Effects of shading and mulch depth on the colonisation of habitat patches by arthropods of rainforest soil and litter

By Akihiro Nakamura1*, Carla P. Catterall1, Chris J. Burwell1,2, Roger L. Kitching1, and Alan P. N. House3

1 Centre for Innovative Conservation Strategies and Griffith School of Environment, Griffith University, 170 Kessels Road, Nathan, Queensland 4111, Australia
2 Queensland Museum, Cnr Grey and Melbourne Streets, South Brisbane, Queensland 4101, Australia
3 CSIRO Sustainable Ecosystems, 306 Carmody Road, St Lucia, Queensland 4067, Australia

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*Corresponding author

Corresponding author’s current address: Queensland Museum, Cnr Grey and Melbourne Streets, South Brisbane, Queensland 4101, Australia

Telephone: +61 (0)7 3840 7703
Fax: +61 (0)7 3735 7014
E-mail: a.nakamura@griffith.edu.au

RUNNING TITLE: arthropod colonisation in forest restoration
1. Development of foliage cover and a layer of leaf litter are two factors considered important for the successful recolonisation of soil and litter arthropods during the early stages of rainforest restoration; however, this needs to be tested explicitly.

2. We employed a manipulative field experiment to assess the effects of shading and litter depth on colonisation patterns of soil and litter arthropods in created habitat patches at five replicated sites within pasture adjacent to rainforest remnants on the Maleny plateau of subtropical eastern Australia.

3. Habitat patches were created by adding sterilised mulch at two depths (shallow 3-5 cm, deep 10-15 cm) under three levels of shading (none, 50%, 90%). Responses of arthropods to treatments were analysed at two levels of taxonomic resolution: ‘ordinal-sorted arthropods’ (all arthropods sorted to order/class) and ant species (Hymenoptera: Formicidae).

4. Shading, at both 50% and 90%, encouraged colonisation by arthropods characteristic of rainforest. Colonisation by pasture-associated arthropods declined progressively with increased shading. Effects of mulch depth were significant only for rainforest-associated ant species, which responded positively to shallow mulch within shaded plots.

5. The results confirm that canopy cover is indeed one of the primary attributes influencing colonisation patterns of arthropods in restored vegetation. More widely-spaced plantings may facilitate some colonisation by rainforest arthropods. However, in order to suppress invasion by pasture-associated arthropods, it may be necessary to establish a fully closed canopy.
KEYWORDS

Biodiversity, bio-indicators, epigaeic invertebrates, reforestation
Australian tropical and subtropical rainforests are some of the few worldwide in which deforestation has all but ceased, and increasing effort is being invested in rainforest restoration, often with the aim of recovering biota characteristic of pre-disturbed habitats (Catterall & Harrison, 2006). The last decade has seen a growing number of studies of tropical and subtropical rainforest restoration, investigating recolonisation by various faunal groups including arthropods (see Nakamura, 2007). Studies have assessed a range of factors that may influence recolonisation patterns of rainforest fauna, including spatio-temporal aspects of the restoration (e.g. isolation, age), plant species composition and structural complexity, canopy cover and litter quality and quantity.

Among these factors, canopy closure has been considered a key component facilitating the development of fauna, especially during early stages of rainforest restoration (Catterall et al., 2008; Grimbacher et al., 2007; Jansen, 1997; Kanowski et al., 2006; Nakamura et al., 2003). A closed canopy provides a shaded forest floor which is associated with increased moisture content and reduced temperature fluctuations in soil and litter microhabitats (Neumann, 1973). These factors are significant determinants of the diversity and abundance of soil and litter arthropods (Chikoski et al., 2006; Entling et al., 2007).

The level of shading achieved during rainforest restoration, therefore, has important implications for the development of rainforest-like arthropod assemblages, as different reforestation techniques achieve different degrees of canopy cover. Timber plantations have been advocated to catalyse rainforest reforestation because they also yield
economic returns (Lugo, 1997). However, the density of trees in plantations is generally sparse (400-1000 stems/ha) compared with ecological restoration where a diverse array of rainforest plants are planted at densities of several thousand stems/ha (Catterall & Harrison, 2006). In tropical and subtropical regions, timber plantations achieved much lower levels of canopy cover (25-60%) than ecological restoration plantings (75-80%) and intact rainforest (93-95%), at least during the earlier stages of reforestation (5-22 years since establishment) (Kanowski et al., 2003). However, increasing the amount of litter in plantations may help offset a more open canopy, by providing better insulation against temperature and moisture extremes, and more resources for colonising soil and litter arthropods (Greenslade & Majer, 1993; Koivula et al., 1999; Majer et al., 1984; Nakamura et al., 2003). This may be achieved through the addition of a layer of organic mulch (such as woodchips or hay) during the early stages of restoration. Mulch is often used in ecological plantings to improve the survival of tree seedlings by suppressing grass and exotic herbs and conserving moisture. However, we do not know if mulching also benefits soil and litter arthropods, as the effects of shading and litter depth on colonisation patterns have not been systematically studied in restored rainforests.

We investigated the effects of shading and mulch depth on the development of assemblages of soil and litter arthropods in experimentally-created habitat patches within a rainforest landscape now dominated by pasture. This experimental approach enabled us to test systematically the focal factors without interactions with extraneous factors, such as plant species and litter composition, habitat area and proximity to the nearest rainforest, which are inherently variable in studies of actual restoration programs. We test the hypothesis that the abundance and diversity of rainforest-associated arthropods in restored patches will increase with increased shading and that an opposite
pattern will occur for pasture-associated arthropods. Further, we test whether increased mulch depth compensates for reduced shading.

METHODS

Study area

The study was undertaken on the Maleny plateau, in the Sunshine Coast hinterland of eastern Australia (26° 40’- 50’ S, 152° 45’- 53’ E, elevation 350 to 530 m). Mean daily maximum and minimum temperatures in mid-summer (January) are 28.9° and 18.8°C respectively, and 19.5° and 7.1°C in mid-winter (July). Average annual rainfall in the region is 1851 mm, with most falling between December and April. Total precipitation during the study period (1437 mm between August 2003 and April 2004) was below average for those months (1633 mm).

Five replicated experimental sites, each comprising an area of pasture abutting a fenced rainforest remnant, were dispersed across a study region of approximately 170 km². Remnants varied from 1.15 ha at one site to over 10 ha at other sites, and were either old regrowth (age of ca.100 years) or had been selectively logged until recently. Further details of study sites are provided in Nakamura et al. (2007).

Experimental design

At each site, we established a series of 3 m x 3 m experimental plots that simulated conditions experienced by soil and litter arthropods within areas of rainforest restoration. All plots were situated in pasture within two metres of a rainforest remnant, so that the results were not confounded by distance effects on colonisation (see Nakamura et al., 2008b). Plots were at least 5 m apart (Fig 1).
Plots were first sprayed with approximately 400-600 ml of broad spectrum herbicide (Roundup® Biactive™, 7.2 g/L Glyphosate), in line with actual restoration procedures conducted in the region (Big Scrub Rainforest Landcare Group, 2005; Goosem & Tucker, 1995). A companion study found no short- or long-term impacts of the herbicide on soil and litter arthropods inhabiting rainforest litter (Nakamura et al., 2008a). Plots were then fenced with barbed wire to a height of 1.2m to exclude stock. Three weeks after herbicide application, all visible vegetation (dead and alive) was removed by hand.

Plots were either unshaded or covered with Sarlon® shadecloth rated at either 50% or 90% protection from insolation. Shadecloth was placed over the top of the plot and 20-40 cm down each side and cut in 15 – 20 places with a slit length of 10 – 15 cm to permit sunflecks and throughfall of rain. No live plants were planted within experimental plots as this was pragmatically difficult and would confound effects of the focal factors.

A mulch of woodchip and leaf material was placed in either a ‘shallow’ (3-5 cm) or ‘deep’ (10-15 cm) layer in a square quadrat (2.5 m x 2.5 m) within each plot. The mulched area was bordered by wire netting (40 cm high, hexagonal mesh size of 1.5 cm (maximum height) x 2 cm (maximum width)) to minimise loss of mulch due to wind or disturbance by larger wildlife. Mulch was derived from vegetation lopped from around powerlines in various locations within about 150 km of the study region, and comprised a mix of foliage and wood derived from rainforest and eucalypt species. Mulch was steam-sterilised for 100 minutes before application to minimise the introduction of exotic species and to create ‘empty’ habitat patches. Sterilised mulch was stored
beneath plastic sheets to minimise any casual arthropod colonisation and distributed to plots within seven days after steam-treatment.

Seven plots were constructed at each of the five sites. Six plots were experimental treatments, with three levels of shading (0%, 50%, 90%) and two levels of mulch depth (shallow, deep). The seventh was a control plot which received herbicide treatment and vegetation removal but no shadecloth or mulch (Fig 1). Construction of the field experiment took place between May and August 2003.

**Sampling methodology**

**Arthropods**

Pitfall trapping and litter extraction was carried out between 9 April and 7 May 2004, approximately nine months after the plots were established. Four pitfall traps were installed on the diagonal lines of each plot, approximately 80 cm from the centre. Each trap was a 120 ml plastic vial (44 mm in diameter), buried in the ground with the lip flush with the surface. Vials were filled with 70 to 80 ml of 70% ethanol with a small amount of glycerol. Pitfall traps were operated for five days. Before data analyses, samples from the four pitfall traps were pooled. Litter samples were taken immediately before pitfall trapping. One litre of litter and surface soil (approx. 20% surface soil and 80% litter by volume to a depth of 1 to 2 cm) was collected in small amounts evenly over the entire plot area. Samples were placed in Tullgren funnels within 12 hours of sampling, and extracted for 4.5 days using 40 watt clear light bulbs.

During sampling, care was taken to avoid cross-contamination among the experimental plots. All footwear was covered with thick polythene film and researchers were thoroughly brush-cleaned before and after visiting each plot.
Identification of arthropods was to order except (a) Hymenoptera which were split into Formicidae and ‘others’; and (b) myriapods, which were sorted to class. Acari and Collembola were not sorted due to their high abundance and ubiquitous occurrence regardless of the experimental treatments. Ants (Hymenoptera: Formicidae) were selected as a target taxon, and sorted to species. Where possible, ants were identified as described species by CJB, using published taxonomic literature, otherwise they were assigned species codes. Voucher specimens are deposited at Griffith School of Environment, Griffith University.

Soil moisture content and temperature

During arthropod sampling (between 15 April and 7 May 2004), soil moisture content was measured by hand-collecting approximately 50 cm³ of topsoil (up to 2 – 3 cm in depth) from each experimental plot at the five sites as well as their adjacent rainforest and pasture areas. Small amounts of topsoil were collected evenly over the plot area, and within 2.5 m x 2.5 m quadrats established within rainforest and pasture at each site. Each soil sample was kept in an airtight plastic bag, and weighed before and after it was oven dried for 24 hours at 105°C. Ground temperature was recorded at 30 minute intervals for 5.5 days (14 to 20 April 2004) using temperature loggers (HOBO® Temperature Data Logger, Onset Computer Corporation, MA), deployed at the experimental plots and surrounding rainforest and pasture areas in one site only. The temperature sensor was placed on the ground surface (beneath the mulch, except in the un-mulched control plot), in the centre of each plot.

Data processing

Data were analysed in three different sets: (i) arthropods sorted to order/class
(referred to as ‘ordinal-sorted arthropods’ hereafter), (ii) ant species and (iii) ant functional groups (Andersen et al., 2003). Each dataset was further divided into two subsets comprising data sampled using pitfall traps and litter extraction. Abundances of ordinal-sorted arthropods were log transformed before analysis. Abundances of ant species were scored on a seven-point ordinal scale following Andersen et al. (2003): 1 = 1, 2 = 2-5, 3 = 6-20, 4 = 21-50, 5 = 51–100, 6 = 101-1000, 7 = >1000 individuals. Abundances within ant functional groups were expressed as proportions of all ants at each plot, and arcsine-transformed for analysis.

In addition to data from the present study, we incorporated data from a preceding survey (Nakamura et al., 2007), which provided baseline information on the difference between the arthropod assemblages of rainforest and pasture habitats in the study region. That survey was carried out in the same location and in a similar season the previous year (8 January to 6 May 2003). Arthropods were collected from three sampling points at each of 24 sites (12 in rainforest remnants and 12 in pasture) across the Maleny region, including the five used for the present study. Although the baseline arthropod sampling was carried out over a slightly larger area than in the present experimental study (each sampling point comprising a circular area of 3 m radius), sampling and sorting protocols were otherwise identical, so that direct comparison was possible.

Baseline survey data were used to identify indicator taxa for either rainforest or pasture habitats, based on the Indicator Value protocol (Dufrene & Legendre, 1997). Rainforest/pasture indicators were classed as either ‘specialist’ (found exclusively in either rainforest or pasture) or ‘increaser’ (found in both habitat types but significantly more abundant in one). Taxa that did not have significant habitat preferences were
classed as ‘generalist’ (see Nakamura et al., 2007 for more details).

Many individual habitat indicator taxa were of limited usefulness due to their patchy distributions (Nakamura et al., 2007). To develop a more robust indicator statistic, additional ‘composite rainforest/pasture indices’ were generated for only two of the selected data sets (viz. ordinal-sorted arthropods, ant species). To calculate composite indices of ordinal-sorted arthropods, abundance values of each of the indicator taxa (as defined by the baseline survey) were first individually range-standardised to give values between 0 and 1 for each taxon at each site (site-specific abundance minus minimum abundance across all sites / maximum minus minimum abundance across all sites). This was done to remove the effects of large differences in taxon-specific abundance. The range-standardisation procedure was not carried out for ant species, as most indicator species had similar abundance scores (most from 0 to 4, with a maximum of 6). The range-standardised abundance (ordinal-sorted arthropods) or abundance scores (ant species) of rainforest or pasture indicator taxa were then summed to give composite indices of rainforest or pasture habitat at each site. Composite indices provided a single value quantifying the extent to which a site resembled rainforest or pasture. Composite indices were calculated separately for ordinal-sorted arthropods and ant species collected by either pitfall traps or litter extraction and were calculated only if two or more of the component indicator taxa/species were present.

Data analysis

Two-factor crossed ANOVAs with randomised complete block design were carried out, using SPSS (Rel.13.0) statistical software (SPSS Inc., 2004) to evaluate the responses of variables (total abundances, taxon richness, individual arthropod
abundances, composite rainforest/pasture indices, soil moisture contents) to the experimental treatments. Factors tested were shading (0%, 50%, 90%), mulch depth (shallow, deep) and their interaction. Between-site variation (blocks) was included as a random factor. Analyses of variance were carried out on the abundance of an individual taxon only if it occurred in at least four of the total experimental plots used for the analyses (N = 30). To enable direct comparison with rainforest and pasture reference sites, we also present baseline survey data from the same five sites (one randomly selected sampling point from the three at a site).

Nonparametric multivariate analyses of variance (MANOVA) were carried out with PERMANOVA software (Anderson, 2005) to test for responses of arthropod assemblages to the experimental treatments. Factors tested were the same as in the univariate analyses of variance. Between-site variation (blocks) was accounted for by including sites in the program as covariates, in a manner specified by M. Anderson (personal communication).

**RESULTS**

**Arthropod assemblages and their response to shading and mulch**

**Overall abundances**

A total of 8839 arthropods was sampled from the experiment, the majority from pitfall traps (7162 individuals). Among 28 ordinal-sorted taxa identified, ants were the most abundant with 3633 individuals (2897 from pitfall traps), followed by Coleoptera with 1846 and Araneae with 582 individuals. Of the 52 ant species identified, 26 were
rare, occurring at less than four plots.

A significant effect of shading was found for the total abundances of pitfall-trapped ants (ANOVA for the effect of shading and mulch depth: $P = 0.019$, $P = 0.272$ respectively, with interaction $P = 0.558$); a post-hoc LSD test showed that abundances were greater in 0% (mean = 106.6) and 50% shading (95.3) than in 90% shading (44.9).

Neither the abundance nor taxon richness of ordinal-sorted arthropods, nor the species richness of ants responded significantly to the shading or mulch depth treatments (results not shown).

**Ordinal-sorted arthropods**

Among pitfall-trapped ordinal-sorted arthropods, two taxa were rainforest ‘specialists’ (Archaeognatha, Opilionida), as defined by Nakamura et al. (2007); nine rainforest ‘increasers’ (Blattodea, Coleoptera, Dermaptera, Diplopoda, Diplura, Heteroptera, Isopoda, Pseudoscorpionida, Psocoptera); and three pasture ‘increasers’ (Araneae, Homoptera, Orthoptera). Among litter-extracted arthropods, there were 14 rainforest ‘increasers’ (Amphipoda, Blattodea, Chilopoda, Coleoptera, Dermaptera, Diplopoda, Diplura, Formicidae, Heteroptera, Isopoda, ‘other Hymenoptera’, Pauropoda, Pseudoscorpionida, Symphyla) and a single pasture ‘increaser’ (Orthoptera).

Despite the large number of indicator taxa, few showed statistically significant responses to shading and litter depth (Table 1). A number of ‘generalists’ significantly responded to shading, mostly showing elevated abundances in plots at 0% and/or 50% shading, while abundances at 90% were lower.

Despite the lack of responses from individual indicator taxa, the composite index of rainforest ‘increasers’ based on pitfall-trapped ordinal-sorted arthropods responded...
positively to an increase in shading from 0% to 50% (Fig. 2a, Table 2). No experimental
treatments affected the composite index of litter-extracted rainforest ‘increasers’ (Fig.
2b, Table 2). Shading also had a significant negative effect on the composite index of
pasture ‘increasers’: abundances of pasture-associated arthropods were lower in the
plots under 50% and 90% shading than in plots without shading, with no significant
interaction between shading and mulch depth (Fig. 2c, Table 2). Composite habitat
indices were not calculated for any habitat ‘specialists’ due to very rare occurrences
(presence in less than four plots) of their component taxa.

Multivariate analyses using PERMANOVA showed statistically significant effects
of shading on the composition of pitfall-trapped ordinal-sorted arthropod assemblages
(Table 2). A post-hoc permutation test showed that the coarse taxonomic composition of
arthropod assemblages under 0% shading differed significantly from those under both
50% and 90% shading. Shading and litter depth treatments did not have a significant
influence on the taxonomic composition of litter-extracted ordinal-sorted arthropods.

Ant species

Among pitfall-trapped ants, there were six rainforest ‘specialists’, as defined by
Nakamura et al. (2007) (*Anonychomyrma* QM3, *Leptomyrmex erythrocephalus*
*rufithorax, Monomorium tambourinense, Pheidole QM1, Pheidole QM2, Pheidole sp.2)*,
two rainforest ‘increasers’ (*Notoncus capitatus, Rhytidoponera chalybaeae*), three
pasture ‘specialists’ (*Cardiocondyla nuda, Pheidole QM3, Rhytidoponera metallica*),
and one pasture ‘increaser’ (*Carebara QM1*). Among litter-extracted ants, a single
species of each group was found: a rainforest ‘specialist’ (*Carebara QM2*), a rainforest
‘increaser’ (*Hypoponera* sp.1), a pasture ‘specialist’ (*Pheidole QM3*), and a pasture
As the occurrences of most ant indicators were patchy, only eight satisfied the frequency requirement for statistical analysis (presence in at least four of the 30 plots).

Of the four rainforest indicators tested, *Hypoponera* sp.1 (litter-extracted rainforest ‘increaser’) responded significantly to the experimental treatments (Table 3), progressively increasing in abundance with increased shading.

Within pitfall-trapped ants, the composite index value for rainforest ‘specialists’ was greater in plots with shallow than deep mulch (Fig. 3a, Table 4). No experimental treatments influenced the composite index of rainforest ‘increasers’ significantly (Fig. 3b, Table 4). Levels of the composite index of pasture ‘specialists’ were significantly lower in plots with 90% shading compared with those with 0% shading (Fig. 3c, Table 4). Composite habitat indices were not calculated for litter-extracted ants, as only one component species was identified for each group of habitat indicators.

Multivariate analysis showed statistically significant effects of shading on species composition of pitfall-trapped ant assemblages (Table 4). The response was similar to that observed for ordinal-sorted arthropods: assemblages of pitfall-trapped ant species in plots under 0% shading were different from those under 90% shading, and assemblages under 50% shading were intermediate.

No ant functional groups responded significantly to the experimental treatments. The strongest response within ant functional groups was that pitfall-trapped ‘cryptic species’ showed a non-significant trend to increase in relative abundance with increased mulch depth (ANOVA for the effect of shading and mulch depth: $P = 0.226$, $P = 0.083$ respectively; interaction $P = 0.520$).
Soil moisture content and temperature

Mean soil moisture content was higher in pasture (at least 100 m away from the forest edge) than in rainforest (Fig. 4). Compared with control plots (no mulch or shading), a relatively high soil moisture content was maintained by all experimental plots regardless of differences in shading and mulch depth; however, none were as moist as the pasture or rainforest reference sites. No significant effects of shading or mulch depth were found on soil moisture content across the experimental treatments (two-factor ANOVA for the effect of shading and mulch depth: $P = 0.885$, $P = 0.158$ respectively; interaction $P = 0.670$), whereas a single factor ANOVA found significant differences among pasture, rainforest, no mulch (control) and the combined experimental treatments ($P < 0.001$), with pairwise tests showing that all were different.

Temperatures recorded in rainforest were lower on average than those in pasture, and the coefficient of variation of half-hourly temperatures over five days in rainforest was about half that of pasture (Fig. 5a). The provision of mulch in the experimental plots suppressed extreme temperature fluctuations (compare the control plot in Fig. 5a with mulched, unshaded plots in Fig. 5b). The presence of shading further reduced average temperatures and their coefficients of variation (Fig. 5b).

DISCUSSION

Responses of arthropods to shading and litter depth

Previous studies of soil and litter fauna development in revegetated sites have reported an initial colonisation by species tolerant of harsh environmental conditions (e.g. Andersen, 1993; Dunger et al., 2001; Fox & Fox, 1982; van Aarde et al., 1996). As
the restored habitat developed, these species were gradually or abruptly replaced by others characteristic of undisturbed habitats. In the context of rainforest restoration, our results suggest that successional patterns of this type could occur as a function of increased shading alone. The effects of shading shown here are consistent with the findings of other studies emphasising the importance of structural attributes, including canopy cover, for the organisation of soil and litter arthropod assemblages (e.g. Grimbacher et al., 2007; Holmes et al., 1993; Lassau & Hochuli, 2004; Proctor et al., 2003; Watts & Gibbs, 2002). Exceptions to this pattern include some groups of arthropods that are linked strongly with biological traits of live plant species (e.g. herbivores, which show strong host-plant affinities, Hunter & Price, 1992; Wardle, 2006).

The observed patterns of arthropod colonisation may be due, at least in part, to ameliorated temperature regimes in shaded plots. Temperature tolerance is important in influencing the distribution of ground-dwelling arthropods (Addo-Bediako et al., 2000; Pearson & Lederhouse, 1987), and a number of restoration studies have shown that arthropods characteristic of rainforest prefer cooler microclimatic conditions (Grimbacher et al., 2006; King et al., 1998). In contrast, soil moisture content did not explain colonisation patterns of arthropod assemblages (as it did not vary significantly among the experimental plots), even though small arthropods could arguably be more sensitive to reduced moisture levels (Levings & Windsor, 1984; Shure & Phillips, 1991). Had we conducted sampling in winter (typically cool and dry), the patterns and role of soil moisture may have been different, although arthropod activity and abundance would have been lower.
In addition to the effects of microclimatic conditions, growth of herbaceous vegetation may have affected arthropod colonisation patterns, particularly those characteristic of pastures. Unshaded plots and some of the plots with 50% shade showed increased levels of colonisation by pasture-associated taxa (Fig 2c). In these types of plot there was visible regrowth of herbaceous pasture plants, which potentially provided food and habitat for pasture-associated herbivorous arthropods, such as Homoptera and Orthoptera. Colonisation patterns of pasture ant species may have also been influenced by the supply of food resources (e.g. seeds from pasture, honeydew from Homoptera) associated with the growth of pasture plants.

In contrast to the strong effects of shading, our results suggest that the amount of litter may not be a strong determinant of arthropod assemblages in the context of rainforest restoration. Our results were consistent with the findings of other restoration studies of soil and litter arthropods colonising revegetated landscapes in various habitats (viz. sclerophyllous and temperate forest, shrubland, grassland, dune forest, heathland and rainforest), mainly from Australasia, Europe, North America and South Africa (53 studies reviewed by Nakamura (2007)). Using empirical and anecdotal evidence, these studies evaluated a large number of biotic and abiotic factors that potentially influence the colonisation of arthropod groups, including ants, beetles and spiders. The effects of differing levels of canopy cover and litter have been well studied, investigated by 14 and 21 studies respectively. While significant or potential impacts of shading were reported by all of the 14 studies, this was not the case for the effect of litter quantity. Seven of the 21 studies (including studies conducted in rainforest reforestation of formerly cleared landscapes, Jansen, 1997; King et al., 1998), found no apparent responses in the rate of arthropod colonisation to different amounts of forest litter.
Although rainforest-like arthropod assemblages may require the presence of at least some litter similar to that typically found on the rainforest floor (ca. 3 cm, see King et al., 1998; Nakamura et al., 2003), our results indicate that further addition of mulch does not benefit their colonisation.

It could be argued that the observed results may have been different had we incorporated other arthropod groups (e.g. spiders, beetles) into species-level analyses (Wassenaar et al., 2005). Furthermore, the use of higher taxonomic levels may have obscured significant responses, as individual species within an order may have responded in different manners. However, our results were consistent with other restoration studies incorporating diverse groups of soil and litter arthropods (Nakamura 2007, see above), suggesting that the fundamental patterns of arthropod colonisation would not have differed regardless of the arthropod groups investigated.

Effects of the experimental context

Most restoration studies to date have employed a post-hoc empirical approach to investigate the effects of factors considered important for the development of colonising fauna (Michener, 1997). The ecological effects of the factors under investigation are therefore difficult to elucidate, due to the presence of extraneous factors (Block et al., 2001; Catterall et al., 2004). This problem is further exacerbated by the fact that restoration projects are generally carried out on a site-specific basis with no spatial replication, limiting inference from the data (Block et al., 2001). This study provided an opportunity to test systematically the factors of interest since the experimental approach allowed for the construction of replicated units in which focal factors (i.e. shading and
litter depth) were manipulated, while extraneous factors were controlled.

There were, however, a number of constraints associated with the experimental design, which potentially limited colonisation of the constructed plots by rainforest-dependent arthropods. First, experimental plots lacked some of the habitat components of reforested sites, namely live plants that supply freshly shed foliage and woody debris, both of which may be important for the colonisation and persistence of rainforest-dependent arthropods (Andrew et al., 2000; Majer et al., 1984). Second, the mulch used in the experiment had been sterilised with steam, which may have killed potential food resources (e.g. prey micro-invertebrates, bacteria, fungi), and may have altered the chemical composition of the mulch, making it more or less favourable to arthropods. Third, the spatial and temporal scale of the experiment may have been insufficient for successful colonisation, although the location of plots adjacent to the forest edge maximised the probability of rainforest-associated taxa moving into the plots (Nakamura et al., 2008b). These limitations may be reflected by the low colonisation rates of litter-associated rainforest ant species (e.g. *Mayriella abstinens* complex, *Strumigenys harpya*, *Discothyrea* and *Lordomyrma* spp., see Nakamura et al. 2007), which were either very low in abundance or absent from the experimental plots. Nevertheless, a diverse array of arthropods, including rainforest-dependent taxa (albeit not as diverse as those commonly found in rainforest), did colonise the experimental plots and their assemblage composition responded differentially to the experimental treatments.

**Implications for practice**

In order to maximise rainforest biodiversity values (the occurrence of biota and
ecological process typical of intact rainforest; Catterall et al., 2004), restored habitat patches need to facilitate colonisation by fauna characteristic of rainforests, while inhibiting (re-)invasion by taxa characteristic of the matrix habitat (i.e. pasture). Our results show that rainforest restoration using lower density plantings, such as timber plantations, may facilitate colonisation by rainforest soil and litter arthropods even though canopy cover is not developed as rapidly, or to the same extent, as in ecologically-designed restoration plantings. However, the establishment of a fully closed canopy (90%) appeared to inhibit invasion by arthropods characteristic of the matrix habitat most effectively. Using deeper mulch did not create more suitable conditions for rainforest arthropods or offset the deleterious effects of less shade.

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Table 1. Effects of shading and mulch depth on abundances of ordinal-sorted arthropod taxa: results only for taxa where the main effects of ANOVA $P < 0.05$. Between-site effects are also shown. ‘Difference’ shows the results of LSD tests (levels with different letters are significantly different; A smaller, B larger, $P < 0.05$). Degrees of freedom (df) for shading, mulch depth, interaction and site are 2, 1, 2, and 4 respectively.

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<td>Other Hymenoptera</td>
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<td>0.035</td>
<td>0.911</td>
<td>0.468</td>
<td></td>
<td>0.001</td>
<td>0%(A) 50%(B) 90%(A)</td>
</tr>
<tr>
<td>Pauropoda</td>
<td>9</td>
<td>0.041</td>
<td>0.561</td>
<td>0.165</td>
<td></td>
<td>&lt;0.001</td>
<td>0%(B) 50%(A) 90%(A)</td>
</tr>
<tr>
<td>Thysanoptera</td>
<td>17</td>
<td>0.009</td>
<td>0.677</td>
<td>0.915</td>
<td>0.112</td>
<td></td>
<td>0%(B) 50%(A) 90%(A)</td>
</tr>
<tr>
<td>Litter extraction</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thysanoptera</td>
<td>4</td>
<td>0.025</td>
<td>0.877</td>
<td>0.976</td>
<td>0.561</td>
<td></td>
<td>0%(B) 50%(A) 90%(A)</td>
</tr>
</tbody>
</table>

†Number of plots ($N = 30$) where that taxon was present. Significant values ($P < 0.05$) are highlighted in bold.
### Table 2. Effects of shading and mulch depth on composite rainforest and pasture indices (ANOVA) and assemblage composition (PERMANOVA) of ordinal-sorted arthropods. Between-site effects are also shown. ‘Difference’ shows the results of post-hoc LSD (for composite indices) or permutation (for assemblage composition) tests (% levels with different letters are significantly different, $P < 0.05$). Df for shading, mulch depth, interaction and site are 2, 1, 2, and 4 respectively. Composite habitat indices were not calculated for all ‘specialist’ indicators as they occurred at less than four plots, or were absent altogether.

<table>
<thead>
<tr>
<th>$P$ value</th>
<th>Shading (S)</th>
<th>Depth (D)</th>
<th>S x D</th>
<th>Site</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Composite rainforest index</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>‘Increaser’ indicators (Pitfall traps)</td>
<td>9</td>
<td>0.045</td>
<td>0.669</td>
<td>0.993</td>
<td>0%(A) 50%(B) 90%(AB)</td>
</tr>
<tr>
<td>‘Increaser’ indicators (Litter extraction)</td>
<td>14</td>
<td>0.337</td>
<td>0.320</td>
<td>0.483</td>
<td>0.110</td>
</tr>
<tr>
<td><strong>Composite pasture index</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>‘Increaser’ indicators (Pitfall traps)</td>
<td>3</td>
<td>0.022</td>
<td>0.347</td>
<td>0.100</td>
<td>0%(B) 50%(AB) 90%(A)</td>
</tr>
<tr>
<td>‘Increaser’ indicators (Litter extraction)$^{\dagger}$</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Assemblage composition</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pitfall traps</td>
<td>n/a</td>
<td>0.006</td>
<td>0.448</td>
<td>0.548</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Litter extraction</td>
<td>n/a</td>
<td>0.252</td>
<td>0.339</td>
<td>0.994</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

$^{\dagger}$Number of taxa used for that composite indicator.

$^{\dagger}$Composite habitat index was not calculated as only one component taxon was found.

Significant values ($P < 0.05$) are highlighted in bold.
Table 3. Effects of shading and mulch depth on abundance scales of ant species: results only for species where the main effects of ANOVA \( P \leq 0.05 \). Between-site effects are also shown. ‘Difference’ shows the results of LSD tests (levels with different letters are significantly different; A smaller, B larger, \( P < 0.05 \)). Df for shading, mulch depth, interaction and site are 2, 1, 2, and 4 respectively.

<table>
<thead>
<tr>
<th>Indicator category</th>
<th>Freq†</th>
<th>Shading (S)</th>
<th>Depth (D)</th>
<th>S x D</th>
<th>Site</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pitfall traps</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Paratrechina</em> QM1</td>
<td>‘Generalist’</td>
<td>13</td>
<td>0.051</td>
<td>0.838</td>
<td>0.026</td>
<td>0.051</td>
</tr>
<tr>
<td><em>Pheidole</em> QM8 (mjobergi grp.)</td>
<td>‘Generalist’</td>
<td>10</td>
<td>0.022</td>
<td>0.652</td>
<td>0.288</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><em>Solenopsis</em> QM1</td>
<td>‘Generalist’</td>
<td>28</td>
<td>0.051</td>
<td>0.503</td>
<td>0.857</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Litter extraction</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hypoponera</em> sp.1</td>
<td>Rainforest ‘increaser’</td>
<td>8</td>
<td>0.044</td>
<td>0.210</td>
<td>0.871</td>
<td>0.099</td>
</tr>
</tbody>
</table>

† Number of plots (N = 30) where that species was present.

Significant values (\( P \leq 0.05 \)) are highlighted in bold.
Table 4. Effects of shading and mulch depth on composite rainforest and pasture indices (ANOVA) and assemblage composition (PERMANOVA) of ant species. Between-site effects are also shown. ‘Difference’ shows the results of post-hoc LSD (for composite indices) or permutation (for assemblage composition) tests (% levels with different letters are significantly different, $P < 0.05$). Df for shading, mulch depth, interaction and site are 2, 1, 2, and 4 respectively. Composite indices were not calculated for all litter-extracted ants, as less than 2 component species ($T^\dagger < 2$) were found from each index.

<table>
<thead>
<tr>
<th></th>
<th>T†</th>
<th>$S$</th>
<th>$D$</th>
<th>$S \times D$</th>
<th>Site</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Composite rainforest index</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>‘Specialist’ indicators (Pitfall traps)</td>
<td>5</td>
<td>0.178</td>
<td><strong>0.049</strong></td>
<td>0.335</td>
<td><strong>0.002</strong></td>
<td>Deep(A) Shallow(B)</td>
</tr>
<tr>
<td>‘Increaser’ indicators (Pitfall traps)</td>
<td>2</td>
<td>0.858</td>
<td>0.441</td>
<td>0.858</td>
<td>0.244</td>
<td>-</td>
</tr>
<tr>
<td><strong>Composite pasture index</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>‘Specialist’ indicators (Pitfall traps)</td>
<td>3</td>
<td><strong>0.048</strong></td>
<td>0.117</td>
<td>0.984</td>
<td><strong>0.009</strong></td>
<td>0%(B) 50%(AB) 90%(A)</td>
</tr>
<tr>
<td>‘Increaser’ indicators (Pitfall traps)$\dagger$</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Assemblage composition</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pitfall traps</td>
<td>n/a</td>
<td><strong>0.025</strong></td>
<td>0.851</td>
<td>0.510</td>
<td>&lt;0.001</td>
<td>0%(A) 50%(AB) 90%(B)</td>
</tr>
<tr>
<td>Litter extraction</td>
<td>n/a</td>
<td>0.387</td>
<td>0.676</td>
<td>0.276</td>
<td><strong>0.025</strong></td>
<td>-</td>
</tr>
</tbody>
</table>

$\dagger$Number of taxa used for that composite indicator.

$\dagger$Composite habitat index was not calculated as only one component taxon was found.

Significant values ($P < 0.05$) are highlighted in bold.
**FIGURE CAPTIONS**

**Fig. 1.** Schematic diagram of one of the field experimental sites (distances not to scale), showing criteria used when positioning experimental plots. ‘Shallow’ indicates sterilised mulch placed at a depth of 3-5 cm, and ‘deep’ is 10-15 cm. The seven plots were located randomly. (see text for more details).

**Fig. 2.** Effect of shading and mulch depth (S, shallow; D, deep) on composite rainforest and pasture indices of ordinal-sorted arthropods. Values for rainforest and pasture reference habitats (sampled the previous year) are also shown. The plots included in the statistical analysis are represented by closed bars.

**Fig. 3.** Effect of shading and mulch depth (S, shallow; D, deep) on composite rainforest and pasture indices of ant species. Values for rainforest and pasture reference habitats (sampled the previous year) are also shown. The plots included in the statistical analysis are represented by closed bars.

**Fig. 4.** Average soil moisture contents across the experimental treatments and unshaded, un-mulched controls. Values for rainforest and pasture reference habitats are also shown. All samples were taken in 2004. The plots included in the statistical analysis are represented by closed bars.

**Fig. 5.** Temperature fluctuations over five days recorded at: (a) un-mulched, unshaded control plots, rainforest and pasture reference habitats, and (b) plots with different shading and mulch depths, with mean values and coefficient of variations (CV). Temperature was recorded only from one site during April 2004. Horizontal lines are drawn at 25°C.
Figure 2

a Composite rainforest index ('Increasers', Pitfall traps)

b Composite rainforest index ('Increasers', Litter extraction)

c Composite pasture index ('Increasers', Pitfall traps)
Figure 3

a Composite rainforest index (‘Specialists’, Pitfall traps)

b Composite rainforest index (‘Increasers’, Pitfall traps)

c Composite pasture index (‘Specialists’, Pitfall traps)
Figure 4

Soil moisture (%)
Figure 5

**a**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Mean</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>20.84</td>
<td>23.92</td>
</tr>
<tr>
<td>Pasture</td>
<td>20.02</td>
<td>6.23</td>
</tr>
<tr>
<td>Rainforest</td>
<td>18.28</td>
<td>3.50</td>
</tr>
</tbody>
</table>

**b**

<table>
<thead>
<tr>
<th>Condition</th>
<th>Mean</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>0% Shallow</td>
<td>23.21</td>
<td>7.66</td>
</tr>
<tr>
<td>0% Deep</td>
<td>22.15</td>
<td>8.43</td>
</tr>
<tr>
<td>50% Shallow</td>
<td>20.01</td>
<td>4.63</td>
</tr>
<tr>
<td>50% Deep</td>
<td>21.18</td>
<td>4.52</td>
</tr>
<tr>
<td>90% Shallow</td>
<td>19.52</td>
<td>3.52</td>
</tr>
<tr>
<td>90% Deep</td>
<td>20.02</td>
<td>3.64</td>
</tr>
</tbody>
</table>