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The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems

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Abstract. We examine the effect of selective timber extraction, and corresponding forest canopy loss, on arboreal dung beetles in the tropical rainforests of Sabah, Malaysian Borneo. Changes in vertical distribution of beetles are measured through differences in the abundance of beetles in ground-based pitfall traps in primary, logged and plantation forest. Previous research has demonstrated that arboreal dung beetles are not generally collected in pitfall traps in primary forest, but are present in large numbers above the ground in canopy vegetation: the presence of arboreal beetles in pitfalls in areas of reduced or modified canopy cover may therefore reflect a response to the absence or modification of their usual habitat, and the proliferation of these beetles nearer to the ground. In this paper, statistically significant differences are found in the abundance of beetles in ground pitfall traps from logged forest compared to primary forest. Results show that virtually no arboreal dung beetles are recorded in primary forest traps, with an increased abundance of arboreal dung beetles in traps from logged and plantation forest, with 1.72% of the total number of arboreal beetles recorded from primary forest, 22.32% from logged forest, and 75.96% from plantation forest. The presence of arboreal dung beetles in plantations demonstrates that arboreal dung beetles can survive outside their normal habitat, and we relate these observations to adaptations to upper rainforest canopy conditions, and proliferation of these microclimatic conditions in man-made habitats. Results are also discussed in terms of their relevance to the measurement of species richness and diversity in logged and other derived ecosystems, where mixing of the ground-based and arboreal faunas occurs.

Key words. Arthropods, rainforest canopy, diversity, dung beetles, selective logging, species richness.

INTRODUCTION

Ecosystem disruption through human activity is judged to pose a major threat to the long term prospects of biodiversity conservation (Whitmore & Sayer, 1992; Myers, 1989). As insects form a significant proportion of global species diversity (May, 1988; Kim, 1993; Stork, 1993), the future of the Earth's biological reserves is very much tied up with the conservation of insect diversity (Sutton & Collins, 1991; Samways, 1993). The importance of the canopy in terms of contributing to the super-diverse faunas found in tropical rainforest, most notably within arthropod groups, is undeniable (e.g. Erwin, 1988; Stork, 1988, 1991; Sutton, 1989; Wilson, 1992). However, few studies have looked at the effects of human anthropogenic disturbance on insect communities in tropical forests (Brown Jr, 1991; Holloway, Kirk-Spriggs & Chey Vun Khen, 1992; Johns, 1992), and virtually nothing is known about the effects of disturbance on arthropod canopy communities in tropical forests. To date, there have been no published reports on the effects of disturbance on arboreal (or canopy) dwelling arthropods in tropical rainforests.

In recent years, particular insect groups have become widely used to show differences between different habitat types (Brown Jr, 1991; Holloway & Stork, 1991; Sutton & Collins, 1991), and to examine the effects of environmental disturbance (e.g. Klein, 1989). Dung beetles are one such useful 'indicator' group, as they tend to illustrate structural differences between habitat types, uncomplicated by phenological differences. The local distribution of dung beetles is known to be strongly influenced by vegetation cover and soil type (Doube, 1983; Nealis, 1977; Janzen, 1983), and the physical structure of the forest appears to be an important determining factor in the structure and distribution of dung beetle communities (Davis, 1993). Dung beetles have been used in several studies to investigate the effects of environmental change on forest diversity and structure (Howden & Nealis, 1975; Nummelin & Hanski, 1989; Klein, 1989; Favila & Halffter, 1992; Halffter & Favila, 1993; Kremen *et al*., 1993; Davis, 1993).

Recent studies have shown that a guild of arboreal dung beetles, found only metres above the forest floor up to the high forest canopy, exists in the lowland tropical forests of Borneo (Davis *et al*., 1997). These arboreal beetles are distinct from the ground-based fauna, and have specific morphological and behavioural adaptations that allow them to be truly arboreal in habit (Davis *et al*., 1997). They are abundant in dung baited traps suspended from trees. Work in Sabah, Malaysian Borneo, showed that these beetles are sometimes collected in ground-based dung baited pitfall traps (Davis, 1993). In this paper we examine for the first time the effects of forest disturbance on the canopy fauna by examining the response of South-east Asian arboreal dung beetles to changes in forest structure through selective logging and conversion to plantation forest. The abundance of arboreal beetles at different heights is not examined specifically, as this has been recorded elsewhere from primary forest at Danum Valley (Davis *et al*., 1997), and changes in vertical stratification measured solely by changes in the abundance of arboreal beetles in ground-based pitfall traps. Comparisons made in this paper are between relative numbers of arboreal dung beetles at ground level and height in primary forest (Davis *et al*., 1997) and numbers collected at ground level in derived ecosystems (logged and plantation forest: this paper). Collections from primary forest at Danum Valley have demonstrated that in traps set at ground level and at 5 m intervals above the forest floor, the arboreal guild of dung beetles shows greatest abundance at 5 m but remains abundant in traps placed up to 20 m: relatively few individuals occur at heights above 25–40 m, and the guild is virtually absent from ground-level traps (Davis *et al*., 1997). The almost complete absence of the arboreal guild from ground-based pitfalls in primary forest, but general abundance at 5 m, is further demonstrated by collections made from two traps in primary forest (Davis, 1993), sampled on five separate occasions over an 18-month period: one at ground level and one at 5 m (the arboreal trap being directly situated above the ground-based trap). A total of 667 arboreal beetles were collected in the trap at 5 m (average = 133.4 beetles per trap, $\pm$SE 42.3), whereas only one specimen of the arboreal guild was collected at ground-level (from a total of 1260 dung beetles).

Although arboreal dung beetle abundance varies both temporally and spatially (Davis *et al*., 1997), and numbers of beetles collected varies between site and over time, the strong dichotomy between ground-based traps and those at 5 m and above in primary forest sites suggests that any change in the numbers of arboreal beetles in ground-based pitfalls may be indicative of a change in the vertical distribution of this guild. Results presented in this paper are taken from traps positioned in primary, logged and plantation forest. The null hypothesis proposed here is that there should be no significant difference in the numbers of arboreal beetles collected in pitfall traps from primary, logged and plantation forest.

METHODS

The study was undertaken at the Danum Valley Field Centre, which lies on the eastern edge of the Danum Valley Conservation Area (4° 58′ N, 117° 48′ E): a 438 km^2 area of primary forest within the Ulu Segama Reserve in South-eastern Sabah (north-east Borneo). Much of the Conservation Area is lowland (<760 m), evergreen dipterocarp forest, where dipterocarps make up approximately 88% of the total volume of large trees (Newbery *et al*., 1992). Forest within the Ulu Segama Reserve, which surrounds the Danum Valley Conservation Area, contains logged forest coupes of different ages, and exotic tree plantations within the logged forest mosaic (Marsh & Greer, 1992). Logged forest has a reduced high forest (or 'upper') canopy compared to primary forest due to the extraction of mature hard-wood trees, and plantation forest lacks

Table 1. Number of pitfalls used on each transect, and description of each transect site.

Transect	Trapping effort*	Description of transect
Riverine A	33	Primary forest adjacent to large river.
Riverine B	35	Primary forest adjacent to large river.
Primary A	25	Primary forest site in DVCA†.
Primary B	40	Primary forest site in DVCA.
Primary C	30	Primary forest site in DVCA.
Logged A	44	Forest site logged in 1988.
Logged B	44	Forest site logged in 1989.
Logged C	10	Forest site logged in 1981.
Logged D	29	Forest site logged in 1981.
Plantation A	27	Adjacent *Acacia* and mahogany plantations.
Plantation B	30	Cocoa plantation with *Albizia* shade cover.

*Number of pitfall traps per transect.
†Danum Valley Conservation Area.

entirely a high forest canopy, being composed instead of low canopy cover of approximately uniform height (generally 10–15 m above ground).

Collections of dung beetles were made between May 1990 and May 1992, as part of an extensive sampling programme (Davis, 1993). Baited pitfall traps were placed along transects in primary, logged and plantation forest. Pitfall traps were made from plastic containers, 12.5 cm in diameter and 13 cm deep, covered by a plastic plate to protect the trap from rain. Pitfalls were baited largely with human faeces: a proven attractant to dung beetles in rainforest habitats (Howden & Nealis, 1975; Hanski, 1983). Some pitfalls were baited with carrion (rotting fish). Insects falling into the trap were killed by a solution of water, chloral hydrate and detergent. Traps were put at intervals of 20 m on transects that ran for 180 m, and were left out for three days and nights.

Here we present data collected from four sites in primary forest, three in logged forest, and two plantation sites, representing a total of 347 traps (1041 trap nights). Table 1 contains a list of the number of pitfalls used at each site, and a summary of the location of each transect. Trapping effort per transect varied according to local conditions (Davis, 1993). Primary site A was situated 300 m from a major river (the Segama), and primary sites B and C deeper within the primary reserve. Four logged forest sites covered different logging coupes: site A, logged in 1988; site B, logged in 1989; and C and D logged in 1981. Plantation transects were placed in *Acacia* and mahogany plantations (plantation site A) and a cocoa plantation interplanted with *Albizia* (plantation site B). Two samples were taken from riverine forest adjacent to the Segama river: riverine site A and riverine site B.

In this paper, pitfall traps are referred specifically as 'ground-based' to contrast with 'aerial' baited pitfall traps which were used to investigate the vertical stratification of the arboreal dung beetle fauna, details of which are published elsewhere (see Davis *et al.*, 1997).

RESULTS

Table 2 contains the abundance of arboreal beetles in ground baited pitfall traps from primary, logged and plantation forest. Table 2 also gives the average number of arboreal dung beetles per trap, and the number of arboreal dung beetles as a percentage of the total number of dung beetles collected. Arboreal beetles form only a small proportion of the beetles from ground-based pitfall traps (of a total of 35,095 beetles collected from baited pitfall traps 196, or 0.56%, were arboreal species), yet the results presented in Table 2 are suggestive. Arboreal dung beetles are almost entirely absent from ground-based pitfalls in primary sites. Analysis shows that the average number of arboreal beetles collected from baited pitfall traps from the collecting programme (adjusting for trapping effort) from three non-riverine primary sites (primary sites A, B and C) are significantly different from the averages recorded at four logged forest sites (logged sites A, B, C and D) ($t = 3.61$, with 5 degrees of freedom; $P =$

Table 2. Total and average number per trap of arboreal dung beetles collected from pitfall traps in primary, riverine, logged and plantation forest within the Ulu Segama Reserve, and percentage of total sample (all dung beetles).

Transect	Total number of arboreal dung beetles collected	Average no. per trap*	Percent of total sample (%)
Riverine A	10	0.30	0.33
Riverine B	15	0.43	0.20
Primary A	3	0.12	0.18
Primary B	0	0.00	0.00
Primary C	1	0.03	0.06
Logged A	15	0.34	0.44
Logged B	28	0.64	0.75
Logged C	3	0.30	0.43
Logged D	20	0.69	0.30
Plantation A	57	2.11	1.85
Plantation B	44	1.47	5.43

*See Table 1 for number of traps per transect.
Averages and percent figures to two significant places.

0.0154). Pitfalls in riverine forest (riverine sites A and B) contained significantly more arboreal beetles than those in non-riverine sites (primary sites A, B and C) ($t = 4.69$, with 3 degrees of freedom: $P = 0.0183$). Although both riverine and logged forest sites showed increased abundance of arboreal dung beetles, the greatest numbers of arboreal dung beetles in ground pitfall traps were recorded from plantation forest: of the total number collected in ground pitfall traps, 1.72% or arboreal beetles were from primary forest, 22.32% from logged forest, and 75.96% from plantation forest.

DISCUSSION

Arboreal dung beetles are found in increased numbers in ground-based baited pitfalls in logged and plantation forest. This suggests a change in vertical distribution of this guild of beetles in disturbed or man-made habitats, with greater numbers of beetles found nearer the ground in derived ecosystems than is the case in primary rainforest (where arboreal dung beetles are largely entirely absent from ground-based pitfalls). Increased abundance of arboreal dung beetles in riverine forest is also suggestive, and is discussed below. Arboreal dung beetles are most abundant in group pitfall traps in plantation forest. Plantations represent a very different set of biotic parameters to those found in primary rainforest: this not only raises questions as to why arboreal beetles are collected in pitfall traps in such numbers at these locations, but also, more importantly, what they are doing there at all?

Walter (1984) commented that the canopy habitat conditions found at his research site in Gabon, where he discovered a guild of arboreal dung beetles, bore close resemblance to savannah habitats, and speculated that this similarity in habitat type may allow savannah species to become established in the canopy as an intermediate between two savannah sites (Walter called this a ‘canopy effect’, which is comparable to ‘edge’ effects). This hypothesis is based on the microclimatic similarities (light, humidity and temperature) between savannah and canopy environments. It could also be hypothesized that similar microclimatic effects could also account for the distribution of arboreal beetles in plantation forests within the Ulu Segama Reserve, as the behavioural and physiological responses required to live in the canopy and sub-canopy conditions would pre-adapt these Bornean arboreal beetles for conditions found in such exposed habitats. It could also be argued that, following Walter’s hypothesis, that these arboreal beetles may, conversely, represent species adapted to live in clear forest habitats which have then been able to adapt to the canopy environment: however, given the pristine nature of the forest at Danum Valley (where these beetles seem to reach their peak diversity and abundance) and the lack of clear forest habitats within Borneo until the recent past, it seems more likely that the species became adapted to conditions in rainforest canopy which has pre-adapted them to conditions in open forest ecosystems (i.e. a reverse of Walter's hypothesis).

The observed decrease in foraging height seen in edge (i.e. riverine) and disturbed sites, to levels that would be non-typical in non-riverine primary forest, could also be explained by dung beetles responding to changes in light and temperature regimes within the forest environment. Associations between beetle abundance and increased levels of insolation have also been attributed to dung beetle distributions in forest and open habitat in southern Mexico (Halffter *et al.*, 1992), and it is possible that this phenomenon is widespread. Walter (1984) observed that two of the five canopy dung beetle species from Gabon were captured in some numbers from ground pitfall traps on the same spot as the arboreal traps during the early dry season (Cambefort & Walter, 1991), indicating a microclimatic base to changes in vertical distribution of these arboreal dung beetles. Several studies have looked at the vertical distribution of plants in tropical rainforests (e.g. Bourgeron, 1983; Terborgh, 1985; Koike & Syahbuddin, 1993) and microclimate (e.g. Lemon, Allen & Muller, 1970; Shuttleworth *et al.*, 1985; Kira & Yoda, 1989; Smith, Hogan & Idol, 1992; Barker, 1996), and it has been suggested that height-related differences in these characteristics may affect the vertical distribution of invertebrates (Barker, 1996). Studies on the behaviour and ecology of the Bornean arboreal dung beetles suggest an association between canopy conditions, specifically microclimate, and the distribution of these beetles (Davis *et al.*, 1997). Results presented here also suggest a relationship between the distribution of arboreal dung beetles and microclimate (and associated parameters). The observed increased abundance of arboreal dung beetles in baited pitfalls at ground level may indicate that in forest where high forest canopy is reduced or absent, canopy conditions (in terms of light, humidity, etc.) are found nearer to the ground, and a 'vertical compression' of the arboreal fauna has taken place. Similarly, increased number of arboreal beetles in ground traps in riverine forest may be attributed to canopy conditions proliferating towards the ground in these 'edge' environments. Reduced stratification due to the absence of high canopy is at its more extreme in plantation forest.

Results presented here have implications for the measurement of species richness and abundance in derived ecosystems. Collections from primary (non-riverine) sites generally show complete spatial separation of the arboreal and ground-based faunas (Davis *et al.*, 1997). In riverine, logged and plantation forest, however, arboreal and ground-based faunas show greater spatial overlap, as illustrated by the increased abundance of arboreal beetles in ground baited pitfall traps. More species can therefore be expected to be collected in pitfalls in riverine, logged and plantation forests, simply because the arboreal fauna is sampled by ground-based pitfall traps in these locations. The environment does not contain any more species *per se*, although the pitfalls seem to suggest this. Unfamiliarity with the fauna could therefore lead to the wrong deductions being made: in this case a lack of knowledge about the arboreal fauna could lead to the conclusion that these beetles 'prefer' logged and plantation forest, rather than simply representing changes in their vertical distribution. Increased species richness is often associated with increased habitat complexity (Magurran, 1988). In the case presented here, however, increased richness simply reflects spatial overlap of species that are normally spatially distinct in primary forest. The dung beetle collection assembled during this study is not as species rich as other invertebrate faunas can be in tropical forests (although some 101 species have been identified to date—Davis, 1993): any mixing of canopy and ground faunas of more diverse faunas will have an even more significant affect on measurements of species richness and abundance, and the potential for serious misinterpretation of samples from such species assemblages would be even more pronounced. The extent of this phenomenon may also depend on the degree of insect specificity in the upper canopy: similarly, the degree to which canopy-based faunas can survive in man-made habitats will depend largely on the degree to which they are specific to plants found only in rainforest canopy environments. Arboreal dung beetles can survive in plantation forests as the resource upon which they feed is found there also: insects which show greater resource specificity are unlikely to be found in similar environments. This work therefore suggests that knowledge of the strato-orientation and resource specificity of individual species within primary rainforest is therefore of key importance in the comparison of primary and disturbed sites, as without such information it is not possible to judge whether enhanced species richness is due to qualitative differences between communities within equivalent biotopes, or to structural and physical changes in forest conditions. Increased local species richness can, in the case presented in this paper, be interpreted as a result of habitat perturbation, rather than an increase in the forest's structural complexity. The link between increased local species diversity and habitat fragmentation, through creation of additional 'edge' conditions (Lovejoy *et al*., 1986), has also been made elsewhere (Murphy, 1989).

This paper has examined the response of an arboreal fauna by examining changes in abundance in ground-based pitfall traps. Results suggest that differences exist between primary and disturbed or man-made habitats, and that the arboreal fauna is found nearer to the ground in disturbed or 'edge' habitats. Data suggest that research on the vertical profiles of insects in tropical forests, combined with information regarding resource specificity, is needed to correctly determine the effects of high forest canopy loss on arthropod canopy communities. This work also indicates that such information is necessary to correctly interpret species richness and diversity measurements at ground level in disturbed and man-made ecosystems, where mixing of canopy and ground-based faunas may occur.

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