Journal of Biogeography (J. Biogeogr.) (2011) 38, 792–804

ORIGINAL ARTICLE

Dung beetle assemblages on tropical land-bridge islands: small island effect and vulnerable species

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ABSTRACT

Aim Using dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in a tropical land-bridge island system, we test for the small island effect (SIE) in the species–area relationship and evaluate its effects on species richness and community composition. We also examine the determinants of species richness across island size and investigate the traits of dung beetle species in relation to their local extinction vulnerability following forest fragmentation.

Location Lake Kenyir, a hydroelectric reservoir in north-eastern Peninsular Malaysia.

Methods We sampled dung beetles using human dung baited pitfall traps on 24 land-bridge islands and three mainland sites. We used regression tree analyses to test for the SIE, as well as species traits related to local rarity, as an indication of extinction vulnerability. We employed generalized linear models (GLMs) to examine determinants for species richness at different scales and compared the results with those from conventional linear and breakpoint regressions. Community analyses included non-metric multidimensional scaling, partial Mantel tests, nestedness analysis and abundance spectra.

Results Regression tree analysis revealed an area threshold at 35.8 ha indicating an SIE. Tree basal area was the most important predictor of species richness on small islands (<35.8 ha). Results from GLMs supported these findings, with isolation and edge index also being important for small islands. The SIE also manifested in patterns of dung beetle community composition where communities on small islands (<35.8 ha) departed from those on the mainland and larger islands, and were highly variable with no significant nestedness, probably as a result of unexpected species occurrences on several small islands. The communities exhibited a low degree of spatial autocorrelation, suggesting that dispersal limitation plays a part in structuring dung beetle assemblages. Species with lower baseline density and an inability to forage on the forest edge were found to be rarer among sites and hence more prone to local extinction.

Main conclusions We highlight the stochastic nature of dung beetle community composition on small islands and argue that this results in reduced ecosystem functionality. A better understanding of the minimum fragment size required for retaining functional ecological communities will be important for effective conservation management and the maintenance of tropical forest ecosystem stability.

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Keywords

Coleoptera, dispersal limitation, forest fragmentation, Peninsular Malaysia, rarity, regression tree, Scarabaeidae, species traits, species–area relationship, tree basal area.

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/j.1365-2699.2010.02439.x

INTRODUCTION

Anthropogenic habitat loss and associated fragmentation is the leading cause of terrestrial biodiversity loss (Brooks *et al.*, 2002; Reed, 2004; Brook *et al.*, 2008). Numerous studies have determined the effects of forest fragments on biotic communities embedded in a matrix of man-made landscape, e.g. agricultural land, plantations or even urban areas (Fahrig, 2003; Bickford *et al.*, 2010). The equilibrium theory of island biogeography (ETIB) has been the theoretical basis for habitat fragmentation studies where patches are treated as islands (Rosenzweig, 1995). However, unlike real islands, terrestrial habitat patches are not surrounded by a uniform matrix (e.g. water) but by mosaic habitats with variable degrees of hostility and permeability for different taxa (Ricketts, 2001; Revilla *et al.*, 2004). As a result, patterns in these studies cannot be extrapolated unless the effect of the matrix is taken into consideration (Prugh *et al.*, 2008; Umetsu *et al.*, 2008; Koh & Ghazoul, 2010). On the other hand, forested land-bridge archipelagos created by hydroelectric reservoirs may be the closest representation to the real island biogeography setting, providing highly valuable opportunities for the study of the effects of anthropogenic forest fragmentation on biodiversity (Diamond, 2001).

The species–area curve has frequently been used to describe the decrease in species richness in habitat fragments. The typical observed pattern is a species–area relationship (SAR) (Arrhenius, 1921; Gleason, 1922) based on the log–log model ($\log S = c + z \log A$, where S is the number of species, A is the area, c is the intercept and z is the slope) (Arrhenius, 1921). Due to near-ubiquitous support, the SAR has been referred to as one of nature's most general patterns (Lomolino, 2000). Despite its universal recognition, a potentially important feature of the SAR – the small island effect (SIE) – has been largely overlooked (Lomolino, 2000; Lomolino & Weiser, 2001). The SIE is the pattern where below a certain area, species richness may vary independently of island area. Higher richness in larger areas may have to do with factors that correlate with larger size, such as greater habitat heterogeneity and higher population levels, and thus lower extinction risks. These effects may disappear on small islands where population sizes are generally low, suggesting that stochastic events may play more significant roles than area (Lomolino & Weiser, 2001). In some cases certain habitat conditions such as those pertaining to soil maturity and moisture can only occur on islands above a certain size, posing a natural threshold on the species diversity an island may support (Niering, 1963). Based on a meta-analysis across diverse taxa and archipelagos, Lomolino & Weiser (2001) found support for SIEs in 73% of the 102 cases using breakpoint regressions based on the log–log SAR model. The upper limit of the SIE varies among different taxa and types of archipelagos, with a median value of around 40 ha (Lomolino & Weiser, 2001). However, there are still debates over the existence of the SIE (Burns *et al.*, 2009) and the appropriate methodology to identify it [e.g. path analysis (Triantis *et al.*, 2006) and multi-model comparison based on an information-theoretic approach (Dengler, 2010)]. With increasingly rapid anthropogenic habitat fragmentation, it is important to understand how this potential area threshold varies, in order to improve conservation management strategies.

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are key bioindicators and are important for ecosystem functioning. Most species utilize mammalian dung for food and breeding although some feed on other types of decomposing materials: carrion, rotting fruits or fungi. They have been shown to be sensitive to tropical forest modification and fragmentation (Halffter & Arellano, 2002; Davis *et al.*, 2004; Davis & Philips, 2005; Nichols *et al.*, 2007), and to changes in mammalian communities (Estrada *et al.*, 1999; Andresen & Laurance, 2007; Nichols *et al.*, 2009). They may also provide a cost-effective indicator group for tropical forest disturbances (Davis *et al.*, 2001; Gardner *et al.*, 2008). Results from dung beetle studies in fragmented tropical forests show that species richness is positively correlated with area (Klein, 1989; Andresen, 2003; Feer & Hingrat, 2005) and negatively correlated with isolation (Estrada *et al.*, 1999). However, few studies have examined the community shift of dung beetles in tropical forest fragments (Larsen *et al.*, 2005). Even fewer studies have looked at how geographical and environmental characters, together with species traits, influence dung beetle community structure in forest fragments (Larsen *et al.*, 2008). Both decreases in dung beetle diversity and changes in their community structure may have negative consequences on ecosystem functioning, including dung burial and nutrient recycling (Stokstad, 2004; Horgan, 2005; Slade *et al.*, 2007; Yamada *et al.*, 2007), secondary seed dispersal (Feer, 1999; Andresen, 2001, 2003; Bang *et al.*, 2005) and biological control (Bornemissza, 1970; Fincher, 1973; Gronvold *et al.*, 1992; Nichols *et al.*, 2008).

Here, by examining dung beetle assemblages in 24 land-bridge islands and three mainland control sites in the tropical forests of Peninsular Malaysia we ask the following questions. (1) Is there support for the SIE in the study archipelago? (2) What are the determinants of species richness on the islands? (3) Do patterns in community composition support the existence of an SIE? We hypothesize that on small islands, idiosyncratic processes not only render species richness independent of area but also cause community composition to be more variable (Levin, 1992; Leibold *et al.*, 2004). (4) What traits of dung beetles are correlated with species' rarity and hence vulnerability to local extinction in forest fragments? We hope that our results will be relevant for the management of biodiversity in Southeast Asian forest fragments, a region experiencing the highest deforestation in the tropics (Sodhi *et al.*, 2010).

MATERIALS AND METHODS

Study site

This research was conducted in Lake Kenyir, a hydroelectric reservoir in the state of Terengganu, north-eastern Peninsular

Malaysia (5°00′ N, 102°48′ E; 145 m a.s.l.) formed by the damming of the upper tributaries of the Terengganu River in 1986. The dam flooded 36,900 ha within the 260,000 ha catchment area of dense hilly forest. Over 340 land-bridge islands were formed from former hill tops, ranging in size from less than 1 ha to over 1000 ha. Most of them have steep banks and narrow littoral zones. Forests on the islands and surrounding mainland were selectively logged before the creation of the dam. The vegetation type in the area is tropical humid forests and consists mainly of lowland and mid-elevation dipterocarp forests. The region generally experiences heavy rain due to the north-east monsoon from November to March and a relatively hot and dry season from May to October, with annual precipitation varying between 2700 and 4000 mm (Furtado *et al.*, 1977).

Dung beetle sampling

Twenty-four islands ranging in size from less than 1 ha to 383.3 ha were selected for this study together with three mainland forest patches as baseline references (Fig. 1; see also Table S1 in Supporting Information). Fieldwork was conducted between June 2008 and October 2009. Each island/mainland site was surveyed at least twice (Table S1). Coprophagous (faeces-feeding) dung beetles were sampled using pitfall traps (200 mL plastic cups) buried in the ground and filled with *c.* 50 mL salt water and a small amount of detergent to reduce surface tension (Larsen & Forsyth, 2005). Approximately 15–20 g human dung was suspended above each trap, in plastic mesh, with a rain cover above. Human dung has been shown to be able to attract a great diversity of dung beetles species in rain forests, including those that feed on carrion and other resources (Howden & Nealis, 1975; Hanski, 1983), and is more effective than herbivorous dung (Doube & Wardhaugh, 1991). Traps were spaced to a minimum 50 m interval to achieve trap independence (Larsen & Forsyth, 2005) and left open for 48 h before the beetles were collected. For islands below 5 ha, three to five traps were set up during each sampling round. For larger islands and the mainland, two to six sampling locations were systematically chosen depending on forest area, and at each location three traps were set up during each sampling round (Table S1).

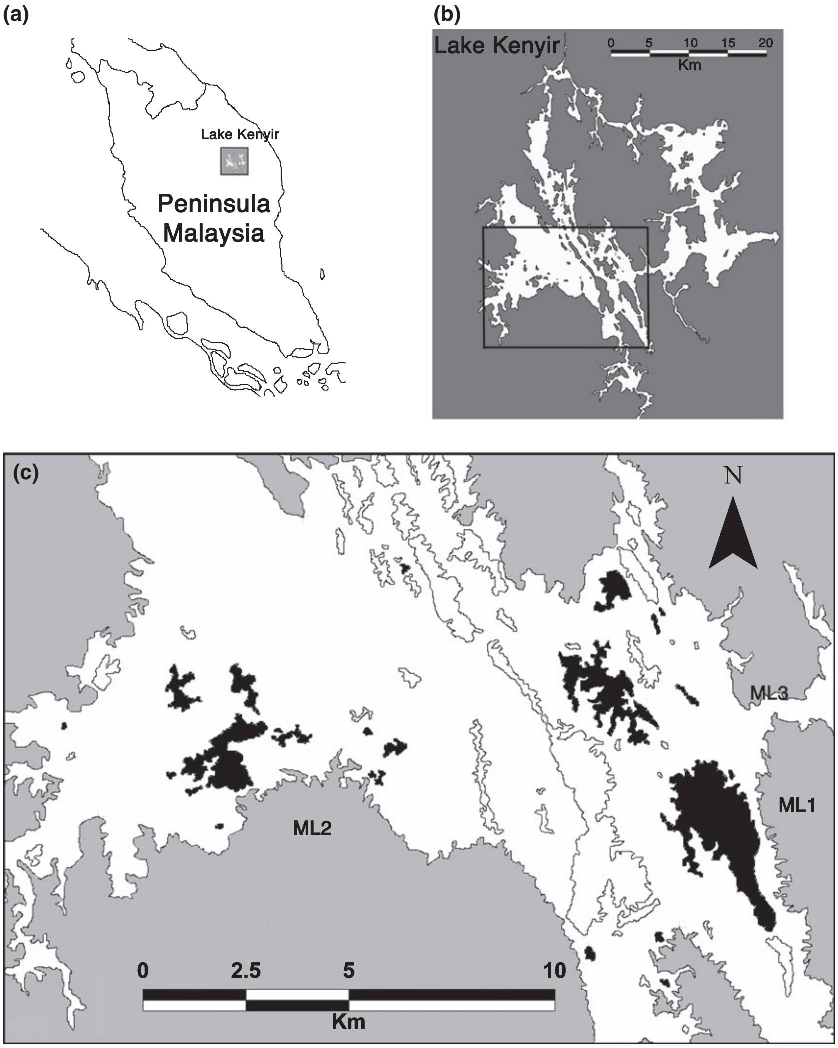

Figure 1 Map showing the relative position of Lake Kenyir within Peninsular Malaysia (a & b). In panel (c) study sites are highlighted in black: there are 24 islands and three mainland sites (ML).

Species traits

In total, six ecologically relevant species traits were obtained: body size, diet breadth, diel activity, guild, baseline density, and edge tolerance (see Appendix S1 and Table S2).

Geographical and environmental variables

To examine potential factors affecting dung beetle assemblages we measured four geographical variables [island area, isolation (distance from the nearest landmass >100 ha), edge index, geographical coordinates (UTM system)] and three environmental variables (basal area of woody species, leaf litter depth, and soil pH) (see Appendix S2).

Statistical analyses

All statistical analyses were conducted in the R environment (R Development Core Team, 2009) with specified packages unless otherwise noted. Two arboreal specialists, *Onthophagus deliensis* and *Onthophagus* sp. 1, were excluded from all analyses (except for the species sampling adequacy analysis) because they forage mostly above 5 m from the forest floor (Davis *et al.*, 1997) and pitfall traps on the ground will not accurately represent their populations (Davis & Sutton, 1998; Tregidgo *et al.*, 2010).

Species sampling adequacy

Sampling adequacy for all sites was evaluated using randomized (100x) sample-based species accumulation curves computed in EstimateS (version 8.0, R.K. Colwell, http://viceroy.eeb.uconn.edu/estimates) (Colwell & Coddington, 1994; curves not shown here). For each site, we examined both the asymptotic richness based on the Michaelis–Menten equation (Colwell & Coddington, 1994) as well as the final slope of the randomized species accumulation curve (Hortal *et al.*, 2004), that is, the gradient between the final two sampling points. The criteria we used for adequate sampling were observed species richness of no less than 80% of the asymptotic value or a final slope of the species accumulation curve of no higher than 0.2 species per sample.

Regression tree for island species richness and dung beetle local rarity

We used regression tree analysis to evaluate the effects of geographical and environmental variables on species richness in a hierarchical manner. Regression tree analysis uses dichotomous keys to recursively partition the data into mutually exclusive subsets that are increasingly homogeneous with respect to the defined groups, providing a tree-like model (McCune & Grace, 2002). As a nonparametric method, the regression tree is robust to many data issues such as nonlinear relationships and missing values, providing a useful tool to analyse complex ecological data (De'ath & Fabricius, 2000). It is therefore powerful in detecting any potential threshold in the effect of area on species richness. We assume that if an SIE exists, its upper limit will be the splitting factor at the top node in the tree, which represents the predictor that explains the largest deviance in the data, and subsequently area should be a predictor for islands above the threshold size but not for those below the threshold size. Mainland forests were not included in the regression analyses because of the difficulty in assigning areas to these forests. We used the $\log_{10}$-transformed species richness on 24 islands as the response variable and four potential predictors, including the three geographical variables of area, isolation, edge index, and one environmental variable of basal area. These were used to grow an overlarge tree with a minimum splitting group of size two and cost complexity measure of 0.0001. This was subsequently pruned to the optimum tree size (i.e. a tree size that minimizes the cost-complexity measure by snipping off the least important splits and hence reducing data overfitting and is within 1 SE of the minimum-error tree) through 10-fold cross-validations. We then regressed the log-species richness against the predicted values by this tree to generate an R^2 measure of model fit. We used the package *rpart* (Therneau & Atkinson, 2009).

To test the robustness of our regression model we used a random forest analysis, which combines the predictions of many independent models for a more-accurate classification (Breiman, 2001). We used the package *randomForest* (Liaw & Wiener, 2002) to generate 1000 trees and examined the relative importance of the candidate traits in predicting the species richness based on the overall accuracy of these models.

We also used the regression tree approach to identify the key traits of dung beetle species associated with their local rarity, measured as the proportion of sites where a species was not detected. We adopted a similar set of criteria as before in generating an optimum tree with rarity as the response and six traits (body size, diet breadth, diel activity, guild, baseline density and edge tolerance) as predictors.

Generalized linear models

To cross-examine the effects of the geographical and environmental variables on dung beetle species richness in a heuristic manner, we employed an information-theoretic approach (Burnham & Anderson, 2002). A set of generalized linear models (GLMs) with Gaussian error structure was assembled using all combinations of candidate predictors potentially important for dung beetle species richness: area, isolation, edge index and basal area (Table 1). The global model included all the predictors and the null model included none of the predictors. Species richness, area, isolation and edge index were $\log_{10}$-transformed to account for non-normality and to achieve equal variances in model residuals. The same model set was first evaluated for all islands (n = 24) and then for islands with sizes equal to and below the upper limit of the SIE. We compared and ranked models using Akaike's information criterion corrected for small sample size (AIC_c). ΔAIC_c denotes the difference in AIC_c from the model with the minimum AIC_c

Table 1 Best approximating generalized linear models of species richness of dung beetles for all islands (n = 24) and for islands ≤35.8 ha (n = 19) in Lake Kenyir, Peninsular Malaysia. Global model: log(richness) ~ log(area) + log(distance) + basal + log(edge index) with Gaussian error structure.

Model description	K	AIC_c	ΔAIC_c	$wAIC_c$	%DE
All islands (n = 24)					
~ area + basal	4	7.654	0	0.265	36.0
~ area	3	7.858	0.205	0.239	27.2
~ area + distance	4	8.605	0.952	0.165	33.5
~ area + basal + distance	5	9.923	2.269	0.085	38.6
Islands < = 35.8 ha (n = 19)					
~ basal	3	6.077	0	0.171	14.9
~ distance	3	6.203	0.126	0.161	14.3
~ 1	2	6.307	0.230	0.153	0
~ basal + edge	4	6.65	0.573	0.129	26.1
~ edge	3	7.619	1.542	0.079	7.7
~ basal + distance	4	7.983	1.906	0.066	20.8

Area, island area; distance, distance from the nearest large landmass (>100 ha); basal, basal area estimate for woody species; edge, edge index (ratio between perimeter of island and perimeter of a circle with the same area, to assess the influence of edge); K, number of model parameters; AIC_c, Akaike's information criterion corrected for small sample size; ΔAIC_c, difference between AIC_c of the top-ranked and current model; $wAIC_c$, AIC_c weight; %DE, percentage deviance explained by the model.

and models with $\Delta AIC_c \leq 2$ are considered to have substantial support. AIC_c weights ($wAIC_c$) provided relative weight of any particular model, which varied from 0 (no support) to 1 (complete support) relative to the entire model set (Burnham & Anderson, 2002). Model fit was assessed using percentage deviance explained (%DE).

SAR curves

To provide comparison with conventional approach to the SIE, three regression models were fitted to the $\log_{10}$-species richness and $\log_{10}$-area data for 24 islands surveyed – the simple linear regression, hockey stick regression and piecewise linear regression. The simple linear regression model represents the classic log–log model of SAR, implemented using the lm() function. If an SIE exists, it should be represented by a breakpoint in the linear relationship and the latter two regression models tested this. The hockey stick regression consists of two segments, a flat line (slope equals zero) joined by a non-zero-slope regression line at the break point (Lomolino & Weiser, 2001). This was implemented using the thresholddose081117() function developed by Lutz & Lutz (2009). The piecewise regression consists of two linear regression lines joined together at the break point (Gentile & Argano, 2005, equation 3), and was implemented using the piecewise.linear() function in the package *SiZer* (Sonderegger, 2008). The significance of the break points was evaluated by their 95% confidence intervals (CIs) in the latter two regressions. We compared model parsimony using AIC_c (Burnham & Anderson, 2002).

Community analyses

The variation in dung beetle community composition among the 24 islands and three mainland sites was visualized using non-metric multidimensional scaling (NMDS) based on the Bray–Curtis distance metric with a two-dimensional solution, as well as using the abundance spectra (Mac Nally, 2007). We used the nested NODF metric (Almeida-Neto *et al.*, 2008) to examine the nestedness of the metacommunity. To test for spatial autocorrelation in dung beetle community composition among sites, we conducted a partial Mantel test. Details of these analyses are presented in Appendix S3.

RESULTS

General sampling results

Across all 27 sites, we collected 49 dung beetle species representing 11 genera totalling 7121 individuals from pitfall traps baited with human dung (Tables S1 & S2). The Michaelis–Menten estimator indicated that between 82.4% and 93.6% species were sampled for sites with at least 10 individuals caught per trap. However, for 14 islands (0.54–32.4 ha) with beetle density lower than that, the use of this parametric estimator appeared to be problematic, producing zero richness estimates on three of these islands and spurious estimates on others (Table S1, in bold). For these low-density islands we based our judgement of sampling adequacy on the final slopes of the species accumulation curves, all of which were within the plateauing range of 0–0.2 species per trap and significantly lower than those of high-density sites ($P < 0.01$). The numbers of traps set on these low-density islands were also relatively high (Table S1). Taken together, we are confident that all sites were adequately sampled.

Traps baited with fish caught 151 individuals belonging to 18 coprophagous species. However, traps baited with banana did not catch any coprophagous dung beetles. Therefore the diet breadth of all species was either 1 (dung only), or 2 (dung and carrion) (Table S2).

Regression tree for island species richness supported a breakpoint in area

Only island area and basal area of trees were selected in the optimal tree model and they explained 76% of the variation in the data (Fig. 2). An island size of 35.8 ha was the splitting factor at the first node, representing a potential SIE threshold (i.e. a breakpoint). According to this model, five islands above this size have a mean species richness of 14 (first terminal node from the right; Fig. 2). For islands below this size threshold, species richness is best explained by tree basal area. Sixteen islands with mean basal area less than 30.4 m^2 ha^{-1} have on average 4.8 species (first terminal node from the left; Fig. 2),

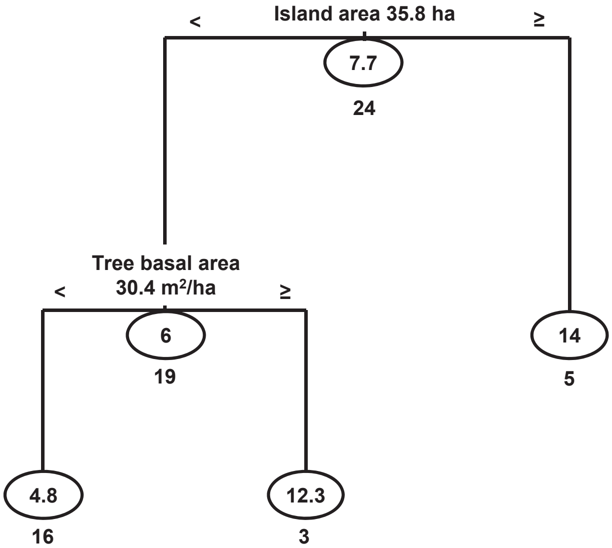

Figure 2 Optimum regression tree for predicting dung beetle species richness on 24 islands in Lake Kenyir, Peninsular Malaysia. Variables tested were island area, isolation, edge index and tree basal area. See Appendix S2 for details of these variables.

whereas three islands with basal area above 30.4 m^2 ha^{-1} have on average 12.3 species (second terminal node from the left; Fig. 2). The variable importance ranking generated by the random forest also showed that island area was the most important predictor according to the percentage increase in the mean square errors (68.4%) followed by basal area (21.3%).

Generalized linear models for dung beetle species richness

We tested GLMs on species richness for the all islands ($n = 24$) and for islands below the 35.8 ha breakpoint suggested by the regression tree analysis ($n = 19$). For all islands area was most important in determining species richness; basal area and isolation were also present in the top three models (Table 1). Together these three predictors explained 38.6% of the total deviance in the data (fourth ranked model). For islands below 35.8 ha area, the top ranked model has only basal area as the predictor, explaining 14.9% of the deviance, which supports the regression tree result (Fig. 2). Two other factors, distance and edge, were also included in the competing models, explaining 14.3% and 7.7% of the deviance, respectively, as single predictors. This suggests relatively important roles of isolation and island edge in explaining species richness on these small islands. Island area did not appear in any top ranked models. The null model closely followed the two best approximating models and all other top ranked models ($\Delta AIC_c < 2$) explained 7.7–26% of the deviance in the data, suggesting an increased stochasticity on islands below 35.8 ha.

Non-significant breakpoint in the species–area relationship

The hockey stick and piecewise linear regression estimated a breakpoint at 21.6 ha (upper and lower 95% CI = 0 and 383.2 ha) and 32.4 ha (upper and lower 95% CI = 1.5 and 129.7 ha), respectively (Fig. 3). Given the large range of the CIs with the lower limits close to zero, neither of the breakpoint estimates is considered significant in an ecologically meaningful sense. Based on model AIC_c, the simple linear model (slope $z = 0.19$) was still the most parsimonious model although both breakpoint regression models have marginally higher R^2 values (Fig. 3).

Dung beetle community composition

While mainland forests and large islands resembled each other in dung beetle community composition, most islands

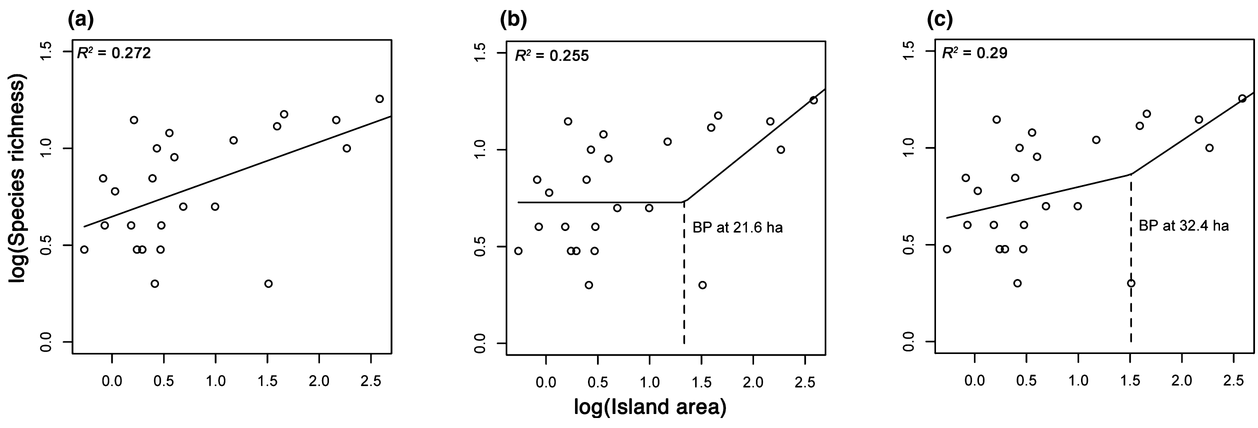

Figure 3 Modelling the species–area relationship for dung beetles across 24 islands in Lake Kenyir, Peninsular Malaysia, with three regression models. The most parsimonious model was a simple linear model (a): $K = 3$, $AIC_c = -62.2$, $\Delta AIC_c = 0$, $wAIC_c = 0.822$; the second ranked model was the hockey stick regression (b): $K = 4$, $AIC_c = -58.5$, $\Delta AIC_c = 3.61$, $wAIC_c = 0.135$; the third ranked model was the piecewise linear regression (c): $K = 5$, $AIC_c = -56.2$, $\Delta AIC_c = 5.90$, $wAIC_c = 0.043$. Breakpoints (BP) and R^2 values are shown on the plots. K, number of model parameters; AIC_c, Akaike's information criterion corrected for small sample size; ΔAIC_c, difference between AIC_c of the top-ranked and current model; $wAIC_c$, AIC_c weight.

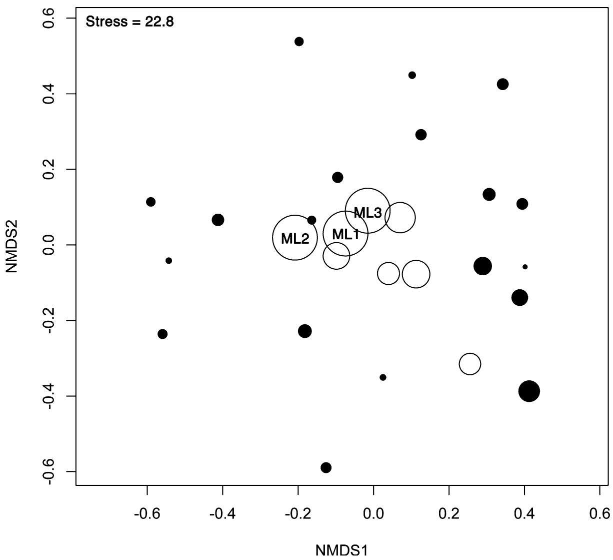

Figure 4 The two-dimensional solution of non-metric multidimensional scaling (NMDS) of dung beetle assemblages at all 27 island and mainland sites in Lake Kenyir, Peninsular Malaysia. The size of the circles represents the size of the site rescaled for visualization. The largest circles represent mainland sites (ML). Dark circles represent islands below 35.8 ha, the small island effect (SIE) threshold estimated from the regression tree analysis. Stress is a measure of the mismatch between the Bray–Curtis distance between communities and the distance in ordination space of the optimal solution.

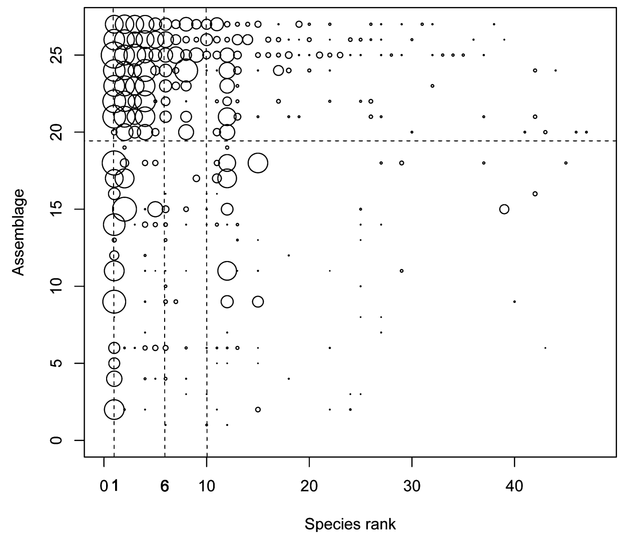

Figure 5 Abundance spectra of dung beetle assemblages at all 27 sites in Lake Kenyir, Peninsular Malaysia. The top three rows are mainland sites, followed by islands in descending order of area. The horizontal dotted line delimits the 35.8 ha threshold. The *x*-axis shows species ranked by their baseline abundance. Species highlighted by vertical dotted lines are rank 1: *Paragymnopleurus maurus*; rank 6: *Copris doriae*; and rank 10: *Catharsius molossus*. The size of the circle represents the local abundance of the species rescaled for visualization.

below 35.8 ha differed largely from the mainland communities as well as from each other, forming a 'dust cloud' around the centre of the ordination chart (Fig. 4; NMDS stress = 22.8). The two small islands located near the centre of the NMDS chart are geographically very close to the site Mainland 2 (Table S1; Islands 11 and 19, which were connected by a narrow land bridge when water level of the lake was extremely low). An orderly area-related nested pattern was not found among the dung beetle metacommunity (NODF = 58.3, $P = 0.64$). Using the abundance spectra, those species occurrences that departed from a perfectly nested pattern can be visualized as isolated points on the lower right of the panel (Fig. 5). The changes in species relative abundance from the mainland sites to the small islands were also shown in this figure. A partial Mantel test showed a marginally significant but low degree of spatial autocorrelation in dung beetle community composition among sites ($P < 0.05$, $r = 0.12$) after accounting for other environmental variables.

Regression tree for dung beetle local rarity

The optimum tree identified three traits important in affecting species local rarity – baseline density, edge tolerance and diet breadth (Fig. 6) – explaining 81.4% of the variance in the data. The results from the random forest confirmed the reliability of this tree model. In particular, the most important traits ranked by the percentage increase in mean square errors are as follows: baseline density (46.0%), edge tolerance (11.5%) and diet breadth (5.6%). According to the optimum tree model, the mean proportion of islands in Lake Kenyir where a species was absent varies between 37.7% and 94.0%. For instance, 20 out of 47 species that are naturally uncommon (with <0.035 individuals per trap in mainland forests) are estimated to be absent on 94.0% of the islands (the first terminal node from the right; Fig. 6). Conversely, six species that are most common (with ≥0.374 individuals per trap in mainland forests), able to forage on the forest edge and feed on both dung and carrion, have the highest occurrences among islands (absent from 37.7% of the islands; the first terminal node from the left; Fig. 6).

DISCUSSION

Overall, our results show that for islands below 35.8 ha at Lake Kenyir, species richness and community composition were driven by a small island effect, rather than by a direct relationship with area. This was supported by the regression tree analysis and GLMs. In comparison, the breakpoints in the SAR estimated by conventional regressions did not have enough statistical support (Fig. 3). The regression tree analysis and GLMs were of more heuristic value as they took into consideration the effects of other geographical and environmental variables on island species richness. Regression tree analysis also did not assume an overall linear relationship

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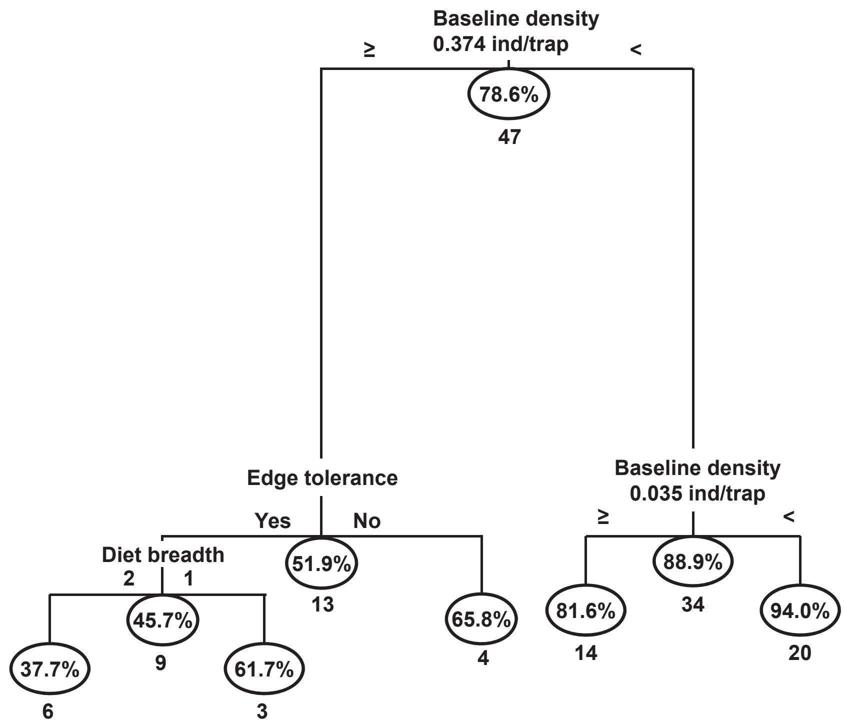

Figure 6 Optimum regression tree for predicting the vulnerability of dung beetles to local extinction in Lake Kenyir, Peninsular Malaysia. Species traits tested were baseline density (as in mainland forests), edge tolerance, diet breadth, diel activity, body size and guild. See Appendix S1 for details of the species traits.

between the predictors and the response, therefore providing a more flexible and powerful tool for investigating ecological relationships (De'ath & Fabricius, 2000). The breakpoint linear regressions did not appear to be well supported, probably due to the small sample size of large islands (only five islands above 35.8 ha were available). Although the hockey stick and piecewise regression models explained more variation in the data, they had additionally one and two parameters, respectively (Fig. 3), which made them less parsimonious. For these reasons, we interpret our results according to the regression tree analysis and GLMs.

Our estimated upper limit of the SIE is at 35.8 ha, lower than the 100 ha estimated by Lomolino & Weiser (2001) using a scarab beetle data set from the Florida Keys, a marine and thus more isolated archipelago, which included much larger islands ($63–1.6 \times 10^7$ ha, Peck & Howden, 1985). Although we note that the method they used has received some criticism (Burns *et al.*, 2009), Lomolino & Weiser (2001) suggested that the upper limits of SIEs should be higher for biotas of more isolated archipelagos than those of lakes and rivers, because the former typically have infrequent immigration as well as lower extinction rates. Compared to other fragmentation studies (Fig. 3 in Lomolino & Weiser, 2001) we sampled a notably higher proportion of islands that fell within the range of the SIE, which enabled us to gain more insights to this understudied ecological pattern. The overall slope of the SAR ($z = 0.19$) was much lower than for true oceanic archipelagos ($z = 0.35$) and close to that for continental habitat islands ($z = 0.22$) (MacArthur & Wilson, 1967), which may have valuable implications for understanding real world habitat fragmentation (Laurance, 2008; Koh & Ghazoul, 2010).

The observed ecological patterns are likely to be caused by multiple underlying mechanisms that operate at different scales (Levin, 1992; Leibold *et al.*, 2004). In Lake Kenyir, area was the primary underlying driver of species richness across the entire range of island sizes under study (0.5–383.3 ha). However, its role in determining species richness diminished in comparison with other geographical and environmental characteristics on small islands. We show that below 35.8 ha, area becomes unimportant and tree basal area has the strongest positive effect on species richness; isolation and the relative amount of forest edge are also important. This pattern is consistent with the explanation that below the upper limit of the SIE species richness is largely related to the inter-island differences in habitat and resource availability characteristics (Lomolino & Weiser, 2001). The topography of Lake Kenyir is irregular and the position of an island and its exposure to different climatic conditions or other environmental forces are potentially relevant but difficult to quantify. We are also unable to assess the availability of mammalian dung on these small islands because most of the mammals are non-resident and opportunistic visitors. Sights and signs of the Asian elephant (*Elephas maximus*), wild boar (*Sus scrofa*) and primates have been recorded on most of these islands (L. Qie, pers. obs.) but these mammals can cross water barriers. The types of food resource on an island can influence the type and visitation rate of mammals, for which we are unable to give an unbiased measure. These and other stochastic events may jointly influence the dung beetle diversity on small islands and contribute to the observed large amount of unexplained deviance in the GLMs (Table 1).

The community composition on islands below 35.8 ha noticeably departed from that of the mainland sites and larger islands, but instead of forming a separate cluster they radiated from the original community in all directions in the NMDS graph (Fig. 4). This confirmed our prediction that if idiosyncratic island characteristics override area effects, the resulting community composition would be more variable. A significant nested pattern was missing in this archipelago. The nested NODF metric has been shown to be relatively sensitive to rare species on poor islands (Santos *et al.*, 2010). A number of such incidences were observed where on some small and poor islands there were still 'surprise' species (Fig. 5). Furthermore, highly variable community composition on small islands has also been observed in birds (Terborgh *et al.*, 1997; Lees & Peres, 2006). We argue that the SIE not only manifests itself in terms of species richness, but also in terms of community composition.

We used local rarity of dung beetle species to estimate their vulnerability to local extinction. Because sampling effort on these islands was adequate, the probability of pseudo-absences confounding our results is low. Our regression tree model on the local rarity of 47 dung beetle species show that common species and species that are able to forage at the forest edge have higher occurrences and hence are less prone to extinction. This is consistent with the conclusion of Larsen *et al.* (2008) in a similar system in Venezuela. However, body size is not as important in explaining rarity as opposed to their finding, where large-bodied dung beetles were more prone to extinction. In particular, two of the most widespread species, *Paragymnopleurus maurus* and *Copris doriae* (rank 1 and 6 in Fig. 5), are also among the larger species (Table S2), and the largest species, *Catharsius molossus*, was present in some of the most depauperate islands (rank 10 in Fig. 5). We also show that species that feed on both dung and carrion have higher occurrences on islands and hence are more resilient to local extinction (Fig. 6). This is not surprising because mammalian dung is probably an ephemeral resource, especially on most of the small islands that lack resident mammals. Dung beetle species that can utilize other decomposing materials such as carrion will improve their chances of persistence.

An interesting finding in our study is the spatial autocorrelation of the community composition among the study sites. There may be two reasons for this pattern. First, the landscape consisted of numerous mountain ridges oriented from north-west to south-east, which were partially submerged after the area was flooded (Fig. 1). These may have acted as terrestrial barriers to dung beetle dispersals before the hydroelectric dam was built, causing species distribution to be more dissimilar along the longitudinal gradient. Therefore, the observed spatial autocorrelation may partially reflect the historical regional distribution of dung beetles. However, the lack of pre-fragmentation data prevented us from verifying this hypothesis. Second, and more importantly, this spatial autocorrelation suggests dispersal limitation of dung beetles after the former hill tops became islands. Dung beetles living in the rain forest foraging close to the forest floor may not be adapted to navigate outside the forest or across large expanse of open water (Stokstad, 2004). Exceptions may be the canopy specialists (Davis *et al.*, 1997; Davis & Sutton, 1998), which are excluded from our data analyses here. Experimental evidence showed that variation in flight ability of tropical forest birds correlated strongly with the species distributions on lake islands in Panama (Moore *et al.*, 2008). Dispersal was also shown to be a key in structuring ground beetle communities on lake islands in northern Poland (Zalewski & Ulrich, 2006). Unfortunately, the relative flight abilities of different dung beetle species are poorly known. It is suggested that there are two forage-flight patterns in dung beetles: large-bodied dung beetles tend to fly rapidly and continuously for long distance, while small-bodied species perch on leaves and fly occasionally for short distances (Larsen *et al.*, 2008). The question here is, however, not only whether the dung beetles can, but also whether they will, fly across open water between the islands. Using floating pitfall traps, we found that dung beetle captures declined significantly and sharply from exposed soil bank to water (L. Qie, unpublished data). Dung beetles are shown to be able to utilize polarized light for navigation (Dacke *et al.*, 2003, 2004). It is possible therefore that they can use the polarized light from the water surface to avoid water and hence limit their dispersal.

In addition, less isolated islands harbour more species in our study (Table 1), which provides indirect evidence for differences in the dispersal ability among dung beetle species. Hence, source–sink dynamics may exist between neighbouring sites for species that do cross the water barrier, and this may explain why some rare species are found on some of the species-poor islands. Many common species were also in much lower densities on the smaller islands (rank 2 to 11 in Fig. 5) with some having notable temporal fluctuations (L. Qie, unpublished data), hence we postulate that some of these populations are in fact being maintained by immigrations from mainland or large islands located nearby. If this is the case, the source–sink dynamics may have lowered the SIE threshold below that expected if all islands had closed populations. Furthermore, these islands have been isolated for 24 years and the faunal relaxation on some islands may still be ongoing. Although it is still uncertain how long the process of relaxation will take and it may vary among taxa, the species richness decay of tropical forest birds was estimated to have an *c.* 50-year half-life (Brooks *et al.*, 1999). It is possible that our study merely captured a snapshot of the dung beetle communities in this lake archipelago and given time, many extant species of dung beetles on the islands may go locally extinct, resulting in a different species–area relationship altogether (Triantis *et al.*, 2010).

In conclusion, our study sheds light on the small island effects on dung beetle richness and communities. Along with our understanding of correlates of local rarity, we show that common species and those able to forage on the forest edge have a higher chance of survival on small islands. Species richness and community composition on islands below 35.8 ha in area clearly exhibited increased variability. Dung beetle assemblage on any such island is probably a random selection from the pool of resilient species, thus representing a community greatly shifted from the intact one on mainland sites. This compositional shift also affects the functional role of the dung beetle group, which results in a decreased level of ecosystem functioning, such as dung removal and secondary seed dispersal (Slade *et al.*, 2007; Nichols *et al.*, 2008; L. Qie, unpublished data). Because these small islands are more susceptible to stochastic events, their communities can be drastically altered over time and species already in low abundance (Table S1) are likely to face an elevated risk of local extinction. Therefore, to fully understand the importance of community dynamics in small fragments, more long-term monitoring programmes are urgently needed, e.g. those at Barro Colorado Island, Panama (Robinson, 1999), and the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon (Ferraz *et al.*, 2007). Such projects should also address long-term fragmentation effects on functionally important groups, such as dung beetles. Our results also add to the ongoing debate on the conservation values of small habitat fragments. We highlight the need to understand minimum fragment size, capable of retaining predictable and functional ecological communities, for effective conservation management and maintenance of tropical forest ecosystem stability.

ACKNOWLEDGEMENTS

We thank the Economic Planning Unit (Malaysia) for permission to conduct this study. We thank Johannes Huijbregts from the National Museum of Natural History Naturalis, Leiden, The Netherlands for his indispensable help in species identification. We further thank L.P. Koh, K.S.H. Peh, J.S.H. Lee, A. Campos-Arceiz, T. Wanger, D. Bickford and especially S. Howard for comments on earlier drafts of the manuscript. This study was supported by the National University of Singapore (Grant no. R-154-000-331-112).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Definition and measurement of dung beetle species traits.

Appendix S2 Geographical and environmental variables measured for Lake Kenyir sites.

Appendix S3 Details of statistical procedures for community analyses.

Table S1 Summary of geographical and environmental variables, and species accumulation for all study sites.

Table S2 Lake Kenyir dung beetle species list, with associated ecological traits.

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BIOSKETCH

Lan Qie conducted this study as part of her PhD at the National University of Singapore. Coming from an engineering background, she is interested in arthropod ecology, particularly relating to questions at the population, community and ecosystem level.

Author contributions: L.Q., N.S.S. and S.L.H.L. conceived the idea for this study; L.Q. collected the data; L.Q. and T.M.L. analysed the data; L.Q. led the writing. All authors read and approved the final manuscript.

Editor: Kostas Triantis