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ORIGINAL PAPER

Beetle assemblages in rainforest gaps along a subtropical to tropical latitudinal gradient

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Abstract Successional processes in forest gaps created by tree falls are often considered a principal mechanism maintaining species diversity within forests. Although insects are important as mediators of forest recovery processes, there have been few observations of how they differ between forest gaps and non-gaps across latitudes. Here we tested the impacts of gap habitat on beetle assemblage composition at three locations spanning subtropical and tropical biomes (28°S, 16°S, 5°N: Lamington and Daintree in Australia, and Danum in Borneo). Beetles were collected by flight interception traps and sorted to family and feeding guilds. Despite clear differences in environmental conditions between gaps and non-gaps at all three location, we found weak and inconsistent differences in beetle family and feeding guild composition across a latitudinal gradient. PERMANOVA results showed no significant differences in beetle family and feeding guild composition between gaps and non-gaps. For beetle families, however, the interaction effect (between gap vs. non-gap treatment and location) was significant. Post-hoc analysis and NMDS ordinations showed significant and clear separation of family assemblages between gaps and non-gaps within the Danum samples but not within samples from either the Lamington or Daintree sites. Using IndVal, when all three locations were combined, Chrysomelidae and Tenebrionidae were found to be indicators for gaps and Scarabaeinae and Leiodidae for non-

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gaps. Analysed separately, gap indicators were only Chrysomelidae at Daintree, whereas non-gap indicators were Scarabaeinae at Lamington, Scarabaeinae, all other Scarabaeidae, Anthicidae, Scydmaeninae, and Hybosoridae at Danum. We suggest the scale of changes in insect composition and richness with the creation of a natural light gap in forests contrast with those resulting from anthropogenic disturbance such as logging and clearing of forests and the greater adaptability of forests to small-scale changes rather than large-scale changes.

Keywords Gap dynamics · Disturbance · Light regimes · Coleoptera · Tree-fall gaps

Introduction

Light gaps created by asynchronous tree-falls create an intrinsic heterogeneity within forested landscapes (Brokaw 1982). The gradual recovery of canopy cover within such gaps through successional processes has been proposed as a principal mechanism maintaining species diversity within forests (Denslow 1987; Grove et al. 2000; Lawton and Putz 1988; Nicotra et al. 1999)—the so-called 'intermediate disturbance hypothesis' of Connell and Slatyer (Brokaw and Busing 2000; Connell 1978; Connell and Slayter 1977; Molino and Sabatier 2001; Sheil 1999). Much of the ensuing debate has focussed on the species diversity of trees within forests. While there seems little doubt that the existence of pioneer tree species within tree assemblages in tropical forests depends on light gap dynamics (Brokaw 1982; Pearson et al. 2003; van der Meer et al. 1998), the role of such gaps in maintaining or enhancing the diversity of shade-trees, and hence overall tree diversity, within rainforests has been challenged (Brokaw and Busing 2000; Brown and Jennings 1998; Hubbell et al. 1999). In particular the development of neutral explanations of forest diversity in which landscape species richness may be approximated by stochastic models of tree replacement, has emerged as an apparent alternative to the deterministic explanations based on the intermediate disturbance hypothesis (Hubbell 2001). The 'truth' probably lies somewhere between these two competing explanations with spatial scale playing a key role (Kitching 2013).

As Schnitzer et al. (2008) noted, the debate has been clouded, and restricted, by the focus on tree species. They advocate greater attention be paid to other plant life-forms particularly lianas. Their argument is readily extended to considerations of animal diversity, particularly of invertebrates which mediate ecological processes. What is beyond dispute is that rainforests are complex and dynamic ecosystems with inter-correlated biotic and abiotic factors affecting their structure and function (Hill et al. 2001; Whitmore 1984). Light gaps influence many biologically important variables and processes (Brokaw 1982; Denslow 1987; Denslow et al. 1998; Hubbell et al. 1999; Schnitzer and Carson 2001). Light, solar radiation, temperature, humidity, rainfall, soil moisture, and vegetation structure all change within light gaps. These in turn affect rates of plant growth and decomposition at the ground level and, hence, impact upon the availability of resources for animals. This creates a feedback mechanism impacting upon those ecological processes in which animals play a key role such as decomposition, herbivory and pollination.

The ways in which bird assemblages respond to light gap formation have been well studied (Levey 1988; Schemske and Brokaw 1981) but there have been many fewer examinations of how insects and insect-related processes respond (Bouget and Duelli 2004; Feener and Schupp 1998; Hill et al. 2001; Richards and Windsor 2007; Shelly 1988).

Here we present novel results on gap and non-gap faunas of the most diverse of terrestrial insect orders, the beetles (Coleoptera). Beetles comprise roughly 25% of all named species of insects (Grimaldi and Engel 2005; Hunt et al. 2007; Ødegaard 2000) and occur across a wide spectrum of environments occupying a range of feeding guilds including herbivores, fungivores, predators, scavengers and decomposers (Evans et al. 2000). We have chosen to examine the beetle fauna at the family level since, although beetles represent a wide range of feeding guilds and habitats, most of the 150 plus beetle families around the world are conservative in their biology (with a few notable exceptions where the families have diversified in their biologies and feeding strategies) (Hammond 1990). Hammond et al. (1996) previously showed that the forest beetle faunas of several biogeographically distinct regions were surprisingly similar in terms of the rank order of the number of species in beetle families, hence validating our choice to examine at the family level. To test whether the differences we find between the beetle assemblages of light gaps and non-gaps are consistent across forests we have examined their diversity and distribution at the family and feeding guild level in three latitudinally contrasting rainforest locations: Lamington National Park in Australia's sub-tropics in southern Queensland, Daintree lowlands in tropical north Queensland and Danum Valley in Sabah, Borneo. Previously, beetles have been the subject of forest gap studies in deciduous temperate forests where the focus has been on the impact of gap size and isolation, and environmental influences on beetle communities (Bouget 2005a, b). Further, Sugiura et al. (2009) examined how the beetle community changed within artificially created forest gaps.

Specifically we ask the following questions.

1. Are there differences in richness or composition of assemblages of beetle families between gaps and non-gap sites and, if so, do particular beetle families or species drive these differences in composition consistently across latitudes?
2. Are there differences in the distribution of beetles across feeding guilds in gap versus non-gap sites and are any such differences driven by resource availability?
3. Do gaps and non-gaps actually represent different environments for insects and which environmental variables, if any, are responsible for any of the observed differences from the two questions posed above?

Methods

Study locations

The study was conducted from December 2011 to March 2012 at three locations.

Lamington

This sub-tropical study location is in the Green Mountains section of Lamington National Park (28°13.20S, 153°07.30E) within the Gondwana Rainforests of Australia World Heritage Area. The area falls within the McPherson-Macleay region (Burbidge 1960) where the humid sub-tropical and warm temperate regions overlap resulting in a mixture of both tropical and temperate plant species (Laidlaw et al. 2000). The sub-tropical study sites were located at 900 m a s l. Laidlaw et al. (2000) established a one hectare reference plot at this location recording 1266 stems with a dbh greater than 5 cm representing 76 species from 29 families. Dominant species (in descending importance of basal area) were *Argyrodendron trifoliolatum* (Sterculiaceae), *Ficus watkinsiana* (Moraceae), *A. actinophyllum* (Sterculiaceae), *Pseudoweinmannia lachnocarpa* (Cunoniaceae) and *Ackama paniculata* (Cunonaceae) (formerly *Caldcluvia paniculosa*). The location has an average rainfall of ca 1600 mm, with lowest falls in August (ca 100 mm) and highest in February & March (ca 500 mm/month). Mean daily temperatures vary from 22 °C in July to 28 °C in January.

Daintree

This location is in the lowland tropical rainforest of the Cape Tribulation Section of the Daintree National Park at the Daintree Rainforest Observatory (16°06′20″S 145°26′40″E). Study sites were located in forest covered by the Australian Canopy Crane. This forest is part the Wet Tropics of Queensland World Heritage Area, the largest remaining area of continuous rainforest in Australia (Grove 2001; Kitching 1986). The forest is complex mesophyll vine forest with a canopy height ranging from 10 to 40 m with occasional emergent trees to 45 m (Grove et al. 2000). In 2000, all trees above 10 cm dbh were measured and identified to species within the one hectare under the arc of the canopy crane with repeated surveys in 2005 indicating 82 species of trees (Laidlaw et al. 2007). The canopy is dominated by *Cleistanthus myrianthus* (Euphorbiaceae), *Alstonia scholaris (*Apocynaceae), *Myristica insipida* (Myristicaceae), *Normanbya normanbyi* (Arecaceae) and *Rockinghamia angustifolia* (Euphorbiaceae) (Laidlaw et al. 2007). The location has an average rainfall of 3600 mm, with lowest falls in August (80 mm) and the highest in March (550 mm). The region is subject to periodic intense cyclones. Mean daily temperatures vary from 22 °C in July to 28 °C in January.

Danum

The Danum Valley Conservation Area in Sabah, Malaysia covers 43,800 ha of unlogged lowland dipterocarp forest and is one of the few remaining protected forests in Sabah within which the native large mammal fauna remains intact. More than 1300 described plant species have been found in Danum Valley to date and the number is increasing with more intensive study (Hazebroek et al. 2012; SEARRP 2012). The canopy is generally up to 60–70 m with taller emergent individual dipterocarps. The study sites were within a 50 ha permanent plot (4°57′50.23″N, 117°48′42.51″E) established by the South-east Asia Rainforest Research Program (SEARRP). All trees with a diameter at breast height (dbh) $\geq$1 cm in the 50 ha plot have been tagged, measured, mapped and identified to species (Burslem 2010). Newbery et al. (1992) recorded 17,985 individuals of 511 species of tree with dbh >10 cm across two nearby four-hectare plots within the primary forest. The forest is dominated by species of Dipterocarpaceae and Euphorbiaceae, including five co-existing species of the dipterocarp genus, *Shorea.* The climate in Borneo is equatorial with high temperatures and high rainfall (Hazebroek et al. 2012). It is affected by the Indo-Australian Monsoon System from November to March and seasonal migrations of the Intertropical Convergence Zone (ITCZ) from June to August (SEARRP 2012). Mean annual rainfall is 2881 mm (1985–2011) with monthly means ranging from ca 315 mm in January to ca 160 mm in April. The area does not, in general, receive destructive cyclones. Mean daily temperatures range from 27.7 °C in May to 26 °C in January (www.searrp.org/danum-valley/the-conservation-area/climate/, accessed July 24 2015).

Plot selection

At each location a total of ten sites was selected consisting of five gap and five non-gap plots. The sites were more than 50 m apart and, for the gaps, were identified by the presence of a recent (in the last 2 years) large fallen tree trunk ($\geq$80 cm dbh) and an obvious resulting canopy opening. Flight intercept traps (FIT) were generally located close to the middle of gaps and for non-gaps in areas in surrounding areas of continuous forest. Precise locations were determined by available clear space on the ground to allow installation of the FIT. Gap size varied depending on how big the tree fall that created the gap had been. At Lamington (the only site where precise measurements were made) gaps ranged in size from 85 to 792 m^2. In the Supplementary material we present the vegetation and environmental assessments we made to confirm differences between gaps and non-gaps. These confirmed that the amount of light reaching the understorey was higher in the gap sites. The mean number of stems greater than one cm in diameter at 1.3 m in height was lower in light gap sites compared with non-gap sites at the two higher latitude locations (Daintree and Lamington), but not at Danum (Supporting Table 1; Supporting Fig. 1). Basal area was greater in non-gap habitats than light gap, whereas the opposite pattern was found for woody debris (Supporting Table 1; Supporting Fig. 1).

Beetle sampling

Beetles were sampled using a single ground-based flight intercept traps (FIT) in each gap and non-gap site. FITs were run for a 10-day period in 2012 in January (Daintree), March (Lamington) and July (Danum), respectively. We chose to sample in these periods for logistical reasons but also because this was the wet season for the Australian sites. For Danum there is much less monthly variation in temperature and precipitation and July has an average of 203 mm precipitation compared to the 25 year monthly range of 167–318 mm (http://www.searrp.org/danum-valley/the-conservation-area/climate/). Each FIT was positioned in the centre of each site. The FITs were constructed using 1 m^2 clear plastic sheets tied vertically between two stakes or trees with a tray of water and propylene glycol located beneath and a plastic roof to prevent rain from overfilling the collection trays. Flying insects hit the vertical plastic sheet and drop into the preservative in the tray below. Previous studies have found that there is relatively low variability in the assemblage composition of FIT catches among traps compared with those for Malaise traps and their sampling efficiency is less reliant on precise site location, or how well the trap is erected, than for either light traps or Malaise traps (Stork and Grimbacher 2006). Beetles were identified to family level for all three locations following the classification of Lawrence and Newton (1995). Sub-families with distinct biologies were separated out (e.g. Scarabaeinae separated from the remaining Scarabaeidae). The beetles were sorted into five feeding guilds; fungivores, herbivores, predators, saprophages and xylophages (Hammond1990, 1994). A few families were allocated to mixed feeding guilds.

Statistical analysis

We recognise that sampling for a 10 day period at each study location is a relatively short period. Insufficient sampling tends to collect common taxa and miss out rare ones, causing biased assemblage composition. If this is apparent in one or the other habitat type, the results may be highly misleading. To test the sampling sufficiency within each habitat type and location, we generated coverage-based rarefaction curves by plotting the number of beetles against rarefied sample coverage of families. Sample coverage is the estimated proportion of individuals in a community represented by the families sampled (Chao and Jost 2012). We also generated individual-based rarefaction curves which plot the number of beetles against rarefied family richness. The rarefaction curves were extrapolated by doubling the number of collected individuals to estimate the total number of families which would have been collected with increased sampling intensity. The bootstrap method (based on 100 simulations) was used to generate 95% confidence intervals for both interpolated and extrapolated family richness, so that the differences in species richness between gap and non-gap habitats could be analysed. All rarefaction curves were generated using the iNEXT ver. 1.0 (Hsieh et al. 2013) available within R ver. 3.1.0 (Team 2014).

We investigated the differences in family richness and total abundance between gap and non-gap with two-way ANOVAs (using *aov* procedure available within R ver. 3.1.0) incorporating the influence of location, as well as gap versus non-gap effects, into the analyses. Abundances of beetles were log-transformed before analysis to reduce the influence of extremely abundant families and to meet the assumptions of parametric analyses.

To test the differences in beetle assemblage composition between gap and non-gap habitats, we employed permutational multivariate analysis of variance (PERMANOVA) available in PRIMER6 and PERMANOVA + add-on software (Anderson et al. 2008). PERMANOVA calculates distance-based *pseudo-F* statistics based on a given resemblance measure (we used the Bray-Curtis index based on square-root transformed abundances), in a way analogous to ANOVAs. *P* values were calculated using a permutational method with 4999 randomizations. When main and/or interaction effects were found to be significant, post hoc pairwise t-tests were conducted using permutation methods. For some of the tests where inadequate numbers of unique combinations were available for permutation, a Monte-Carlo asymptotic permutation was used. Beetle assemblages were also assessed visually using non-metric multi-dimensional scaling (NMDS) ordinations, with 25 random restarts, using PRIMER6 (Clarke and Gorley 2006). Beetle assemblages were analysed based on family and feeding guild with abundances square-root transformed before analysis.

We further assessed whether differences in configuration of the gap habitats (i.e. excluding the sites from non-gaps) influenced assemblage composition and taxon richness of beetles, using a distance-based linear model (DistLM) in PRIMER6 and PERMANOVA + add-on software (Anderson et al. 2008). DistLM seeks the combination of explanatory variables that explains the most variation in a data cloud described by a resemblance matrix. We used a step-wise selection procedure, based on the adjusted Akaike information criterion (AICc), and force-included two dummy predictors in the model to account for the differences among the three sites. Explanatory variables tested included gap size (m^2), light intensity index (mol/m^2/day), canopy cover (%), woody debris cover (%), basal area (m^2) and tree stem count. We conducted separate analyses for woody debris and basal area, as these variables were not measured at the Daintree site. All explanatory variables were normalised before analysis. All assemblage data were based on the Bray-Curtis similarity values of square-root transformed abundances. Differences in family richness values were quantified using Euclidean distances.

To determine whether particular families or feeding guilds are characteristic of either gap or non-gap habitats, we used the indicator value protocol, IndVal (Dufrêne and Legendre 1997), using the LABDSV R package (version 1.6, Roberts 2015). This method creates an index which combines species abundances with their frequency of occurrence within various groups of samples. We pooled data for all traps from either gaps or non-gaps at each location. This index is maximal when all individuals of a species/family are found in a single group of sites and minimal when individuals are equally shared among all sites. We selected indicator groups which had significant *P* values based on a randomization method based on 4999 runs.

Results

Abundance and richness of beetles sampled

A total of 21,864 beetles of 56 families were collected across the three locations (Table 1, Supporting Table 2). The Daintree sites had the most individuals and at this location and at Lamington, Ptiliidae and Pselaphinae (Staphylinidae) and other Staphylinidae were the most abundant groups (Supporting Table 2). At Danum, Scolytinae (Curculionidae) comprised about half of all beetles and non-pselaphine and non-scaphidiine Staphylinidae comprised a further 15–17% (Supporting Table 2). Despite larger number of individuals collected at non-gap habitats at Danum and Daintree, average family richness and abundance did not vary significantly between gap and non-gap plots across the three locations (Table 2).

Coverage-based rarefaction curves showed that nearly 100% of the beetles were represented by the families sampled in all three locations (Supporting Fig. 2). Individual-based rarefaction curves showed that there was no difference in the total number of beetle

Table 1 Numbers of beetles caught using FIT traps in light gaps and non-gaps at the three sampled locations

	28°S (Lamington)		16°S (Daintree)		5°N (Danum)	
	Gap	Non-gap	Gap	Non-gap	Gap	Non-gap
Individuals (total)	3784	3282	3805	5071	2368	4404
Individuals (mean)	756	656	761	1014	474	881
±SE	*139.15*	*134.70*	*132.13*	*340.27*	*66.46*	*251.93*
Families (total)	42	33	35	34	39	37
Families (mean)	26	21.8	21	18.8	20.2	20.8
±SE	*1.55*	*1.60*	*0.77*	*1.53*	*1.77*	*3.92*

Table 2 Summary of ANOVA results based on family richness and abundance, showing *F* and *P* values of the effects of gap versus non-gap treatments, location and their interactions

	Gap versus Non-gap		Location		Interaction	
	F	*P*	*F*	*P*	*F*	*P*
Family richness	1.95	0.175	9.53	**<0.001**	0.76	0.480
Abundance	1.22	0.280	0.91	0.417	0.81	0.458

Significant *P* values are shown in bold

Degrees of freedom for habitat, location, their interaction and residuals are 1, 2, 2 and 24, respectively families between gap and non-gap habitats across all three locations, even when relatively under-sampled habitats were extrapolated (Fig. 1).

Assemblage differences and indicator species

PERMANOVA results showed no significant differences in beetle family and feeding guild composition between gaps and non-gaps (Table 3). For beetle families, however, the interaction effect (between gap vs non-gap treatment and location) was significant. Post-hoc analysis and NMDS ordinations (Fig. 2) showed significant and clear separation of family assemblages between gaps and non-gaps within the Danum samples (post hoc Monte-Carlo $P = 0.018$), but not within samples from either the Lamington ($P = 0.084$)

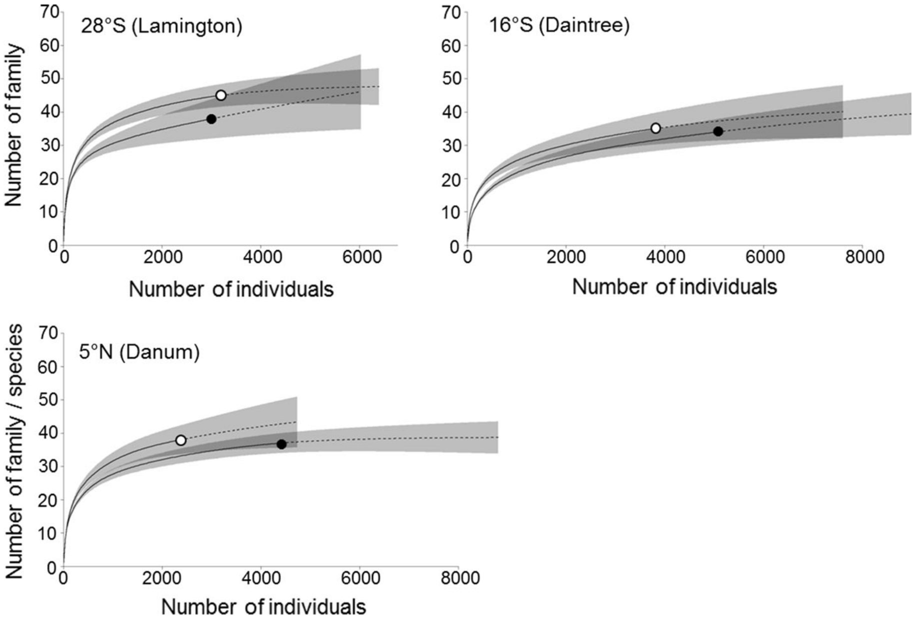

Fig. 1 Individual-based rarefaction and extrapolation curves of the number of families from **a** Lamington, **b** Daintree and **c** Danum. *Open* and *closed circles* represent the sampling extent from gap and non-gap, respectively. *Dashed lines* are extrapolations by a factor of 2 with 95% confidence intervals (*grey area*)

Table 3 Summary of PERMANOVA results based on beetle family and feeding guilds, showing Pseudo-*F* and *P* values of the effects of gap vs non-gap treatments, subregion and their interactions

	Gap vs non-gap		Location		Interaction	
	Pseudo-*F*	*P*	Pseudo-*F*	*P*	Pseudo-*F*	*P*
Family	1.28	0.322[a]	16.89	**<0.001**	2.18	**0.003**
Feeding guild	1.12	0.410[a]	20.96	**<0.001**	1.83	0.101

Degrees of freedom for habitat, location, their interaction and residuals are 1, 2, 2 and 24, respectively

Significant *P* values are shown in bold

[a] Due to limited number of unique permutations (n = 38), *P* values were calculated using Monte-Carlo asymptotic permutation

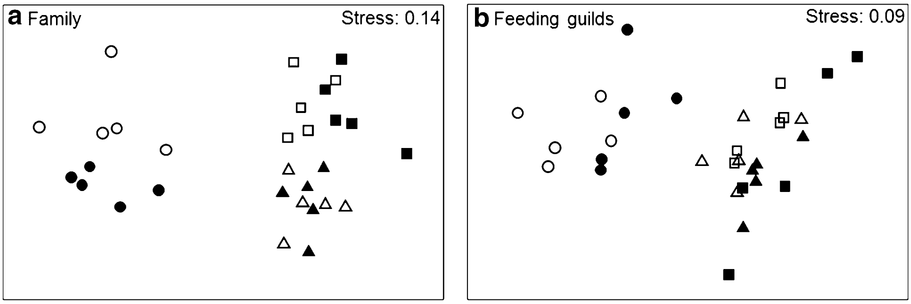

Fig. 2 NMDS ordinations of beetles based on family (**a**) and feeding guilds (**b**) collected from Lamington (*triangles*), Daintree (*squares*) and Danum (*circles*). *Open symbols* represent gap sites and *closed symbols*, non-gap sites

or Daintree sites ($P = 0.213$). Dispersion of samples from Daintree non-gap sites was larger than that of Lamington, which may have resulted in larger P values in Daintree (Fig. 2a). As there was no significant differences in family richness between gap and non-gap sites (Fig. 1), the significant difference between gap and non-gap sites in Danum was likely to have resulted from high family turnover between the two habitats.

DistLM showed that none of the predictor environmental variables measured explained significant variations in any assemblage composition or taxon richness within gap habitats.

When all three locations were combined, IndVal found four families or sub-families indicative of gaps (Chrysomelidae, Tenebrionidae) or non-gaps (Scarabaeidae: Scarabaeinae, Leiodidae) (Table 4). IndVal indices for Chrysomelidae and Tenebrionidae were, however, both low and P values were marginally significant. When individual locations were analysed separately, we found one such taxon at Lamington and two at Daintree whereas five indicator taxa were found at Danum (Table 4). This clearly reflected the results of multivariate analysis where a significant difference between gap and non-gap

Table 4 Summary of the families found to be significant indicators of either gap or non-gap habitat showing Indicator Values (IndVal), P values and their habitat. None of the feeding guilds were found to be significant indicators

	IndVal (%)	P	Habitat
All locations combined			
Chrysomelidae	56.8	0.049	Gap
Tenebrionidae	51.8	0.014	Gap
Scarabaeidae Scarabaeinae	73.5	0.001	Non-gap
Leiodidae	62.7	0.024	Non-gap
28°S (Lamington)			
Scarabaeidae Scarabaeinae	82.4	0.039	Non-gap
16°S (Daintree)			
Chrysomelidae	86.1	0.035	Gap
Leiodidae	77.7	0.008	Non-gap
5°N (Danum)			
Scarabaeidae Scarabaeinae	80.1	0.009	Non-gap
Anthicidae	80.0	0.045	Non-gap
Scydmaenidae	73.3	0.032	Non-gap
Hybosoridae	72.9	0.007	Non-gap
Remaining Scarabaeidae	71.6	0.016	Non-gap

habitats was found only at Danum. All of the five indicator families found at Danum were indicative of the non-gap habitat. None of the feeding guilds were found to be indicators of either gaps or non-gaps either collectively or separately for the three locations.

Discussion

Our analyses appear to show no significant differences in beetle family richness between gap and non-gap at rainforest locations from 28° to 5° latitude. Here we explore these and our other findings further. In this discussion we examine how our results are able to answer the three key questions we asked.

1. Are there differences in richness or composition of assemblages of beetle families between gaps and non-gap sites and, if so, do particular beetle families or species drive these differences in composition consistently across latitudes?

Sample coverage analysis showed that we had sampled a high proportion of the families at all three sites that might be expected to be caught using FITs, which suggests that our sampling was sufficient to test for differences in beetle family richness and composition between gaps and non-gaps. There was no significant differences in the beetle abundance and family richness between light gaps and non-gaps across the three locations (Table 2), which was also confirmed by the individual-based rarefaction curves (Fig. 1). In terms of family composition, we found that there was a clear difference between gap and non-gap plots at the family level at Danum, but not at either Daintree or Lamington (Fig. 2). Of course, in addition to differences in climate and seasonality driven by latitude, the Danum and Australian sites are located in different biogeographical regions with concomitant contrasting tectonic, evolutionary and invasion histories. The observation that results from both gap and non-gap sites from Borneo cluster together in the ordination space, and contrast with the 'super-cluster' which represent the Australian site (Fig. 2), is clear evidence that, in addition to gap/non-gap dynamics additional, overarching drivers are involved. Parsimony suggests that biogeographical region is the most likely explanation.

Previous studies show somewhat conflicting results. Several studies have been made in Panama. Shelly (1988) investigated day-flying insect assemblages in light gaps and closed understorey forest using sticky traps observing that Coleoptera, Formicidae and Psocoptera were more abundant in the closed sites than in light gaps but the size distributions of taxa were similar across sites. Richards and Winsor (2007) used Malaise traps to survey a wide range of insect species finding higher levels of abundance in light gaps in the wet season: a trend which was reversed in the dry season. Feener and Shupp (1998) found no difference in ant abundance, diversity or assemblage composition in gaps compared with non-gaps. Hill et al. (2001) found that butterfly assemblages in rainforests in Borneo were more diverse in gap sites compared with those in adjacent forest and species usually associated with the canopy were to be found at ground level (see also Houlihan et al. (2013)). They suggested that a distinctive 'gap fauna' existed and anticipated that generalist species are more widespread and are more likely to occupy gaps than are specialist species. Pardonnet et al. (2013) also found that in Peru fruit feeding Nymphalidae were more diverse in gaps than non-gaps.

Our results remain the only cross-regional ones which have used the same sampling protocols and trapping methods and, as is apparent, are not readily combined with others to produce a coherent global picture of how insects respond to the creation or existence of light gaps. Overall results to date are conflicting with some of the differences perhaps being the result of different locations, sampling protocol, taxonomic groups and, not least, exactly what was being measured. There is an urgent need for cross-location comparisons using the same or a standard set of sampling methods. In this respect, Coleoptera remain the insect taxon of choice inasmuch as they contain species from widely differing trophic groups but study of a wider range of taxa will be useful. Some taxa may utilize gaps only as foraging adults because particular resources are available there (e.g. nectaring Lepidoptera), others because particular larval habitats are abundant within gaps (e.g. xylophagous beetles). Analyses below the family or subfamily level may be needed given the great diversity of particular life styles, even within insect families.

Within our results, use of the indicator value protocol showed that only a few families were specialized to either of the contrasting habitats, perhaps reflecting the fact that a few families dominate in terms of abundance and number of species. It was also interesting to note that across all three locations Tenebrionidae and Chrysomelidae were indicators of gaps. Tenebrionidae are often more tolerant of drier conditions and are commonly found in woody debris. Chrysomelidae, as herbivores, are associated with new vegetation. Family/subfamily indicators across locations of non-gaps were scarabaeines which are likely to be feeding on mammalian dung, and Leiodidae which are fungivores. Both dung and fungi are likely to be more abundant in closed forests than in gaps, the former because of the greater amount of vegetation and food sources and the latter because the ground layer of closed forests is likely to be more moist hence favouring the growth of fungi. When individual sites were analysed separately, we found only one or two indicator taxa at Lamington and Daintree locations, and these reflect some of the previously discussed differences in availability of resources. All of the five indicator families found at Danum were indicative of the non-gap habitat which suggests that in a more equatorial climate these families are less tolerant of open habitats.

2. Are there differences in the distribution of beetles across feeding guilds in gap versus non-gap sites and are any such differences driven by resource availability?

Given the previous results concerning the scarcity of families that were identified as indicators of gaps or non-gaps it was not surprising that none of the feeding guilds were found to be indicators of either habitats. As discussed above, one would expect that availability of key food resources such as dead wood, new leaves, mammal dung and fungi are driving the presence or abundance of some families of beetle*s*. Bouget (2005b) examined whether gaps created by a severe storm in a oak-hornbeam forest resulted in differences in key feeding guilds of saproxlic beetles. The size of gaps (1200–33,000 m^2) is on a very different scale to our study (85–792 m^2) but Bouget used FIT traps to sample as we did. ANOSIM tests confirmed that even small gaps differed from closed-canopy controls in terms of saproxylic species composition. Bray-Curtis similarity between forest controls and gaps reached 29% (small gaps), 35% (large gaps) and 40% (mid-size gaps). The largest difference occurred between midsize gaps and controls. The abundance of pioneer xylophagous beetles, and particularly the scolytids, increased with gap size, but not significantly). Secondary xylophagous, zoophagous (predators) and xylomycetophagous species did not differ in gap size classes, whereas floricolous saproxylic beetles were more abundant in mid-size and large gaps than in small patches (Bouget 2005b).

3. Do gaps and non-gaps actually represent different environments for insects and which environmental variables, if any, are responsible for any of the observed differences from the two questions posed above?

Since we had pre-selected our sites as gap or non-gap it was not surprising that in gaps there was significantly more light and smaller total basal area of large trees, and less canopy cover than in non-gaps. We can say, therefore, that these represent different environments for animals such as invertebrates. However, DistLM showed that none of the predictor environmental variables measured explained significant variations in any assemblage composition or family richness within gap habitats. We found that light gaps were more variable in terms of temperature (based on the coefficient of variation values) than non-gaps. In part this probably reflects the variable size and shapes of the light gaps but also reflects the fact that lack of canopy cover means that in gaps the temperatures experienced are more similar to those normally experience at the top of the canopy. Turton and Siegenthaler (2004), for example, found that temperatures at the top of the canopy at the same Daintree study site used here were more extreme than at ground level but, after a cyclone that had effectively stripped away much of the canopy foliage, the same extreme temperatures previously only found at the top of the canopy were experienced at ground level. The percent coverage of woody debris was higher in gap sites at both Lamington and Danum. This reflects the fact that gaps are created by tree falls resulting, inevitably, in increased woody debris. Annual temperature ranges in forested ecosystems have been observed to increase with latitude (Wright et al. 2009) and hence this most likely reflects the fact that there is a strong cooler and dry season in eastern Australian sub-tropical and tropical rainforests and hence the species of all families of beetles need to be able to tolerate drier conditions and a broader range of temperatures than at Danum where there is less climatic seasonality.

Concluding remarks

Our results and those of others suggests there is still much to be learned about the role of light gaps in introducing taxonomic and functional diversity into primary forest ecosystems. Examined closely enough with sufficient taxonomic focus we suggest that gap/non-gap differences will be found even when this is not evident at the coarse level of the family or sub-family. These differences, where they exist, however, are insignificant and inconsequential compared with those created as a by-product of the extensive loss and change in composition of the fauna and flora of forests following logging, fragmentation, clearing and transformation of tropical forests (Ewers et al. 2015; Lawton et al. 1998; Schulze et al. 2004). Primary rainforests remain irreplaceable for the conservation of biodiversity (Gibson et al. 2011). That biotic contrasts between gaps and non-gaps within primary forests are relatively small underlines the resilience of these systems to the ‘natural’ disturbance regimes to which they have been subjected. Our results do not suggest this resilience will extend to large-scale anthropogenic impacts.

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