

Importance of topography and soil texture in the spatial distribution of two sympatric dipterocarp trees in a Bornean rainforest

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Relationships between spatial distributions and site conditions, namely topography and soil texture, were analyzed for two congeneric emergent trees, *Dryobalanops aromatica* and *Dryobalanops lanceolata* (Dipterocarpaceae), in a tropical rainforest in Sarawak, East Malaysia. A 52-ha permanent plot was divided into 1300 quadrats measuring 20 m × 20 m; for each *Dryobalanops* species, the number and total basal area of trees ≥1 cm in d.b.h. were compared among groups of quadrats with different site conditions. Because spatial distributions of both *Dryobalanops* and site-condition variables were aggregated, Monte-Carlo permutation tests were applied to analyze the relationships. Both single and multifactor statistical tests showed that the density and basal area distributions of the two species were significantly non-random in relation to soil texture and topographic variables. *D. aromatica* was significantly more abundant at higher elevations, in sandy soils, and on convex and steep slopes. In contrast, *D. lanceolata* preferred lower elevations and less sandy soils. In the study plot, there were very few sites (3 of 1150 quadrats tested) where the models of Hayashi's method predicted the co-occurrence of the two species. These results suggest that between-species differences in habitat preferences are so large that they alone explain the spatially segregated distributions of these two species within the 52-ha study plot.

Key words: Dipterocarpaceae; *Dryobalanops*; habitat; spatial distribution; tropical rainforest.

INTRODUCTION

Sympatric distributions of congeneric species are remarkable features of tropical rainforests (Richards 1952; Ashton 1969; Whitmore 1984). Comparative studies on the ecology of such species often provide important information for coexistence mechanisms of rainforest trees because they are likely to have relatively similar niches because of the same ecological and physiological heritage

via their common ancestral lineage (Rogstad 1989). The maintenance of species diversity is, therefore, closely related to the mechanisms of the coexistence of such sympatric congeners.

Habitat divergence is a possible mechanism enabling the coexistence of trees in tropical rainforests (Ashton 1969). Evidence has been accumulating for a significant role of edaphic factors in determining rainforest species' distributions within relatively small areas (e.g. Basnet 1992; Tuomisto & Ruokolainen 1994; Oliveira-Filho *et al.* 1994; Newbery *et al.* 1996; Poulsen 1996; Clark *et al.* 1998, 1999; Harms *et al.* 2001). For example, at a 50-ha plot on Barro Colorado Island, Panama, Harms *et al.* (2001) found that 64% of 171 species were significantly associated with cer-

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tain habitat types that were characterized by edaphic differences.

However, species' habitat associations alone cannot lead to the coexistence of species if their habitats are similar and largely overlap. Harms *et al.* (2001) concluded that, although a majority of species were non-randomly distributed in relation to edaphic factors, the effects of edaphic factors may contribute little to the maintenance of species richness because many species shared similar habitats. Thus, we should check the degree of among-species habitat difference before we discuss the importance of habitat divergence in mechanisms of species coexistence.

Habitat divergence within groups of congeneric and sympatric species has also been reported for many rainforest trees of various life forms, for example, canopy trees (Yamada *et al.* 2000), middle- and under-storey trees (Rogstad 1990) and pioneer species (Davies *et al.* 1998). However, few of these studies correctly analyzed the statistical significance of habitat effects on species' distributions. This is, in part, because the independence assumption required for many conventional statistical analyses, such as the χ^2 and regression analyses, is violated when both trees and habitat distributions are spatially auto-correlated, which is often the case in real forests (Legendre 1993; Plotkin *et al.* 2000; Harms *et al.* 2001).

In this study, we examine differences between habitats in relation to topography and soil texture for two congeneric emergent tree species that are sympatrically distributed in a Bornean rainforest. First, we check the spatial structure of tree distributions and site conditions because spatial auto-correlation, if it exists, must be considered in the habitat analysis. Second, we analyze whether the tree distributions are significantly related to topography and soil texture. Finally, we explore whether the degree of divergence in habitat, if it exists, is so great that it can contribute to the coexistence of the two species.

METHODS

Study site

The study site is a mixed dipterocarp forest (*sensu* Ashton 1964) in the Lambir Hills National Park

(4°12'N, 114°00'E; ~60–450 m a.s.l.) in Sarawak, East Malaysia. The average annual rainfall is 2725 mm (1967–1998) at Miri Airport, which is located approximately 20 km north of the study site. There is no distinct dry season, although the period from February to August has relatively less rainfall. The soil consists of red-yellow podsoles or ultisols derived from Miocene sediments (Mulock Houwer 1968). Two types of ultisols, udult and humult, are distributed side by side within the study site. Udults are relatively rich in clay and have relatively high mineral–nutrient concentrations; humults are relatively rich in sand and relatively poor in mineral concentrations at our site, characteristically with a surface root-matted horizon of raw humus (Baillie *et al.* 1987; Ashton & Hall 1992; Palmiotto 1998). The topography is characterized by hilly, undulating terrain with steep slopes, including scars caused by small landslides (Yamakura *et al.* 1995). Approximately 80% of the park is covered by mixed dipterocarp forests with a remarkable diversity of trees; 1173 tree species were counted in the 52-ha plot established in the forest (Condit *et al.* 2000; Lee *et al.* 2002).

Study species

Dryobalanops aromatica Gartn.f. and *Dryobalanops lanceolata* Bruck (Dipterocarpaceae) are emergent trees in the lowland tropical rainforest in Borneo; *D. aromatica* also occurs in Sumatra and on the Malay Peninsula (Ashton 1982). Their geographic distributions overlap only in the northern part of Borneo (Ashton 1982). In this region, the two species sometimes co-occur in the same forest. Both species often make local stands (~0.2–2 ha) of high canopy dominance up to 30% in total basal area (van Zone 1915 in Richards 1952; Whitmore 1984; Kachi *et al.* 1993; Itoh *et al.* 1995a).

In the study plot, *D. aromatica* is the most abundant species both in tree number (8490/52 ha, 2.5% of all trees ≥ 1 cm d.b.h.) and in basal area (149 m²/52 ha, 6.7% of total basal area). Whereas *D. lanceolata* is less abundant in the plot; the tree number and basal area are the 78th (954 trees/52 ha, 0.3% of all trees) and 39th largest (11.6 m²/52 ha, 0.5% of the total basal area) of the 1173 species, respectively. Despite the large difference in relative importance at the whole-plot scale, both

species make dense populations at smaller scales (Itoh *et al.* 1997; Lee *et al.* 2002). In two 1.6 ha areas in the plot, in which dense stands of each species are found, *D. aromatica* and *D. lanceolata* are the most abundant species; *D. aromatica* occupies 5.5% of total tree number and 19.5% of total basal area of trees ≥ 1 cm d.b.h., whereas *D. lanceolata* occupies 5.3% and 17.3% of tree number and basal area, respectively (Itoh *et al.* 1997).

The two species share similar reproductive properties. They flower and fruit at relatively short intervals (2–4 years) among dipterocarp species (Chan & Appanah 1980; Whitmore 1984; Itoh *et al.* in press). Both species produce large wind-dispersed, one-seeded fruits (2–3 g dry weight). The seeds have no dormancy and germinate within 1 month after dispersal both in gaps and closed forests (Itoh *et al.* 1995b). Their seedlings are shade-tolerant and can survive for more than 10 years without canopy gaps (A. Itoh, pers. obs., 1990–2001), although growth is greater in canopy gaps (Kachi *et al.* 1993; Itoh *et al.* 1995b).

Tree enumeration and topography survey

A permanent 52-ha plot (500 m \times 1040 m) was established from 1990 to 1993 (Yamakura *et al.* 1995). The plot was demarcated and divided into 1300 20 m \times 20 m quadrats. The relative elevation of each corner of all the quadrats was measured. All trees ≥ 1 cm d.b.h. (diameter at 1.3 m) were measured for d.b.h., and were individually labeled, mapped and identified to species. Details of plot demarcation and tree enumeration are described in Yamakura *et al.* (1995).

In this study, we used individual-based data instead of trunk-based data. Trees with more than two trunks at breast height were labeled and each trunk was measured in the field, but these were treated as one individual and only the largest trunk was used to calculate basal area.

Soil survey

Soil texture was used for an edaphic variable because previous studies showed that soil fertility and soil water conditions were closely related to soil texture at Lambir (Baillie & Ahmed 1984; Ashton & Hall 1992; Hirai *et al.* 1997). In general, soil fertility increases with increasing clay con-

tents, whereas soil water drainage depends mostly on sand contents, so that more sandy soils fluctuate greatly in water conditions and are, in general, drier (Hirai *et al.* 1997).

Soil samples, 5–15 cm deep, were collected from the center of all 20 m \times 20 m quadrats. In the field, they were assigned to one of four texture classes following Kimmins (1987), based on the apparent sand content, stickiness and slipperiness. To calibrate the field determination, 145 soil samples were randomly collected and their sand (particles >0.05 mm diameter), silt (0.002–0.05 mm) and clay (<0.002 mm) contents were measured using a dispersion and settling method with a LaMotte Soil Texture Kit (LaMotte Co., Chestertown, MD, USA). Soil texture was graded based on the sand contents in classes ordered 1–4. Average sand contents were $64 \pm 1.4\%$ (SE) ($n = 31$), $54 \pm 0.8\%$ ($n = 35$), $45 \pm 1.0\%$ ($n = 23$) and $39 \pm 0.8\%$ ($n = 56$) for each class, respectively. Average clay contents were $13 \pm 1.0\%$, $27 \pm 0.8\%$, $19 \pm 1.3\%$ and $36 \pm 0.7\%$, respectively. Because class 2 had greater clay content than class 3, the former might be more fertile than the latter.

Topography variables

Three topography variables (i.e. elevation, index of convexity (IC) and inclination) were calculated for all 20 m \times 20 m quadrats ($n = 1300$) using the quantitative method of Yamakura *et al.* (1995).

The elevation of a focal quadrat was defined as the mean elevation of its four corner posts. The IC is an empirical index for the local surface relief of the ground. The IC was defined as the difference in elevation between the focal quadrat and the outer-quadrat, which consisted of the eight surrounding quadrats. The elevation of the outer quadrats was the mean elevation of the 12 survey posts on its margin. Positive and negative values of IC indicate convex (ridge) and concave (valley) land surface forms, respectively. The IC was calculated only for 1150 quadrats. Those adjacent to the margin of the plot were excluded because they lacked outer quadrats for the calculation. Inclination was calculated from a 3-D regressed plane determined for each quadrat by the equation:

$$Z = b_0 + b_1X + b_2Y \quad (1)$$

where Z is elevation, X and Y are the coordinates in a horizontal plane measured from the southeast corner of the plot, and b_0 , b_1 and b_2 are coefficients specific to each quadrat. The values of the coefficients were determined using the least-squares method from X , Y and Z at the corners of each quadrat. The inclination is then given by the equation:

$$\theta = \cos^{-1} \left(\frac{1}{\sqrt{b_1^2 + b_2^2 + 1}} \right) \quad (2)$$

Note that \cos^{-1} in equation 2 is erroneously given as \sin^{-1} in Yamakura *et al.* (1995).

Spatial distribution of site conditions and trees

The spatial structures of site condition variables and tree distributions were analyzed using a geostatistical method, the semivariogram, which has been widely used to analyze spatial structures in ecology (e.g. Phillips 1985; Robertson 1987). The sample semivariance $[\hat{\gamma}(\mathbf{h})]$ is estimated by the equation:

$$\hat{\gamma}(\mathbf{h}) = \frac{1}{2N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} [z(x_i) - z(x_i + \mathbf{h})]^2 \quad (3)$$

where $z(x_i)$ and $z(x_i + \mathbf{h})$ are the values of a given variable at locations x_i and $x_i + \mathbf{h}$, a location separated by a separation vector or lag distance \mathbf{h} from x_i , and $N(\mathbf{h})$ is the total number of pairs of samples separated by \mathbf{h} . The empirical semivariogram, which is a plot of the values of $\hat{\gamma}(\mathbf{h})$ as a function of \mathbf{h} , gives information on the spatial dependency of the variable. In this study, samples were 20 m \times 20 m quadrats, and the variables were the four site variables (i.e. elevation, IC, inclination and soil texture) and the four tree distribution variables (i.e. tree density and basal area per quadrat for each species). For soil texture, we used the mean sand content (%) of the four soil texture classes. The values of tree density and basal area were log-transformed using the equations $\log_{10}(n + 1)$ and $\log_{10}(\text{BA} + 1)$, where n is the number of trees in each quadrat and BA is the total basal area (cm²) of *Dryobalanops* trees in each quadrat.

In general, a variogram levels off at a certain value of semivariance, called the sill, which is

roughly equal to the total variance of variables (Kitanidis 1997). The value of \mathbf{h} at which $\hat{\gamma}(\mathbf{h})$ reaches a sill is termed the 'range'. Variables are spatially dependent when \mathbf{h} is smaller than a 'range'; the nearer two locations are, the more similar their variables. If \mathbf{h} is larger than a 'range', the difference between the variables is independent of their distance, suggesting that the variables have no spatial dependence greater than the scale equal to the 'range'.

To compare the spatial scales of the topography and soil variables, an exponential model was fitted using the weighted least-squares method (Robertson 1987). A model with a nugget effect was adopted for inclination and sand content. The nugget effect includes errors in data and a smaller scale variance than the minimum distance between measured points. This model is defined as:

$$\hat{\gamma}(\mathbf{h}) = C_0 + C_1 \left\{ 1 - \exp\left(-\frac{\mathbf{h}}{a}\right) \right\} \quad (4)$$

where C_0 , C_1 , and a are coefficients identical for each variable (Kitanidis 1997). C_0 and $(C_0 + C_1)$ stand for a nugget effect and a sill, respectively. The 'range' is estimated by the 'practical range' ($3a$), which is the lag distance at which $\hat{\gamma}(\mathbf{h})$ is $\sim 95\%$ of C_1 . An exponential model without the nugget effect was used for IC and tree density because the nugget effect took negative values when we used equation 4. A negative nugget effect is theoretically unattainable. This model is defined by equation 4 with $C_0 = 0$. We did not apply any model for elevation because its semivariogram did not level off until the maximum \mathbf{h} (250 m). For illustration of the goodness of fit, we calculated Pearson's r^2 values for the fit of model predictions to actual sample semivariances.

Analysis of topography/soil and tree distribution

The relationship between topography or soil and *Dryobalanops* distribution was analyzed using single- and multifactor analyses.

As a single-factor analysis, dependence of tree distribution and basal area on topography/soil was analyzed using the χ^2 and Kruskal–Wallis tests, respectively. Topographic variables were categorized into five regular classes: elevation: <160,

<175, <190, <205 and ≥ 205 m; IC: <-3, <-1, <1, <3 and ≥ 3 m; inclination: <12, <18, <24, <30 and $\geq 30^\circ$. Because the spatial distributions of both trees and site condition variables were auto-correlated, as will be shown later in the results, the independence assumption in the χ^2 and Kruskal–Wallis tests was violated. Therefore, we applied a Monte-Carlo permutation test to determine the significance of the observed values of the χ^2 and Kruskal–Wallis statistics.

We conducted random torus shifts of the distribution map of each *Dryobalanops* species (Besag & Diggle 1977). The original tree map was randomly shifted in north–south and east–west directions about a 2-D torus, in which opposite edges of the study plot are adjoined so that shifted trees do not locate outside the study plot. The torus shifts maintain the local spatial patterns of tree distribution, but change the relationship between tree distributions and site variables. Thus, this is an effective method, although not perfect, to avoid the problem of spatial auto-correlation in analyzing habitat associations (Harms *et al.* 2001). The permutation was repeated 500 times for each species, and χ^2 and Kruskal–Wallis statistics were calculated for all topography and soil texture variables. We then assigned the significance level (P) by counting how many times a test statistic as extreme as or more extreme than the observed one was obtained with the permuted data.

As a multifactor analysis, we adopted Hayashi's quantification method (Hayashi 1952). This method is mathematically equivalent to a multiple regression analysis including only dummy categorical independent variables with no continuous independent variables. In this method, dependent variables need not be linearly related to the independent variables. We adopted this method because the response of tree distribution to topography and soil is often non-linear (e.g. Gartlan *et al.* 1986).

In Hayashi's quantification method, a dependent variable is referred to as the 'outside criterion', and independent variables (categorical) are called 'items', each of which has several classes or 'categories'. The predicted value of the i th outside criterion (Y_i) is given by the following equation:

$$Y_i = c + \sum_{j=1}^R \sum_{k=1}^{c_j} a_{jk} \delta_i(jk) \quad (5)$$

where c is a constant, R is the number of items, c_j is the number of categories in the j th item, a_{jk} is the 'standardized score' of the k th category in the j th item, and $\delta_i(jk)$ is a dummy variable. When the i th outside criterion corresponds to the k th category in the j th item, $\delta_i(jk) = 1$; otherwise $\delta_i(jk) = 0$. The standardized scores for each category in all items are calculated so that the sum of residuals between predicted and observed outside criterion will be minimized and at the same time the following equation will be satisfied:

$$\sum_{k=1}^{c_j} n_{jk} a_{jk} = 0 \quad (6)$$

where n_{jk} is the number of data at the k th category of j th item.

In our study, we used two outside criteria for each species (i.e. the tree number (n) and total basal area (BA; cm^2) in a $20 \text{ m} \times 20 \text{ m}$ quadrat). Tree number was largely determined by small saplings, which were generally much more abundant than large adults. In contrast, the total basal area was mostly dependent on the presence or absence of large individuals in the quadrats. The values were log-transformed using the equations $\log_{10}(n + 1)$ and $\log_{10}(\text{BA} + 1)$. The items were elevation, IC, inclination and soil texture; the first three variables were categorized into five classes as in the single-factor analysis.

Hayashi's quantification method calculates the multiple correlation coefficient (R) and the partial correlation coefficient (r) similar to a conventional multiple linear regression. Selection of significant items using their F -values can be accomplished using the same stepwise selection methods as in a multiple linear regression analysis. However, F -values for each item and for the total model must be inflated because tree distribution and site condition variables were spatially auto-correlated in our data (Cliff & Ord 1981). Therefore, we conducted a Monte-Carlo permutation test. The original map of each *Dryobalanops* species was randomly shifted 500 times in the same way as in the single-factor analysis; maps of topography and soil were kept constant as originals. Next, we applied a backward stepwise selection of the items; an item was removed if the F ratio between models with and without the item was larger in the original data than the 50th largest one in the 500 per-

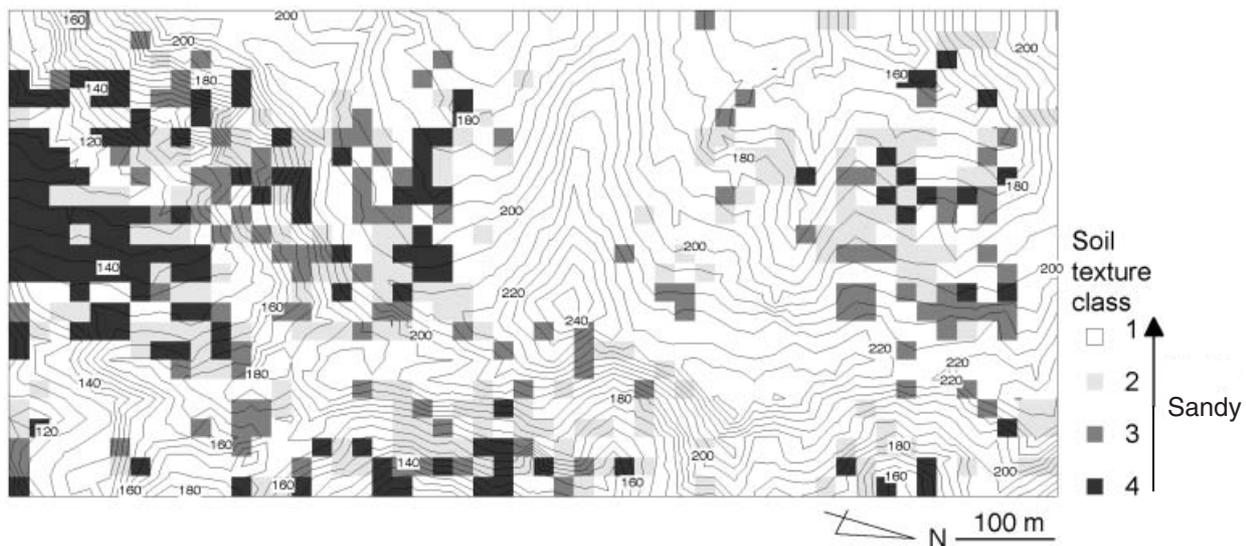


Fig. 1. Topography and soil texture distribution of the study plot. The soil texture is graded relatively rich to poor in sand using classes ordered 1–4.

muted data ($P < 0.1$). Forward stepwise selections were also attempted and provided identical results to the backward selections.

RESULTS

Spatial pattern of site conditions and *Dryobalanops* trees

Topography and soil texture showed complicated spatial patterns within the 52-ha plot (Fig. 1). Correlations between three topographic variables were not significant ($r = -0.043$ – 0.037 , $P = 0.14$ – 0.20) except for elevation and IC ($r = 0.380$, $P < 0.01$). Soil texture class was significantly negatively correlated with all three topographic variables (Spearman's rank correlation coefficients were -0.059 – 0.326 , $P < 0.01$), indicating that sandy soils occurred at higher elevations and on convex and steeper slopes.

Semivariance increased with lag distance (h) on smaller scales than ~ 100 m for all the site variables (Fig. 2), indicating spatial auto-correlation of the variables at local scales. Semivariograms leveled off within a lag distance of < 250 m for IC, inclination and soil texture. The semivariogram of elevation, however, increased more or less linearly with lag distance up to the maximum lag distance (250 m).

The 'range' of each variable indicated that the order of spatial scales in which the variables were auto-correlated was $IC < \text{soil texture} < \text{inclination} < \text{elevation}$ (Table 1).

The distributions of the two *Dryobalanops* trees were clearly segregated; only small trees of the two species overlapped in a few small areas (Fig. 3). The 'ranges' in semivariograms for density and basal area of the two species were 132–160 m (Fig. 4; Table 1), indicating that their distributions were spatially auto-correlated within these spatial scales.

Soil, topography and tree distribution

The single-factor analysis showed that *D. aromatica* and *D. lanceolata* were non-randomly distributed ($P < 0.05$) with respect to elevation, IC, inclination and soil texture in the plot, although randomness in the distribution of *D. lanceolata* was not rejected for IC and inclination ($P = 0.52$ – 0.54) (Table 2). Significantly more *D. aromatica* were found at high elevation, on sandy soils, and on convex and steep slopes. In contrast, the occurrence of *D. lanceolata* was associated with low elevation and less sandy soils. Relationships between basal area and edaphic variables were the same as those of the tree distributions,

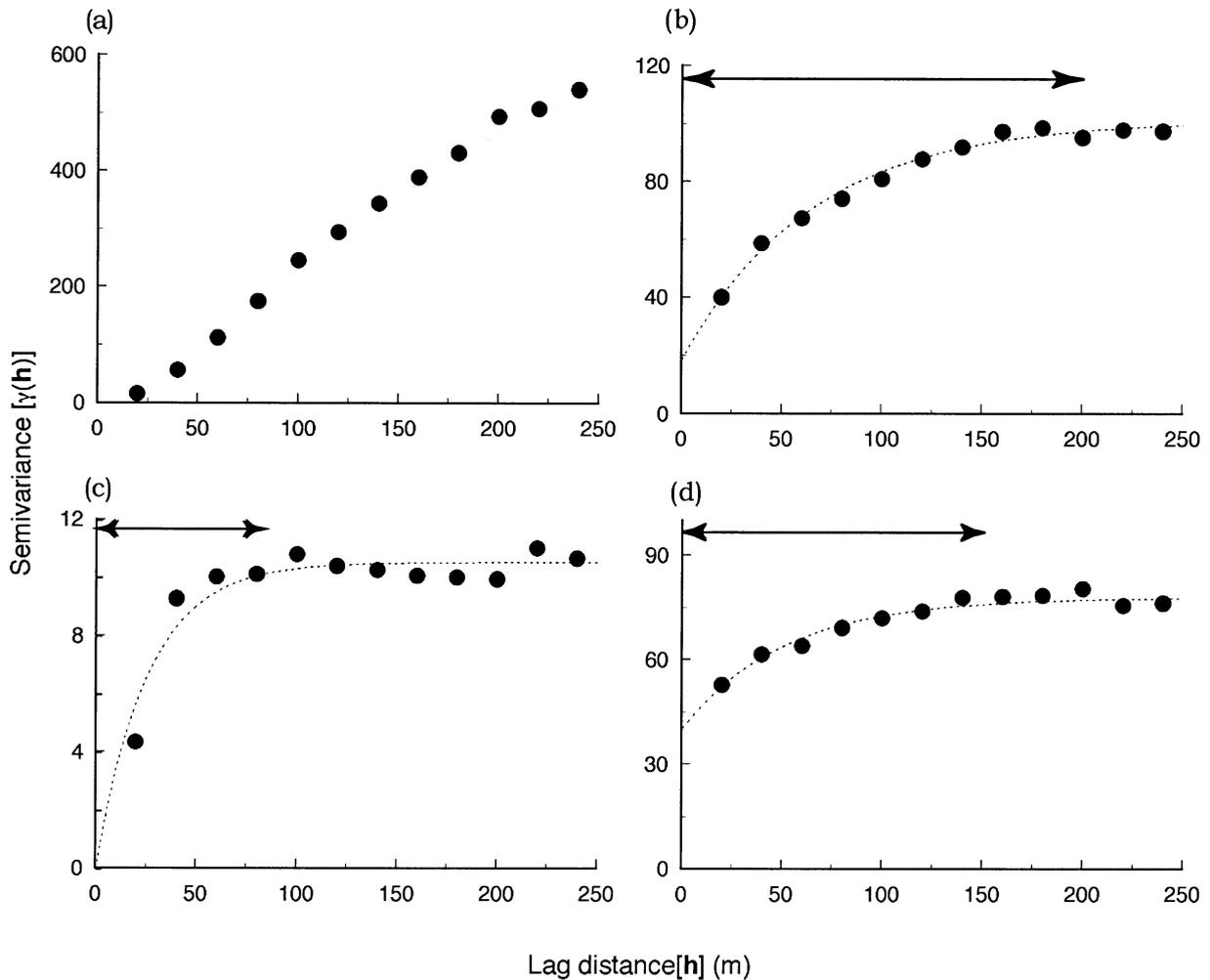


Fig. 2. Semivariograms of (a) elevation, (b) inclination, (c) index of convexity (IC) and (d) soil sand content. Dotted lines are exponential models fitted using a weighted least-squares method (see Table 1 for coefficients). The arrows indicate 'ranges' estimated by the exponential models. Sample sizes are 2523 for the shortest lag distance and 1676 for the longest distance except for IC, for which sample sizes are 2277 and 1474, respectively.

except that the relationship between basal area and inclination was not significant ($P = 0.75$) for *D. aromatica* (Table 2).

The multifactor analysis supported the results of the single-factor analysis when we used the significance level, $P < 0.1$, except that soil texture did not significantly predict *D. aromatica* distribution, both for tree number and basal area (Table 3). This suggests that all the significant relationships in the single-factor analyses, except for soil texture for *D. aromatica*, were not artifacts as a result of correlations between the factors.

Models based on only topography and soil variables predicted segregated distributions of the two species in the study plot (Fig. 3). Of the 1150

quadrats tested, only three were predicted to have positive values of $\log_{10}(n + 1)$, that is $n > 0$, for both species. Although the segregated spatial patterns of the two species at the whole-plot scale were relatively well reconstructed by the models, their spatial distributions were highly clumped within the areas in which their occurrences were expected from the models (Fig. 3)

DISCUSSION

The results suggest that both topography and soil texture were important in determining the spatial distributions of the two *Dryobalanops* species in the

Table 1 Parameters of the exponential model (eqn 4) estimated using a weighted mean least squares method for variograms of inclination, index of convexity (IC), soil texture, log tree density and log basal area of two *Dryobalanops* species: *D. aromatica* and *D. lanceolata*

Variable	C_0	C_1	a	Sill	Range (m)	r^2
Inclination	19.7	82.6	68.5	102.2	205	0.99
IC	0	10.9	26.7	10.9	80	0.94
Soil texture	40.2	37.8	51.1	77.9	153	0.96
Log tree density						
<i>D. aromatica</i>	0	0.29	45.5	0.29	137	0.99
<i>D. lanceolata</i>	0	0.05	49.7	0.05	149	0.94
Log basal area						
<i>D. aromatica</i>	0.42	1.53	53.3	1.95	160	1.00
<i>D. lanceolata</i>	0.05	0.30	44.0	0.35	132	0.95

C_0 , C_1 and a are coefficients of the model. Sill = $C_0 + C_1$; Range = $3a$; (r^2), goodness of fit of the model.

study plot. Their habitats were clearly different; trees of *D. aromatica* were associated with high elevations, steep and convex slopes and sandy soils, whereas those of *D. lanceolata* were associated with low elevations and less sandy soils. The magnitude of the habitat differences between these two species was sufficiently large to explain the segregated spatial patterns in the plot (Fig. 3). These results strongly support the importance of habitat divergence in the coexistence of the two species at the scale of approximately 50 ha.

Although Hayashi's models predicted successfully the segregated distributions at the whole-plot scale, the realized distributions were much narrower than predicted (Fig. 3). Both species were not distributed in all the quadrats in which the models predicted their presence. However, this is not surprising because the spatial pattern of a tree species is the result of various biological processes. Aside from topography and soils, tree distributions are generally affected by many other factors, such as seed dispersal limitation, disturbance, seed predators, pathogens, herbivores and competition. The inconsistency of the model predictions with real distributions at small spatial scales suggests that the effects of topography and soil texture may be less important within their preferable habitats than across their habitats for determining the spatial patterns of the two *Dryobalanops* species.

Some mechanisms of habitat segregation have been reported for these two species. Water stress

can limit seedling establishment of *D. lanceolata* on dry sandy ridges in Lambir (Itoh 1995). One-year mortality of experimentally sown seeds of the two species differed between a valley and a ridge, probably because of the difference in tolerance of their seeds and seedlings to drought. In the valley, *D. lanceolata* had lower mortality than *D. aromatica*. In contrast, *D. lanceolata* showed much higher mortality on the ridge. Itoh (1995) suggested that *D. lanceolata* could not become established on sandy ridges because of the relatively dry conditions there. However, lack of *D. aromatica* in wet sites could not be explained by the experiment because mortality of its seeds and seedlings was also lower in the valley than on the ridge, although the difference was not as large as that in *D. lanceolata*.

Another possible mechanism is a difference in growth under different soil nutrient conditions (Lathman 1992; Burslem *et al.* 1995; Gunatilleke *et al.* 1997). Lathman (1992) showed that rank of seedling growth changed in various nutrient conditions for six sympatric tree species of a temperate forest and that, in general, they grew better on their native soil conditions. Palmiotto (1998) found that seedlings of *D. aromatica* grew better than *D. lanceolata* in less fertile soils, but worse in more fertile soils using nursery and field experiments. Although it is yet to be determined whether differences in seedling growth are so large as to prevent their regeneration outside their natural habitats, his study indicates that each species

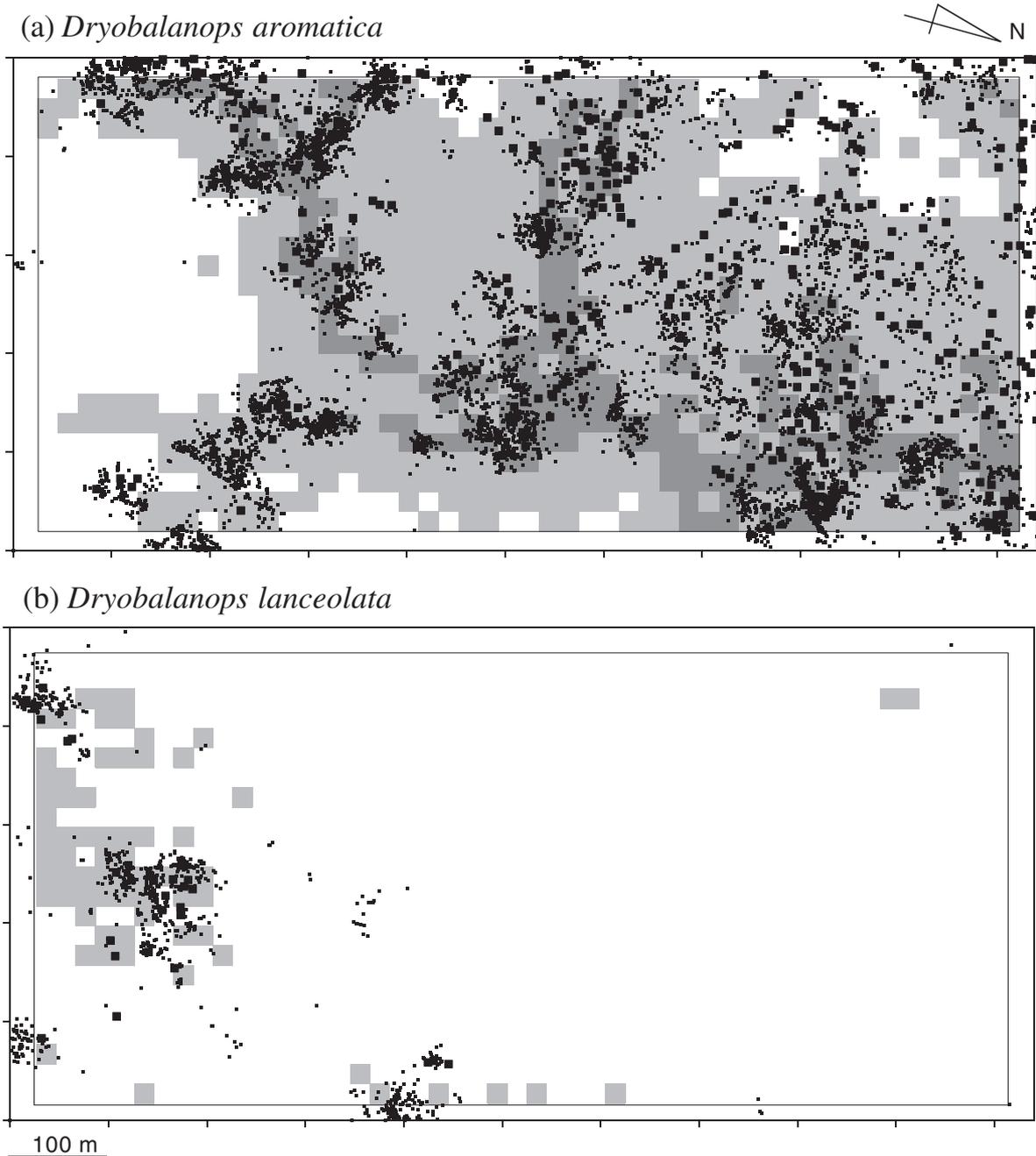


Fig. 3. Spatial distributions of (a) *Dryobalanops aromatica* and (b) *Dryobalanops lanceolata*. Square: d.b.h. ≥ 30 cm; dot: $1 \leq \text{d.b.h.} < 30$ cm. Predicted tree densities using Hayashi's models with topography and soil texture variables were also indicated for each $20 \text{ m} \times 20 \text{ m}$ quadrat (see text and Table 2 for details of the models). Quadrats adjacent to the margin of the plot were excluded from the calculations because values of index of convexity (IC) were unavailable (see text for the calculation of IC). White: tree density (n) ≤ 0 , light shade: $0 < n \leq 4$, dark shade: $n > 4$.

adapts better to the nutrient conditions of its natural habitat (Palmiotto 1998).

The relative importance of soil water conditions and nutrient availability in the habitat divergence

of the two *Dryobalanops* species is not clear because they are often correlated in Lambir (Hirai *et al.* 1997). Both topography and soil texture affect water conditions and nutrients simultaneously.

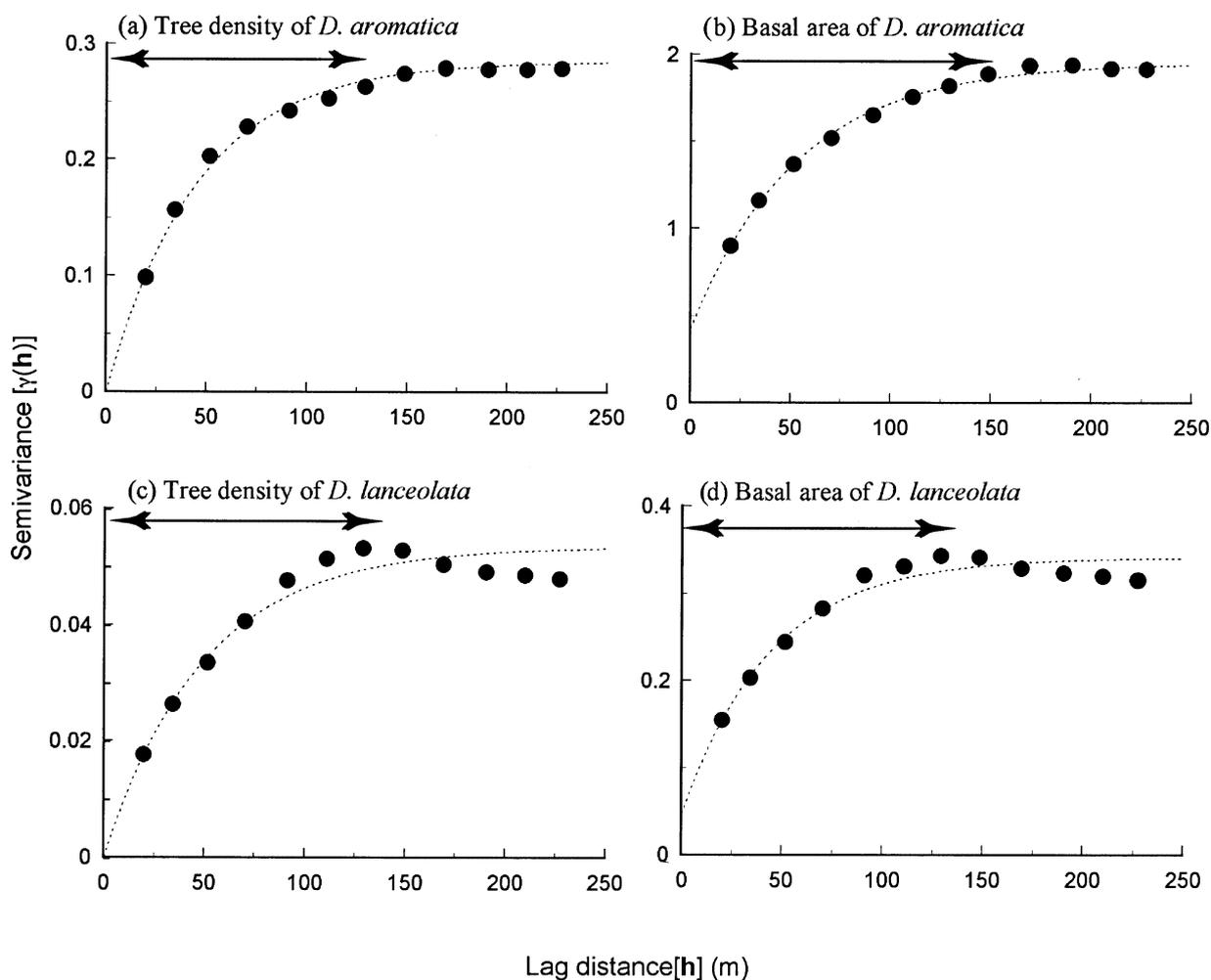


Fig. 4. Semivariograms of tree density and basal area of *Dryobalanops lanceolata* (c, d) and *Dryobalanops aromatica* (a, b). Dotted lines are exponential models fitted using a weighted least-squares method (see Table 1 for coefficients). The arrows indicate 'ranges' estimated by the exponential models. Sample sizes are 2523 for the shortest lag distance and 1676 for the longest distance.

Soils located at the base of mature *D. lanceolata* trees had higher amounts of exchangeable Ca, Mg and K and available P than soils under *D. aromatica* trees (Hirai *et al.* 1997). The water condition of the former soils was ever-wet and more stable over time than that of the latter. Whether nutrients or soil water conditions are more important as mechanisms determining the spatial patterns of *Dryobalanops* remains to be determined.

Although there have been many studies on habitat analysis on trees in tropical rainforests, few of these studies analyzed the degree of among-species differences in their habitats (but see Clark *et al.*

1999; Harms *et al.* 2001). Further studies including more species, especially sympatric congeners, are needed to generalize the importance of habitat divergence in species coexistence in tropical rainforests.

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Table 2 Tree numbers and basal areas (mean \pm se) of *Dryobalanops aromatica* and *Dryobalanops lanceolata* in different topography and soil texture classes

Topography/soil class	<i>n</i>	<i>D. aromatica</i>		<i>D. lanceolata</i>	
		Tree no.	Basal area [cm ² /0.04 ha]	Tree no.	Basal area [cm ² /0.04 ha]
Elevation (m)					
<160	289	137 (0.47)	8.6 \pm 3.1	821 (2.84)	15.4 \pm 3.8
160–175	215	704 (3.27)	30.2 \pm 5.7	88 (0.41)	0.8 \pm 0.5
175–190	267	2268 (8.49)	44.8 \pm 7.1	17 (0.06)	0.02 \pm 0.01
190–205	270	3852 (14.27)	63.1 \pm 7.4	27 (0.10)	0.05 \pm 0.04
>205	259	1529 (5.90)	83.7 \pm 9.3	1 (0.00)	0.01 \pm 0.00
χ^2/KW		2203	333.0	2505	237.5
<i>P</i>		0.003	<0.002	<0.002	<0.002
IC (m)					
<-3	194	772 (3.98)	15.7 \pm 3.6	152 (0.78)	3.1 \pm 1.4
-3 to 1	235	1075 (4.57)	30.0 \pm 5.8	196 (0.83)	5.8 \pm 2.8
-1 to 1	313	1659 (5.30)	43.2 \pm 6.2	300 (0.96)	4.4 \pm 1.9
1–3	178	1651 (9.28)	67.8 \pm 9.9	84 (0.47)	5.8 \pm 3.3
>3	230	2543 (11.10)	81.7 \pm 10.3	26 (0.11)	0.1 \pm 0.1
χ^2/KW		1309	101.6	160	5.8
<i>P</i>		<0.002	<0.002	0.52	0.64
Inclination (°)					
<12	291	1321 (4.54)	40.7 \pm 6.8	170 (0.58)	1.6 \pm 1.1
12–18	289	1179 (4.08)	42.7 \pm 5.6	337 (1.17)	6.6 \pm 2.5
18–24	253	1534 (6.06)	49.1 \pm 6.9	180 (0.71)	3.5 \pm 2.0
24–30	226	2091 (9.25)	57.3 \pm 9.2	171 (0.76)	5.5 \pm 2.6
>30	241	2365 (9.81)	42.0 \pm 6.7	96 (0.40)	0.7 \pm 0.4
χ^2/KW		1028	5.0	174	2.6
<i>P</i>		<0.002	<0.002	0.52	0.64
Soil texture class					
1	837	6485 (7.75)	55.1 \pm 4.1	179 (0.21)	1.2 \pm 0.6
2	181	957 (5.29)	37.2 \pm 8.4	210 (1.16)	5.5 \pm 2.5
3	117	769 (6.57)	29.5 \pm 6.9	113 (0.97)	5.0 \pm 4.0
4	140	279 (1.99)	14.5 \pm 5.4	452 (3.23)	14.5 \pm 5.0
χ^2/KW		495	77.2	1307	77.6
<i>P</i>		0.03	<0.002	0.01	<0.002

Numerals in parentheses in the tree number are mean densities per 20 m \times 20 m quadrat. Positive and negative values of the index of convexity (IC) indicate convex and concave slopes, respectively. Soil texture classes are relatively rich to poor in sand content in the order from 1 to 4. (*n*), number of squares in each topography/soil class. (χ^2), the chi-squared of tree number. (*KW*), the Kruskal–Wallis statistics of basal area. (*P*), significance level of random distribution in relation to topography/soil determined using a Monte-Carlo permutation test.

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Table 3 Standardized scores of topography and soil for the tree number and basal area of *Dryobalanops aromatica* and *Dryobalanops lanceolata* determined using Hayashi's quantification method

Topography/ soil class	<i>D. aromatica</i>		<i>D. lanceolata</i>	
	Tree no.	Basal area	Tree no.	Basal area
Elevation (m)				
<160	-0.39	-1.13	0.18	0.46
160-175	-0.13	-0.38	-0.03	-0.07
175-190	0.02	0.08	-0.05	-0.14
190-205	0.22	0.52	-0.05	-0.13
>205	0.24	0.78	-0.04	-0.12
<i>F</i>	69.8	81.6	45.9	45.5
<i>P</i>	<0.002	<0.002	0.003	0.002
IC (m)				
<-3	-0.05	-0.20	-	-
-3 to 1	-0.07	-0.21	-	-
-1 to 1	-0.05	-0.11	-	-
1-3	0.09	0.32	-	-
>3	0.11	0.29	-	-
<i>F</i>	7.4	9.1	-	-
<i>P</i>	0.006	0.002	-	-
Inclination (°)				
<12	-0.11	-	-	-
12-18	-0.06	-	-	-
18-24	0.02	-	-	-
24-30	0.07	-	-	-
>30	0.12	-	-	-
<i>F</i>	9.0	-	-	-
<i>P</i>	0.04	-	-	-
Soil texture class				
1	-	-	-0.02	-0.05
2	-	-	0.02	0.04
3	-	-	0.03	0.05
4	-	-	0.09	0.20
<i>F</i>	-	-	10.0	6.9
<i>P</i>	-	-	0.02	0.06
Intercept	0.52	1.48	0.06	0.16
<i>R</i> ² of the model	0.27	0.29	0.20	0.19
<i>F</i> of the model	35.2	58.6	41.9	39.1
<i>P</i> of the model	<0.002	<0.002	<0.002	<0.002

Scores were calculated for the models including significant variables only ($P < 0.1$), which were selected using a backward stepwise method based on a Monte-Carlo permutation test.

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