset was the 25-ha Fushan Forest Dynamics Plot (Fushan), which measured 500×500 m and was classified as subtropical submontane evergreen broadleaf forests. Data from 2003-2004 were used in this study and consisted of 114,354 tree records and 110 species (Su *et al.*, 2007). The census protocols were identical for both sites. All plants ≥ 1 cm in diameter at breast height (dbh) in the plot were mapped, measured, and identified to species level in scientific nomenclature.

Plot designs

Four plot design factors were considered in the study: (1) plot configurations (PCONFIG), (2) area of a plot or total area of subplots of a cluster (PAREA), (3) cluster layout as geometrical arrangement of subplots in a cluster (CLAYOUT), and (4) extent of ground area enclosed by the boundaries of a cluster plot (CEXTENT). The combinations of design factors and their respective levels were depicted in Fig. S1 [suppl.]. Only circular plot and subplot were considered to facilitate evaluation of the three study objectives. Güler *et al.* (2016) recommended more compact plot shape such as circular plot when sampling species composition and diversity. The number of subplots of a cluster plot was fixed to four, which was the average among the 18 countries' NFIs (Tomppo *et al.*, 2010).

Two PCONFIG levels were considered: (1) single, and (2) cluster. For PCONFIG = single, a single circular plot was established with the plot center at a sample location, whereas for PCONFIG = cluster, a cluster of four circular subplots was established with the cluster center at a sample location. Three PAREA levels were considered: (1) 250, (2) 500, and (3) 1000 m². For PCONFIG = single, PAREA denoted the whole area of a single plot. For PCONFIG = cluster, PAREA denoted the total area of the four subplots, or equivalently the area of a subplot was PAREA/4. As a result, the area sampled by a plot is identical to that by a cluster for a given PAREA.

The design factors CLAYOUT and CEXTENT were only applied to cluster plot. Three CLAYOUT levels were considered: (1) square, (2) rectangle with width-to-length ratio of 1:3, and (3) equilateral triangle. For CLAYOUT = square and rectangle, four subplots were placed at the vertices. For CLAYOUT = triangle, the geometrical arrangement of subplots followed that of

the USA FIA program (Bechtold & Patterson, 2005) with three subplots at the vertices and one at cluster center. Three CEXTENT levels were considered: (1) 1000, (2) 2500, and (3) 10000 m². Larger CEXTENT implied that subplots were placed further apart. As a result, there were 3 possible combinations of a single plot (3 PAREA) and 27 possible combinations of a cluster plot (3 PAREA \times 3 CLAYOUT \times 3 CEXTENT) with a total of 30 plot designs (Fig. S1 [suppl.]).

Simulation methods

A simulation study was set up to evaluate the three study objectives, and the simulation was reiterated 100 times. In an iteration, 500 sample locations were first randomly generated by random selection of x- and y-coordinates. Then at a random sample location, all 30 plot designs were laid out to observe presence/absence of a plant species for each plot design. This approach was to ensure that species composition between the 30 plot designs could be compared at a single sample location. When PCONFIG = cluster, the orientation of a cluster was randomized by selecting a random azimuth between 0 and 2π . As a result, all 30 plot designs were simulated at all 500 random sample locations.

When a sample location was near the boundaries of Fushan and Pasoh, correction for boundary slopover was applied. For PCONFIG = single, the walkthrough method by Ducey *et al.* (2004) was applied. For the walkthrough method, a sample location was reflected through a sample tree, and the sample tree would be double tallied if the reflected plot center laid outside the forest boundary (Ducey *et al.*, 2004). For PCONFIG = cluster, the reflection method by Valentine *et al.* (2006) was used. For the reflection method, four direction vectors from a sample location to the centers of the four subplots were established. If a direction vector intersected the forest boundary, it was folded back over itself at the boundary with the subplot established at its terminus and sample trees corrected for boundary slopover by the walkthrough method if necessary (Valentine *et al.*, 2006). Different boundary slopover correction methods were necessary to ensure that inclusion probabilities of trees near the boundaries were accurate for the specific PCONFIG (Kershaw *et al.*, 2016). West (2013) found that use of different correction methods in an inventory did not introduce appreciable bias and did not reduce precision when estimating stand attributes, which could be extended to species composition similarity because the similarity indices applied in this study depended only on the presence/absence of a species (Eqns. 1-2). However, this assumption should be examined in a future study.

Sampling intensity was determined by PAREA. It was the ratio of total ground area covered by 500 randomly placed sample plots to the total area of a study site. For example, with PAREA = 250 m², the total area covered by 500 random sample plots was 12.5 ha; thus, sampling intensity was 50% and 25% for Fushan and Pasoh, respectively. However, some sample plots would overlap with each other on the ground. As such, the actual total ground area covered by the 500 random sample plots and the sampling intensity should be less.

Analysis

Species composition between two plot designs was compared at the scale of sample location. At a sample location, two species composition similarity indices were calculated: Jaccard and Sørensen similarity indices as follows (Chao *et al.*, 2005),

Jaccard similarity index (JAC),

$$JAC = \frac{S_{12}}{S_1 + S_2 - S_{12}} \times 100\% \quad (1)$$

Sørensen similarity index (SOR),

$$SOR = \frac{2S_{12}}{S_1 + S_2} \times 100\% \quad (2)$$

where, S_1 = number of observed species in a ground plot of plot design 1 at a sample location, S_2 = number of observed species in a ground plot of plot design 2 at the same sample location, S_{12} = number of shared species between the ground plot of plot design 1 and that of plot design 2 at the same sample location. Thus, similarity is expressed as the number of identical species found in both ground plots of two different plot designs at the same sample location relative to the total number of distinct species in both ground plots. For PCONFIG = cluster, species data were pooled from all four subplots of a cluster plot before the calculation.

When evaluating the three study objectives, species composition between two plot designs was compared on a common ground by identifying a design factor to be analyzed while controlling for other factors. For Objective 1, species composition of a single plot was compared to that of a cluster plot of a cluster layout at a sample location controlling for PAREA and CEXTENT. Under each combination of PAREA and CEXTENT, the comparisons were: (1) PCONFIG = single vs CLAYOUT = square, (2) PCONFIG = single vs CLAYOUT = rectangle, and (3) PCONFIG = single vs CLAYOUT = triangle. For Objective 2, species composition of two cluster plots of two different cluster layouts were compared at a sample location controlling for PAREA and CEXTENT. Under each

combination of PAREA and CEXTENT, the comparisons were: (1) CLAYOUT = square vs CLAYOUT = rectangle, (2) CLAYOUT = square vs CLAYOUT = triangle, and (3) CLAYOUT = triangle vs CLAYOUT = rectangle. For Objective 3, species composition of two cluster plots of two different extent of ground area enclosed by a cluster were compared at a sample location controlling for PAREA and CLAYOUT. Under each combination of PAREA and CLAYOUT, the comparisons were: (1) CEXTENT = 1000 vs CEXTENT = 2500 m², (2) CEXTENT = 1000 vs CEXTENT = 10000 m², and (3) CEXTENT = 2500 vs CEXTENT = 10000 m². For each objective, there were a total of 27 possible combinations of comparison, e.g. 3 comparisons × 3 PAREA × 3 CEXTENT for Objective 1 and so forth. Across all three objectives, we made a total of 81 comparisons. PAREA was the consistent controlling factor so that the set of comparisons that had identical PAREA were carried out on a similar sampling intensity. To reiterate, the two similarity indices were calculated at a sample location for each comparison (i.e., between two plot designs).

For each of the 81 combinations, each simulated iteration produced 500 estimates of JAC and SOR from the 500 random sample locations. Let θ_{ij} be an estimate of JAC or SOR for the j -th random location and the i -th iteration. Mean and standard deviation of θ_{ij} were calculated for the i -th iteration as $\bar{\theta}_i = \sum_{j=1}^{500} \theta_{ij} / 500$ and $s_{\theta_i} = \sqrt{\sum_{j=1}^{500} (\theta_{ij} - \bar{\theta}_i)^2 / 499}$. The coefficient of variation in percent (CV) of θ for the i -th iteration was $CV_{\theta_i} = s_{\theta_i} / \bar{\theta}_i \times 100\%$. The 100 iterations produced 100 means and CVs, which were then averaged as $\bar{\bar{\theta}} = \sum_{i=1}^{100} \bar{\theta}_i / 100$ and $\overline{CV_{\theta}} = \sum_{i=1}^{100} CV_{\theta_i} / 100$. Furthermore, 2.5% and 97.5% quantiles of the 100 means and CVs were estimated. The interval between the two was designated as the empirical 95% confidence interval (E95CI). Lastly, $\bar{\bar{\theta}}$, $\overline{CV_{\theta}}$, and E95CI were reported in the study.

A hierarchical linear mixed effects (HLME) model (Pinheiro & Bates, 2000) was developed for each study objective to assess the significance of the comparisons. For Objective 1, the HLME model was,

$$\begin{aligned} \bar{\theta} = & \left(\alpha_0 + a_{0,PAREA} + a_{0,CEXTENT(PAREA)} \right) + \\ & + \left(\alpha_1 + a_{1,PAREA} + a_{1,CEXTENT(PAREA)} \right) (\text{single v square}) + \\ & + \left(\alpha_2 + a_{2,PAREA} + a_{2,CEXTENT(PAREA)} \right) (\text{single v triangle}) \end{aligned} \quad (3)$$

where, $\bar{\theta}$ was mean of 500 estimates of JAC or SOR, (single v square) was the comparison of a single plot

to a cluster plot of CLAYOUT = square, (single v triangle) was the comparison of a single plot to a cluster plot of CLAYOUT = triangle, α_k was the k -th fixed effect, $a_{k,PAREA}$ was the k -th PAREA random effect, and $a_{k,CEXTENT(PAREA)}$ was the k -th CEXTENT nested under PAREA random effect for $k = 0, \dots, 2$.

For Objective 2, the HLME model was,

$$\begin{aligned} \bar{\theta} = & \left(\beta_0 + b_{0,PAREA} + b_{0,CEXTENT(PAREA)} \right) + \\ & + \left(\beta_1 + b_{1,PAREA} + b_{1,CEXTENT(PAREA)} \right) (\text{square v triangle}) + \\ & + \left(\beta_2 + b_{2,PAREA} + b_{2,CEXTENT(PAREA)} \right) (\text{triangle v rectangle}) \end{aligned} \quad (4)$$

where, (square v triangle) was the comparison of cluster plot with CLAYOUT = square to CLAYOUT = triangle, (triangle v rectangle) was the comparison of cluster plot with CLAYOUT = triangle to CLAYOUT = rectangle, β_k was the k -th fixed effect, $b_{k,PAREA}$ was the k -th PAREA random effect, and $b_{k,CEXTENT(PAREA)}$ was the k -th CEXTENT nested under PAREA random effect for $k = 0, \dots, 2$.

For Objective 3, the HLME model was,

$$\begin{aligned} \bar{\theta} = & \left(\delta_0 + d_{0,PAREA} + d_{0,CLAYOUT(PAREA)} \right) + \\ & + \left(\delta_1 + d_{1,PAREA} + d_{1,CLAYOUT(PAREA)} \right) (1000 \text{ v } 10000) + \\ & + \left(\delta_2 + d_{2,PAREA} + d_{2,CLAYOUT(PAREA)} \right) (2500 \text{ v } 10000) \end{aligned} \quad (5)$$

where, (1000 v 10000) was the comparison of cluster plot with CEXTENT = 1000 m² to CEXTENT = 10000 m², (2500 v 10000) was the comparison of cluster plot with CEXTENT = 2500 m² to CEXTENT = 10000 m², δ_k was the k -th fixed effect, $d_{k,PAREA}$ was the k -th PAREA random effect, and $d_{k,CLAYOUT(PAREA)}$ was the k -th CLAYOUT nested under PAREA random effect for $k = 0, \dots, 2$.

As shown in above three HLME models, both fixed and random effects for $k = 0, \dots, 2$ were estimated. Random effects were estimated using a hierarchical error structure because the comparisons in Eqns. (3-5) were nested with their respective controlling factors. For Objectives 1 and 2, the comparisons were nested within PAREA and CEXTENT under PAREA (Eqns. 3-4). For Objective 3, the comparisons were nested within PAREA and CLAYOUT under PAREA (Eqn. 5). The estimated values of α_k , β_k , and δ_k and their p -values were reported. The HLME models were fitted with R nlme package (Pinheiro *et al.*, 2019). Similar HLME models were also used in Yang *et al.* (2019a) to study sample designs for airborne light detection and ranging application.

Results

Single vs CLAYOUT

Similarity in species composition between a single plot (PCONFIG = single) and a cluster plot of a cluster layout (PCONFIG = cluster and CLAYOUT = rectangle, square, or triangle) was estimated controlling for PAREA and CEXTENT. The estimated mean ($\bar{\theta}$) and mean CV ($\overline{CV_{\theta}}$) were consistent between the two similarity indices and the two study sites (Figs. 1 and S2; Table S1 [suppl.]). Consistently across levels of PAREA and CEXTENT, similarity in species composition was the highest between a single plot and a cluster plot of triangle CLAYOUT (Figs. 1a and S2a [suppl.]), e.g. mean JAC was 53-72% for Fushan and was 35-55% for Pasoh (Table S1 [suppl.]). In contrast, similarity in species composition between a single plot and a cluster plot of rectangle CLAYOUT was the lowest (Figs. 1a and S2a [suppl.]), e.g. mean JAC was 45-67% for Fushan and was 24-47% for Pasoh (Table S1 [suppl.]). Non-overlapping E95CI suggested that the two comparisons were significantly different, which was also supported by the HLME models ($p < 0.0001$ for α_2 ; Table 1). Mean JAC and SOR for the comparison between a single plot and a cluster plot of square CLAYOUT were consistently similar to those for the comparison between a single plot and a cluster plot of rectangle CLAYOUT (Figs. 1a and S2a [suppl.]), but the HLME models suggested significant differences between the two comparisons ($p < 0.0161$ for α_1 ; Table 1). In general, increasing PAREA increased mean JAC and SOR of a particular comparison. On the other hand, increasing CEXTENT for a given PAREA had little effects on the similarity indices.

The trends in $\overline{CV_{\theta}}$ were the opposite of $\bar{\theta}$ (Figs. 1b and S2b [suppl.]). Mean CV was the lowest for the comparison between a single plot and a cluster plot of triangle CLAYOUT (e.g. for JAC, 13-26% for Fushan and 8-15% for Pasoh), and it was the highest for the comparison between a single plot and a cluster plot rectangle CLAYOUT (e.g. for JAC, 14-29% for Fushan and 9-22% for Pasoh) (Table S1 [suppl.]). Increasing PAREA decreased mean CV of a particular comparison. However, increasing CEXTENT for a given PAREA had little effects on mean CV.

Geometrical arrangement of subplots (CLAYOUT)

Controlling for PAREA and CEXTENT, similarity in species composition between two cluster plots of two different cluster layouts or geometrical arrange-

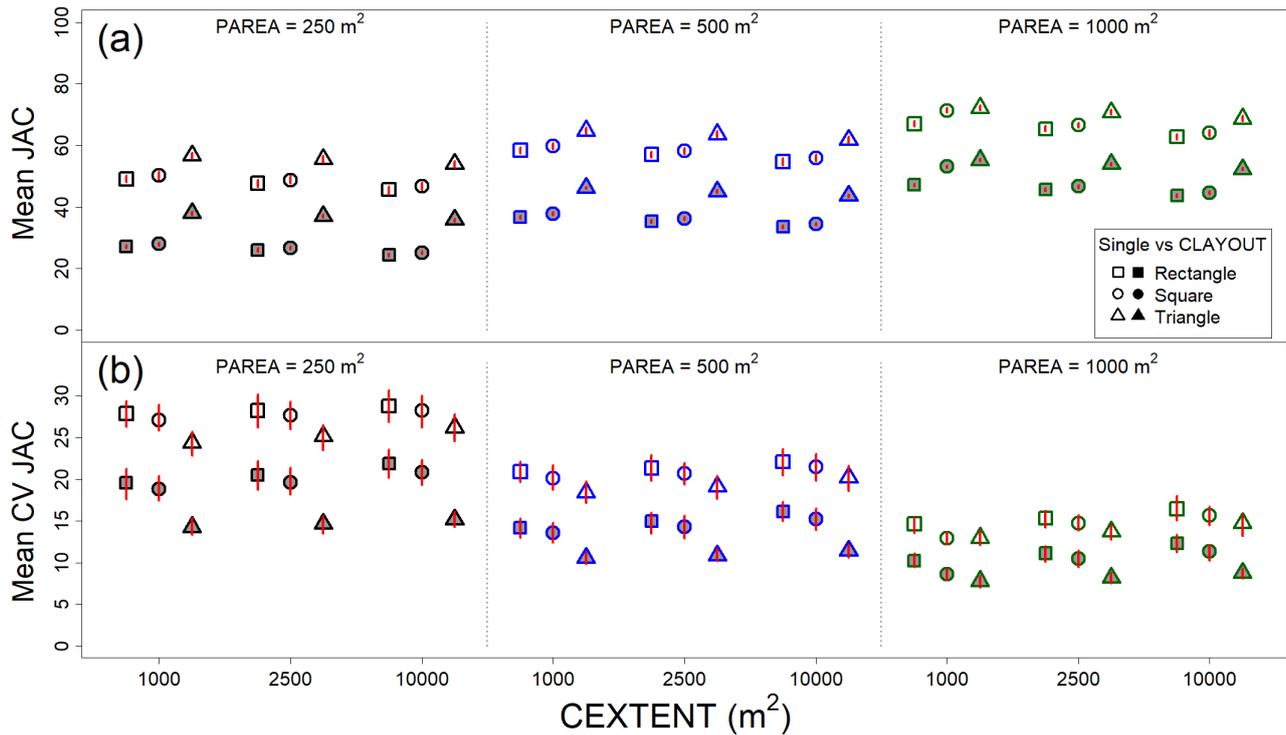


Figure 1. (a) Mean ($\bar{\theta}$) and (b) mean CV ($\overline{CV_{\theta}}$) Jaccard similarity index for comparing species composition between a single plot and a cluster plot of a cluster layout for Fushan (open symbols) and Pasoh (filled grey symbols). The three comparisons are: (1) single vs CLAYOUT = rectangle (\square and \blacksquare), (2) single vs CLAYOUT = square (\circ and \bullet), (3) single vs CLAYOUT = triangle (\triangle and \blacktriangle). The comparisons are controlled for PAREA and CEXTENT. PAREA are 250 (black symbols), 500 (blue symbols), and 1000 m² (green symbols). CEXTENT are 1000, 2500, and 10000 m². Red solid lines depict empirical 95% confidence intervals.

ments of subplots was compared. The estimated mean ($\bar{\theta}$) was consistent between the two similarity indices and the study sites (Figs. 2a and S3a; Table S2 [suppl.]). Increasing PAREA noticeably increased mean JAC and SOR of a particular comparison. For a specific PAREA, increasing CEXTENT led to comparable mean JAC and SOR between the three comparisons of two CLAYOUT. Similarity in species composition between CLAYOUT of square and rectangle was the lowest, e.g. mean JAC was 49-70% for Fushan and was 27-52% for Pasoh (Table S2 [suppl.]). On the other hand, similarity in species composition between CLAYOUT of triangle and rectangle was generally the highest, e.g. mean JAC was 50-75% for Fushan and 27-57% for Pasoh (Table S2 [suppl.]), and it was significantly different from the comparison of square to rectangle CLAYOUT as suggested by E95CI and HLME models ($p < 0.0003$ for β_2 ; Table 1).

The trends in mean CV ($\overline{CV_{\theta}}$) were similar between the two similarity indices but were somewhat different between the two study sites (Figs. 2b and S3b; Table S2 [suppl.]). In general, increasing PAREA consistently reduced mean CV of a particular comparison across similarity indices and study sites. However, for a specific PAREA, increasing CEXTENT decreased

mean CV of a particular comparison for Fushan but instead increased it for Pasoh (Figs. 2b and S3b [suppl.]). For example, the mean CV of the comparison between triangle and rectangle CLAYOUT was either comparable or the lowest for Fushan (e.g. 11-22% for JAC), but it was either comparable or the highest for Pasoh (7-17% for JAC) (Table S2 [suppl.]). Similarly, mean CV of the comparison between square and rectangle CLAYOUT were the opposite, i.e., either comparable or the highest for Fushan (e.g. 13-24% for JAC) but either comparable or the lowest for Pasoh (e.g. 7-16% for JAC) (Table S2 [suppl.]).

Extent of ground cover (CEXTENT)

By controlling for PAREA and CLAYOUT, similarity in species composition between two cluster plots of two different extent of ground area enclosed by the boundaries of a cluster plot was compared. The estimated mean ($\bar{\theta}$) and mean CV ($\overline{CV_{\theta}}$) were consistent between the two similarity indices and the study sites (Figs. 3 and S4; Table S3 [suppl.]). The comparison between the two CEXTENT 1000 and 2500 m² had consistently the highest similarity in species composi-

Table 1. Estimated regression coefficients of hierarchical linear mixed effects models for Fushan and Pasoh for: (1) comparison between a single plot and a cluster plot of a cluster layout (α_k , Eqn. 3), (2) comparison between two cluster plots of two different cluster layouts (β_k , Eqn. 4), and (3) comparison between two cluster plots of two different extent of ground area enclosed by a cluster (δ_k , Eqn. 5). Their corresponding test statistics and p -values are in parentheses

Comparison of single vs CLAYOUT		
	JAC	SOR
Fushan		
α_0 (intercept)	56.4283 ($t_{2689} = 11.11, p < 0.0001$)	71.0356 ($t_{2689} = 16.33, p < 0.0001$)
α_1 (single v square)	1.5381 ($t_{2689} = 4.08, p = 0.0010$)	1.2499 ($t_{2689} = 5.31, p < 0.0001$)
α_2 (single v triangle)	6.7178 ($t_{2689} = 9.73, p < 0.0001$)	5.4410 ($t_{2689} = 6.32, p < 0.0001$)
Pasoh		
α_0 (intercept)	35.5271 ($t_{2689} = 6.26, p < 0.0001$)	51.6754 ($t_{2689} = 8.30, p < 0.0001$)
α_1 (single v square)	1.4690 ($t_{2689} = 2.41, p = 0.0161$)	1.4896 ($t_{2689} = 2.93, p = 0.0035$)
α_2 (single v triangle)	9.7442 ($t_{2689} = 12.23, p < 0.0001$)	10.1687 ($t_{2689} = 6.49, p < 0.0001$)
Comparison of two CLAYOUT		
	JAC	SOR
Fushan		
β_0 (intercept)	59.3476 ($t_{2689} = 11.82, p < 0.0001$)	73.6766 ($t_{2689} = 17.90, p < 0.0001$)
β_1 (square v triangle)	1.5496 ($t_{2689} = 6.01, p < 0.0001$)	1.2239 ($t_{2689} = 7.02, p < 0.0001$)
β_2 (triangle v rectangle)	2.3067 ($t_{2689} = 4.29, p < 0.0001$)	1.7881 ($t_{2689} = 4.49, p < 0.0001$)
Pasoh		
β_0 (intercept)	36.8889 ($t_{2689} = 6.00, p < 0.0001$)	53.1538 ($t_{2689} = 8.09, p < 0.0001$)
β_1 (square v triangle)	1.7055 ($t_{2689} = 3.66, p = 0.0003$)	1.7039 ($t_{2689} = 4.08, p < 0.0001$)
β_2 (triangle v rectangle)	3.3404 ($t_{2689} = 3.60, p = 0.0003$)	3.3137 ($t_{2689} = 3.68, p = 0.0002$)
Comparison of two CEXTENT		
	JAC	SOR
Fushan		
δ_0 (intercept)	62.6810 ($t_{2689} = 12.59, p < 0.0001$)	76.2374 ($t_{2689} = 19.33, p < 0.0001$)
δ_1 (1000 v 10000)	-3.3435 ($t_{2689} = 6.03, p < 0.0001$)	-2.5959 ($t_{2689} = 8.83, p < 0.0001$)
δ_2 (2500 v 10000)	-2.2433 ($t_{2689} = 4.48, p < 0.0001$)	-1.6467 ($t_{2689} = 5.37, p < 0.0001$)
Pasoh		
δ_0 (intercept)	41.4878 ($t_{2689} = 6.70, p < 0.0001$)	57.8319 ($t_{2689} = 9.36, p < 0.0001$)
δ_1 (1000 v 10000)	-3.1077 ($t_{2689} = 3.74, p = 0.0002$)	3.1175 ($t_{2689} = 6.50, p < 0.0001$)
δ_2 (2500 v 10000)	-2.5519 ($t_{2689} = 3.45, p = 0.0006$)	2.5363 ($t_{2689} = 5.57, p < 0.0001$)

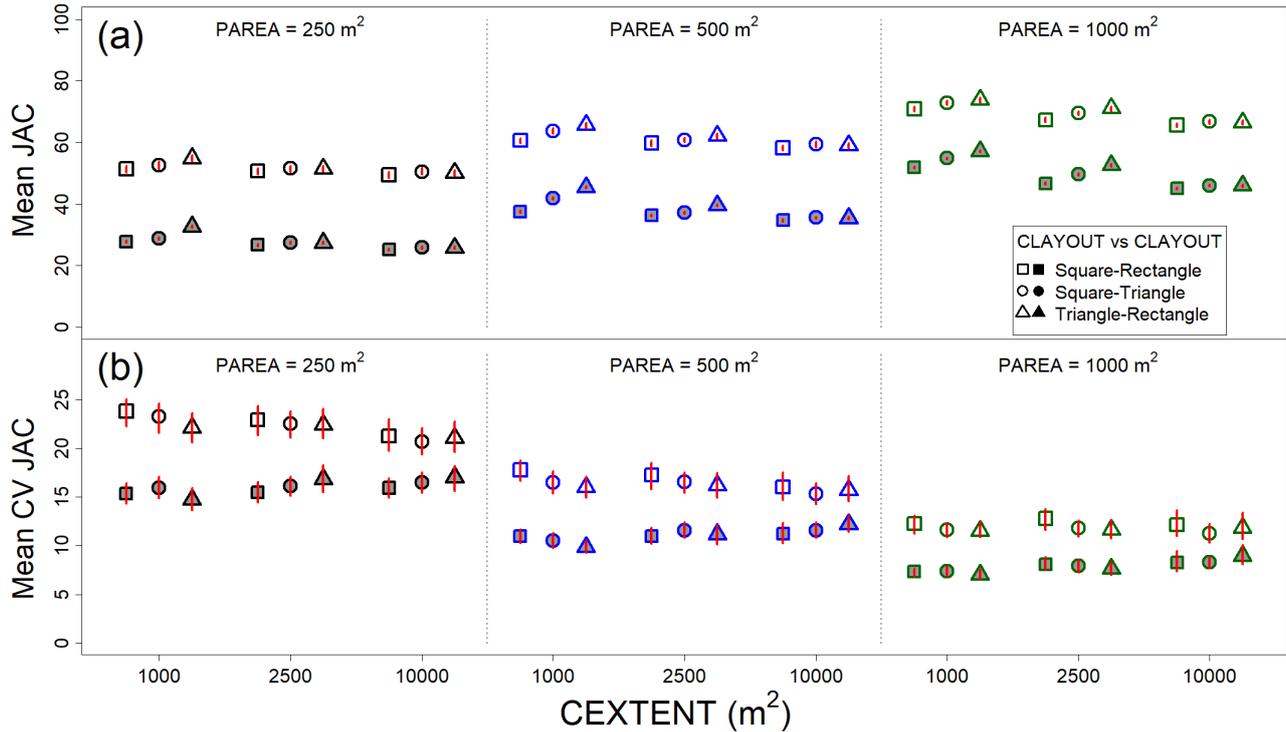


Figure 2. (a) Mean ($\bar{\theta}$) and (b) mean CV (CV_{θ}) Jaccard similarity index for comparing species composition between two cluster plots of two different cluster layouts for Fushan (open symbols) and Pasoh (filled grey symbols). The three comparisons are: (1) CLAYOUT = square vs CLAYOUT = rectangle (\square and \blacksquare), (2) CLAYOUT = square vs CLAYOUT = triangle (\circ and \bullet), (3) CLAYOUT = triangle vs CLAYOUT = rectangle (\triangle and \blacktriangle). The comparisons are controlled for PAREA and CEXTENT. PAREA are 250 (black symbols), 500 (blue symbols), and 1000 m² (green symbols). CEXTENT are 1000, 2500, and 10000 m². Red solid lines depict empirical 95% confidence intervals.

tion, e.g. mean JAC was 51-73% for Fushan and 28-56% for Pasoh (Table S3 [suppl.]). On the other hand, the comparison between the two CEXTENT 1000 and 10000 m² had consistently the lowest similarity in species composition, e.g. mean JAC was 49-70% for Fushan and 25-53% for Pasoh (Table S3 [suppl.]). The HLME models suggested that the similarity in species composition of the two comparisons were significantly different ($p < 0.0002$ for δ_i ; Table 1). As with the above analyses, increasing PAREA noticeably increased mean JAC and SOR of a particular comparison. Under a specific PAREA, triangle CLAYOUT had consistently the highest mean JAC and SOR for a comparison of two CEXTENT (Figs. 3a and S4a [suppl.]).

Mean CV between the three comparisons was majorly comparable. However, mean CV of the comparison between the two CEXTENT 2500 and 10000 m² in some cases was the lowest, e.g. for JAC, 12-22% for Fushan and 8-18% for Pasoh (Table S3 [suppl.]). Moreover, the comparison between the two CEXTENT 1000 and 10000 m² in some cases was the highest, e.g. for JAC, 13-24% for Fushan and 8-19% for Pasoh (Table S3 [suppl.]). Increasing PAREA consistently decreased mean CV of JAC and SOR of a particular comparison. In general, under a specific PAREA, triangle CLAY-

OUT had the lowest mean CV of JAC and SOR for a comparison of two CEXTENT (Figs. 3b and S4b [suppl.]).

Discussion

With increasing emphasis on managing global forests under diverse objectives, forest biodiversity information extracted from a robust forest inventory system has the potential to inform policies on regional and national levels (Winter *et al.*, 2008). Cluster plots have been widely used at these spatial scales because traveling between sample points is considerably costly due to long distances (Yim *et al.*, 2015). Design of a cluster plot is highly flexible, but Yim *et al.* (2015) and Kleinn *et al.* (2002) narrowed down to three main aspects, which were spacing between subplots, geometric shape of cluster plot, and number of subplots per cluster. Two of which corresponded to our simulated factors CLAYOUT and CEXTENT; thus, supporting our choice of design factors in this study. In designing a cluster plot, expenditure is balanced with information gain. Information gain in this study is expressed by the level of similarity in species composition between a

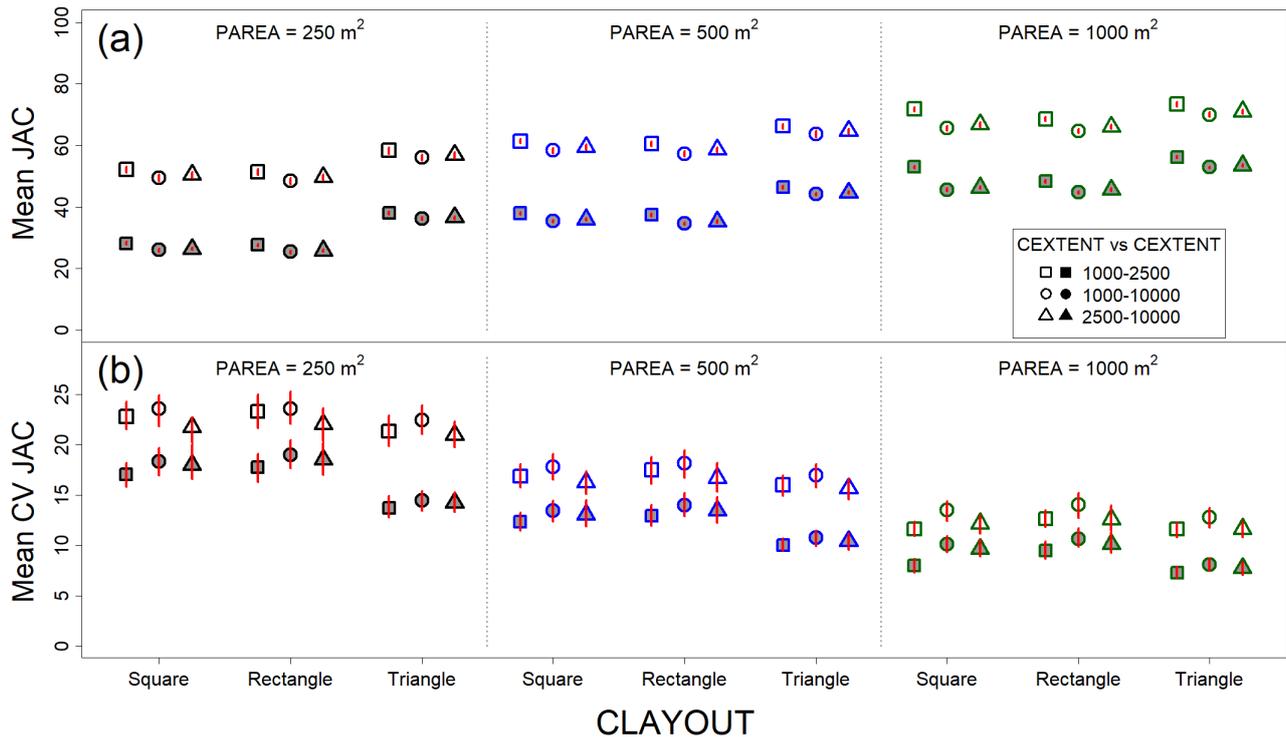


Figure 3. (a) Mean ($\bar{\theta}$) and (b) mean CV (CV_{θ}) Jaccard similarity index for comparing species composition between two cluster plots of two different extent of ground area enclosed by a cluster plot for Fushan (open symbols) and Pasoh (filled grey symbols). The three comparisons are: (1) CEXTENT = 1000 m² vs CEXTENT = 2500 m² (□ and ■), (2) CEXTENT = 1000 m² vs CEXTENT = 10000 m² (○ and ●), (3) CEXTENT = 2500 m² vs CEXTENT = 10000 m² (△ and ▲). The comparisons are controlled for PAREA and CLAYOUT. PAREA are 250 (black symbols), 500 (blue symbols), and 1000 m² (green symbols). CLAYOUT are square, rectangle, and triangle. Red solid lines depict empirical 95% confidence intervals.

more compact and a less compact cluster plot. Everything else being equal, expenditure decreases with a more compact cluster plot. For one, traveling time between subplots is less. If two cluster plots of different compactness produce high similarity in species composition, the more compact is preferable considering the expenditure. This study attempts to recommend the choice of a cluster plot design under each stated objective along this line of reasoning.

This study does not assess accuracy of estimated JAC and SOR for a particular comparison, e.g. PCONFIG = single vs CLAYOUT = square comparison. Quantifying the accuracy requires knowing the true population values of JAC and SOR. The true values are different between the 81 comparisons that we have made because each comparison involves two different plot designs. To know the true values, we also need to sample at all possible sample locations, which is impossible. On the contrary, the mean estimates of JAC and SOR across 500 random sample locations and across 100 iterations ($\bar{\theta}$) for a particular comparison approximate the true population values, especially given the narrow E95CI (Figs. 1a-3a). Thus, this study more importantly looks at how species composition potentially changes when different clus-

ter plot designs are used to assess the stated objectives.

In general, the results of species composition similarity were consistent between study sites and similarity indices. At Pasoh, the plant and species density is 6,707 individual ha⁻¹ and 16.4 species ha⁻¹, respectively. In Fushan, it is 4,576 individual ha⁻¹ and 4.4 species ha⁻¹, respectively. Consistency across study sites suggests that outcomes from this study could potentially be generalized to forests within this range of plant and species density, and forest ecosystems from natural lowland tropical forests to subtropical evergreen broadleaf forests. Although knowing the exact spatial autocorrelation function specific to a forest could lead to optimum cluster plot design (Korhonen & Maltamo, 1991), this consistency suggests that cluster plot designs are versatile. However, forest ecosystems with many common and few rare species such as the Boreal or cold temperate forests need to be further studied as they are exceptional in many studies on species richness estimation (Pitkänen, 1998; Magnussen *et al.*, 2010). Consistency between similarity indices suggests that outcomes of this study could potentially be extended to other indices with similar construction such as the abundance-adjusted Jaccard and Sørensen simi-

larity index (Chao *et al.*, 2005). Yang *et al.* (2019b) have similarly reported consistency in trends between JAC, SOR, and their variants when studying the effects of plot size and shape on sampling species composition.

Comparison of species composition between a single plot and a cluster plot tries to determine whether field effort should be spent in a single large plot or several subplots spread out in different geometrical layouts. A single plot typically requires less field effort without the need to travel between subplots. However, it is expected that a cluster plot would capture a larger variety of plant species. In highly heterogeneous forest ecosystems, Green & Young (1993) proposed that sampling with many small plots spread apart instead of a single large plot would capture many unique plant species. Our study showed that the choice between single and cluster plots depends on PAREA. With larger plots, species composition similarity between a single and a cluster plot increases; thus, the potential gain of a cluster plot in observing diverse species composition diminishes. At small PAREA, results suggest that triangle CLAYOUT is the least effective among the three choices. This might be due to triangle CLAYOUT having a subplot at the center, which leads to it capturing more plant species that are similar to those in a single plot. Despite this, triangle CLAYOUT is still effective to some extent because it captures species not present in a single plot with the maximum species composition similarity between them less than 80%. If the choice is between a single plot or a cluster plot, we recommend that a cluster plot either of square or rectangle CLAYOUT would be preferable than a single plot if PAREA is $\leq 500 \text{ m}^2$. For PAREA $> 500 \text{ m}^2$, we recommend single rectangular plot as suggested by Yang *et al.* (2019b) without the need to travel between subplots. This recommendation is based on a threshold of 50% in similarity in species composition between a single and a cluster plot as we determine that cluster plots are more informative with lower level.

The geometrical arrangement of subplots (CLAYOUT) reflects the spatial compactness of a cluster plot. Spatial compactness is defined as the ratio of CEXTENT to the perimeter of a cluster plot. Among the three CLAYOUT, square is the most compact followed by triangle and rectangle, e.g. the respective compactness is 12.5, 10.97, and 10.83 for CEXTENT of 2500 m^2 . A less compact cluster is attractive because larger perimeter leads to smaller covariance between observed values of subplots and to greater information gain (Kleinn, 1996). This might explain why similarity in species composition is consistently the lowest between square and rectangle CLAYOUT. Assuming CEXTENT

of 2500 m^2 , a moderate 16% increase in travel distance leads to similarity values between the two CLAYOUT to be less than 52% in Pasoh (Table S2 [suppl.]). This implies that local species composition changes quite a bit within a short distance in species rich forests such as Pasoh. Additionally, comparable spatial compactness leads to triangle and rectangle CLAYOUT having the highest similarity in species composition. However, one should note that information gain due to differential spatial compactness diminishes as CEXTENT increases. Past studies have pointed towards uncertain effects of CLAYOUT on sampling forest attributes. Kleinn (1994) and Tokola & Shrestha (1999) found the differences in precision between different CLAYOUT to be relatively small. On the contrary, Yim *et al.* (2015) observed that CLAYOUT affected precision in estimating stand attributes. Spatial compactness directly reflects the effort spent on travel between subplots for square and rectangle CLAYOUT, but not so for triangle CLAYOUT. Assuming moving along the perimeter, the travel distance is 200 and 231 m for square and rectangle CLAYOUT, respectively, for CEXTENT of 2500 m^2 . Assuming starting at the central subplot and then moving along the perimeter, travel distance of triangle CLAYOUT is 196 m for the same CEXTENT. Thus, field effort is generally less for triangle CLAYOUT due to its unique subplot arrangement. Considering the interaction of PAREA and CEXTENT and travel distance, we recommend that if CEXTENT is $\leq 1000 \text{ m}^2$ and PAREA is $\leq 500 \text{ m}^2$, rectangle CLAYOUT is preferred for greater information gain. If the choice of a plot design must be a cluster plot, triangle CLAYOUT is preferred for CEXTENT $> 1000 \text{ m}^2$ and PAREA $> 500 \text{ m}^2$ because it would require less field effort.

Everything else being equal, CEXTENT directly reflects operation costs with larger extent of ground area enclosed by the boundaries of a cluster implying greater travel cost. Spatial autocorrelation between subplots is expected to decrease with greater CEXTENT (Kleinn, 1994; Yim *et al.*, 2015), which should increase information gain on species composition on the cluster level. This explains why sampled species composition between 1000 and 10000 m^2 CEXTENT is the least similar, while species composition between 1000 and 2500 m^2 CEXTENT is the most similar. Comparing species composition between two different CEXTENT is akin to quantifying β -diversity at that scale (Magurran, 2004), which could help us better understand local-level species turnover. For example, JAC is less than 70% for Fushan and 52% for Pasoh for the 1000 to 10000 m^2 CEXTENT comparison (Table S3 [suppl.]) implying that local level species turnover is high for species rich forests even when the

travel distance only increased by about 3 times. One could also potentially calculate local-level γ -diversity, which is an additive of α - and β -diversity (Lande, 1996). We expect similarity in species composition to continue to decrease with larger CEXTENT beyond the levels that we have considered. However, there is a limit to the choice of CEXTENT due to available resources. If the objective is to sample local-level species diversity, we recommend $\text{CEXTENT} \leq 1000 \text{ m}^2$. CEXTENT of 2500 m^2 may not be suitable because of higher operating costs and high similarity in species composition between 1000 and 2500 m^2 CEXTENT. Larger CEXTENT could potentially straddle different ecological strata, which may under-sample a local community.

Mean CV ($\overline{CV_\theta}$) represents average variability in estimated JAC and SOR of 500 random sample locations in a simulated iteration. A low value suggests that similarity in species composition between two plot designs is consistently estimated across a study site. In an actual sampling event, only a single set of sample locations (analogous to a single “iteration”) is established. In that respect, mean CV could be viewed as estimated relative sampling error for the single event. When sampling for forest timber values such as total volume, one strives to lower mean CV by using sample designs that offer higher efficiency or produce narrower confidence widths of the estimates (Kershaw *et al.*, 2016). This is desirable for both management and decision-making aimed to capture such values. However, the opposite may be preferred when sampling species composition. Results show that increasing PAREA effectively lowers mean CV, but it requires greater field effort. For example, when comparing between a single and a cluster plot, mean CV could almost be halved with a four-fold increase in PAREA for certain comparisons. In addition, increasing PAREA increases similarity in species composition between two cluster plot designs, which also implies little information gained between the two designs. Thus, we suggest that mean CV could not be the single deciding factor for the choice of implementing a cluster plot design.

PAREA is the design factor that notably increases estimated similarity indices and decreases mean CV. Larger PAREA means sampling wider local ground area, which leads to greater number of observed species. This is in line with the classic species-area relationship (Condit *et al.*, 1996). To study this relationship, we built a species accumulation curve for each of the 30 plot designs, which represents cumulative number of observed species over number of sample locations (Figs. S5 and S6 [suppl.]). For a plot design, a species accumulation curve was built for each itera-

tion by cumulating the number of observed species from 1 to 500 sampling locations. The 100 species accumulation curves were then averaged for the plot design. Given a number of sample locations, the number of observed species is clearly larger for larger PAREA, especially for number of sampling locations < 100 (solid vs dotted lines in Figs. S5 and S6 [suppl.]). Furthermore, the species accumulation curves of $\text{PAREA} = 1000 \text{ m}^2$ reaches asymptotes at a faster rate than those of $\text{PAREA} = 250 \text{ m}^2$. With a larger number of observed species, it is more likely that two plot designs share a larger number of identical species; thus, it leads to the strong effects of PAREA on similarity in species composition between two plot designs. However, increasing PAREA is associated with greater cost in field plot establishment and species identification work, especially in species rich forests such as Pasoh. Smaller PAREA could potentially minimize the risk of missing individuals (thus, missing species) as field effort is concentrated in locating all plant individuals and species in a small area. Lastly, Green & Young (1993) suggested that many small plots would be better than a few large ones in sampling plant species that showed spatial aggregation in forests.

Kleinn (1996) and Yim *et al.* (2015) both concluded that a generally superior cluster plot design is not possible because the choice of a design depends on the scope of a study, specific forest conditions, and cost function to ensure its practicality in the field. Nevertheless, we have provided some general recommendations on the choice based on the consistent results in this study. To the best of our understanding, this study is the first to explore potentials and limitations of cluster plot design in sampling species composition. There are many potential extensions from this study. For one, many indices are necessary to describe species diversity (Pavoine & Bonsall, 2011). Construction of other similarity indices such as the Bray-Curtis Index and Kulczynski Index (Barwell *et al.*, 2015) are different from JAC and SOR. Thus, it would be interesting to see if these indices behave similarly. Different countries utilize a variety of cluster plot designs such as cross-shape cluster in Brazil, line-shape cluster in Czech Republic, and L-shape cluster in Finland (Tomppo *et al.*, 2010). Hypothetically, different cluster plot designs would inherently account for spatial autocorrelation in species distribution differently, especially with respect to their compactness. Lastly, Yim *et al.* (2015) carried out a time study as they considered time to be an important cost factor for optimizing cluster plot design. The cost of sampling species composition would be different than sampling for forest timber attributes because it involves taxonomic expertise, collection of voucher specimens of unknown species in

the field, and laboratory preparation of samples for identification. These factors need to be accounted for during a forest inventory program. This study has not explicitly quantified the trade-off between costs and information gain. A future cost-and-benefit study could adapt the work from Lynch (2017) and Yang *et al.* (2017). In the context of this study, information gain could be defined as a unit decrease in species composition similarity. A relationship could then be established between total cost and the information gain. Total cost includes measurement, overhead, and travel costs (Yang *et al.*, 2017), which could be obtained from a field study. Lastly, this study should appeal to forest managers and forest ecology communities, who are designing cluster plots for plant diversity assessment.

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