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Evaluating an experimental method for studying twig-dwelling ant communities

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DECLARATION

My two supervisors, Dr Marion Pfeifer and Michael Boyle gave me advice and suggestions throughout the course of the project.

All of the data collected for this study was collected by me with the help of Stability in Altered Forest Ecosystems Project (SAFE) research assistants, with the exception of the above ground biomass data which was collected by SAFE research assistants for a different project, but made available to all SAFE researchers. Some of the ant sample identifications which I made were checked for accuracy by my supervisor, Michael Boyle. I cleaned all of my own data, but the biomass data was provided pre-cleaned.

I was assisted in developing my analyses by Dr. Robert Ewers, my course organiser, who gave me advice on the focus my analyses should take, and by Jim Downie, who assisted me with carrying out the statistical tests and producing graphs in R.

ABSTRACT

Ants are a functionally important part of tropical forest ecosystems. Deforestation in Borneo and in tropical forests worldwide is likely have deleterious effects on ant communities, making it vital to better understand the risks this poses for ants, and by extension the entire forest ecosystem. In this study an experimental method for replicating, manipulating and monitoring twig-dwelling ant communities is trialled. Twig-dwelling ant communities are replicated in artificial twigs across three different deforestation gradients (primary forest, logged forest and oil palm plantation) with variable accuracy. It is also found that it is not possible to accurately assess the colonisation status of large numbers of twigs in a non-destructive manner, demonstrating that the method trialled is inadvisable, and that while they are more limited, destructive methods are likely to produce better results.

Key words: ants; artificial twig nests; Borneo; colonisation; community; deforestation; methods; *Plagiolepis alluardi*

ANTS ARE A HIGHLY DIVERSE FAMILY which inhabit many ecological niches in tropical forest ecosystems. They perform many important ecosystem functions including predation, herbivory, decomposition, (Keller and Gordon 2009) and seed dispersal (Pizo 2007). A loss of some species or change in community composition through logging or conversion to oil palm could therefore have negative effects on other aspects of the ecosystem (Crist 2009). From 2000 to 2010, Borneo lost 5,000,000 ha of forest, the most in SE Asia (Miettinen *et al.* 2011). Logged forest in Borneo has previously been shown to contain 80 percent of the ant species found in primary forest (Woodcock *et al.* 2011) and only 70 percent of the ant abundance (Woodcock *et al.* 2013).

Sunday *et al.* (2014) argue that many ant species (along with other ectotherms) in tropical areas live close to their physiological temperature safety margins, and survive based on behavioural adaptation. They also note that this characteristic is likely to make these species particularly vulnerable to climate change, and is is suggested that it is prudent to preserve environments so that they contain cool havens. Logged tropical forest has been found to be hotter and drier near the ground than primary forest as the thinned canopy permits greater penetration of sunlight (Hardwick *et al.* 2015). The combination of climate change and logging could, therefore, have worrying impacts on ants.

A further potential threat to ant communities due to deforestation is that of invasive ant species. Disturbed habitats often also provide greater opportunities for these species, and have caused huge conservation problems worldwide not only for other ants, but many other taxa. They also can cause significant problems for human activities such as agriculture (Holway *et al.* 2002).

Since ants play such an important role in tropical forest ecosystems, and because of the increasing threats they face, it is important to know exactly how their communities and their functionality within the ecosystem is likely to be impacted by future land use changes, as well as how to mitigate these problems (Crist 2009). To do this, further studies are vital to achieve a fuller understanding of the communities and processes involved.

Observational studies provide invaluable information in ecology, and while they are often simpler and more reliable, experimental manipulations allow a much greater understanding of any underlying processes. They allow the effects of different scenarios to be tested, and thus give the ability to make predictions. To investigate such land-use change scenarios, methods of experimental manipulation of communities must be reliably and comparably replicable in large sample sizes across multiple environments. A successful method would also allow a number of environmental factors to be standardized. Finally, it would be necessary to be able to accurately monitor the subjects of interest without causing disturbance to them.

Twig-dwelling ants can provide a useful model system as they are diverse and found in a wide variety of environments. They are also convenient as their nests are discrete, easy to find objects that can be easily relocated and characterized. Their nests are also easy to fabricate and therefore can be standardized to be made in the same dimensions, from the same plant species, of the same age and level of decay, and to have undergone the same treatments. This allows for much greater comparability of results. A number of studies have also shown that it is possible to create artificial twig nests out of a range of materials, including pine wood, local tropical woods and bamboo sticks, that are readily colonized by at least some species (Byrne 1994, Dornhaus *et al*. 2004, Sagata *et al*. 2010, Armbrecht *et al*. 2004, Levings 1983, Philpott & Foster 2005). Previous studies using artificial twigs have usually involved putting artificial twigs out in either a forest or plantation, leaving them for 60 ds then opening them to see how many were colonised, and by which species. (Sagata *et al*. 2010, Philpott & Foster 2005, Armbrecht *et al*. 2004, Levings 1983) No studies however, have used them for experiments involving several different environments or as a way of monitoring patterns of colonisation and abandonment of individual twigs over time. Byrne (1994), however, did a monitoring study with a similar purpose on natural twigs, and succeeded in accurately monitoring natural twigs that had already been proven to be colonised for abandonment, by watching each individual twig for ten minutes to see if any ants went in or out.

This study firstly aims to test the effectiveness of the artificial twig method and shed new light on the possibilities and caveats of using artificial twig nests for colonisation experiments. As stated above, most previous studies using artificial twigs have been carried out in a single environment. If this method is to be used more widely, it is important to know that it accurately works across a variety of environments. Determining how successful artificial twigs are at replicating a community living in natural twigs in a variety of environments could enable much more elaborate study involving land management change, different environmental treatments and translocations, or inform further use of captive twig-dwelling ant communities.

In addition, this study will also adapt the methods used by Byrne (1994) and investigate if it is possible to make assessments of twig colonisation status on large numbers of experimental communities in a non-destructive way, without disturbing the potential occupants in a way that may affect results. If this is possible, it could provide exciting new possibilities for community and evolutionary experiments on twig-dwelling ants.

The specific questions to be examined are: (1) is it possible to replicate twig-dwelling ant communities using artificial twigs across a range of environmental gradients caused by logging and conversion of forest to oil palm plantation, and (2) is it possible to accurately monitor large numbers of these artificial twigs to determine their colonisation status without causing significant disturbance to any potential colonies inside them? The first question will be determined by the following: (1a) whether the species richness and numbers of colonies can be accurately replicated in communities across environmental gradients; (1b) whether the community composition in the artificial twigs is the same as is found naturally in those environments; (1c) to what extent the differences in species richness and percentage of occupied twigs can be explained by differences in the surrounding environment, compared to differences in whether the communities were found in artificial twigs as opposed to naturally observed twigs.

METHODS

This study was carried out at the SAFE project in Sabah, Malaysia, an experimental landscape of tropical forest in the process of being logged and converted to oil palm (Ewers *et al.* 2011). At the time of this study the majority of the landscape was continuous forest which had experienced varying degrees of logging intensity.

The study incorporated three areas with differing land-use histories within this landscape: primary forest (SAFE plot VJR), heavily logged forest (SAFE plot C) and oil palm plantation (SAFE plot OP3). The virgin jungle reserve in which the primary forest remains were based had been logged around the edges but never in the centre where this study's plots were placed, and is located on the slopes of the highest mountain in the area. The heavily logged area had been logged twice and had just 16 percent forest cover remaining. It was highly variable in terms of ground vegetation type, amount of canopy cover and exposure to direct sunlight, with variously dense thickets of ginger, large numbers of saplings and young trees overgrown by vines, or with almost no vegetation cover other than a few dense shrubs. The oil palm plantation was well established, having been cleared, levelled into terraces, and planted 16 yrs previously. The closest area of natural forest was 1 km from the site (Ewers *et al.* 2011). Additional management practices allowed little vegetation other than the oil palm trees, this consisting solely of patches of grass, moss and ferns growing both on the ground and on the palms' trunks. There were signs of frequent fertilizer application.

Six plots measuring five by five meters were marked out in each forest area. The plot locations were chosen to coincide with one of SAFE's pre-existing fractally-arranged monitoring points in each area, making it possible to use existing datasets on above ground biomass. Each plot was located five meters from each monitoring point, in the direction that had the most similar level of canopy cover to the point itself. All except for two plots were placed at second-order points, each 178 m from one another. The exceptions were located in the virgin jungle reserve and were located at first-order monitoring points, each 56 m apart from one of the monitored second-order points due to logistical considerations (Ewers *et al.* 2011). Within each plot, five non-overlapping 1 m^2 sub-plots were placed at random.

SURVEYING NATURALLY OCCURRING OBSERVED COLONIES - An initial survey was carried out to determine what the species richness and percentage of twigs colonised were in each sub-plot in naturally-occurring twigs. Fifteen person-minutes of searching time was put in at each sub-plot to search for colonies of twig-dwelling ants. To locate potential colonies, all twigs of up to 4 cm in diameter found within the search time were broken open to detect any ants living in twig cavities. The number of twigs broken open was recorded and reference specimens were collected from all colonies found for later identification. A colony was defined as by Sagata *et al.* (2010) as a group of ants with at least one queen, or at least two workers with brood. Identification was carried out using the key written by Fayle (unpubl. data).

CREATING ARTIFICIAL TWIG-DWELLING ANT COMMUNITIES - Ten artificial twigs were placed in each of the sub-plots to create an experimental community. The artificial twigs were made out of freshly harvested oil palm fronds, and all measured 15 cm in length, and between 2 and 4 cm in diameter. Each had a 0.5 cm diameter hole drilled in one end to create a space for colonization. Prior to artificial twig placement, each subplot was cleared of natural colonies and potential twig nests through the initial survey. The twigs were placed down randomly in the sub-plots, so that they were not all pointing in the same direction, and were allowed to move around naturally within the sub-plot due to animal interference and rain throughout the course of the experiment. However, if they moved outside the sub-plot they would be gently picked up and replaced in the centre of the sub-plot. On the rare occasions that artificial twigs were found to be missing, they were replaced with new twigs so that the number of artificial twigs per subplot remained the same. The twigs were left in the field for 4 mos.

COLONISATION DETECTION EXPERIMENT – A non-destructive trial of an experimental method was carried out to investigate colonisation patterns by monitoring twigs in different environments over time. The technique used in this experiment was adapted from the method used by Byrne (1994) of monitoring natural twigs known to contain twig-dwelling ant colonies for abandonment by watching the twig entrance hole. In the present experiment, artificial twigs were watched for signs of colonisation. To do this, one person watched each sub-plot's group of ten twigs for ten minutes to see if any ants were going in or out of the holes in the twigs. If no ants went in or out, the twig was designated as not colonised. If one or two ants were seen going in or out of a twig during the 10 min time frame, the twig was noted down as a potential colony. If more than two ants were seen, the twig was deemed to be colonised. Care was taken to cause minimal disturbance to the twigs; however, at times it was essential to move leaf litter away from the entrance holes in order to allow monitoring to be carried out. Plots were visited between 0930 h and 1600 h. A record was kept of the time at which each sub-plot was worked.

Following being watched, every twig in the subplot was cut open and examined thoroughly for twig-dwelling ant colonies, to give the twig's true colonisation status. Reference specimens were taken from each colony found for later identification. This allowed for a robust test of the accuracy of the method for assessing colonisation status.

ENVIRONMENTAL MEASUREMENTS - Humidity, air temperature, soil temperature, ground surface temperature and light levels were regularly measured at each of the sub-plots.

On each visit, one measurement each was taken for humidity (using a General Tools Calibratable 7-Function Digital Psychrometer, model EP8710) and for air temperature (using a Digi-Sense Professional Thermocouple Thermometer, Model 20250-20) at the centre of each subplot and 20cm from the surface of the ground. Due to surface cover variability, and the frequent difference found between air temperature and surface temperature, surface temperature was also measured in four locations (using a Precision Gold Infrared Thermometer, model N85FR), 20 cm in from the corner of each subplot on every visit. One light level measurement was taken from the centre of each sub-plot, 1 m from the ground (using a SPER Scientific Light meter, Model 840006). Where light levels were above those that the device could measure, the maximum lux measurable by the device was recorded.

Above ground biomass had previously been measured at all second-order monitoring points as part of a different study at SAFE, using methods described by Chave *et al*. (2014). In calculations, the above ground biomass recorded from the nearest second-order point was used for the two points at first order points.

STATISTICAL METHODS - All statistical analyses were carried out using R (R Core Team, 2016).

In order to determine background effects on ant communities, a generalised linear model with Poisson error structure was employed to investigate the effect of forest type, twig type (observed natural community survey or artificial twigs), and different environmental variables on the species richness found per plot. A generalised linear model with quasibinomial error structure was used to investigate the effect of the same variables on the percentage of twigs that were colonised per plot. In cases where forest type was found to be significant, a multiple comparisons test was used to determine if there were significant differences between each of the forest areas.

To determine whether there were differences between natural and artificial communities in each forest area, an NMDS ordination was carried out using the R package *vegan* (Oksanen *et al.*, 2016).

To determine the effectiveness of the monitoring technique at correctly determining colonisation status of the twigs, a chi-squared test was carried out comparing for each twig whether a colony was observed though monitoring, and whether a colony was found once the twig was opened.

RESULTS

REPLICABILITY OF COMMUNITIES - A series of analyses were carried out to determine whether the species richness and number of colonies found remained constant between the observed and artificial twig-dwelling ant communities.

SPECIES RICHNESS - In total, 26 genera of ants were identified between the three forest areas, but only nine of these were found in both observed and artificial twigs, while ten genera were found only in observed twigs and seven were found only in artificial twigs. Of the 26 genera found, only five were found in all three forest types, while three were found in primary forest and logged forest but not oil palm plantation, a further three were found in logged forest and oil palm plantation but not primary forest, while only one was found in primary forest and oil palm but not logged forest. There were also 14 genera found only in one forest area; five in primary forest, five in logged forest and four in oil palm plantation. Overall primary forest had 14 genera, logged had 16 and oil palm plantation had 13 (Fig. 1).

The Generalised Linear Model investigating the relationship between species richness and the environmental factors measured found a significant difference in species richness due to forest type, but no significant relationship was found due to above ground biomass, air temperature, surface temperature, humidity, light levels or, most importantly, whether the twigs were observed or artificial (Table 1). Using a multiple comparisons test, the effect of forest area was further elucidated and a significant difference in species richness per plot was found between primary and logged forest but not between primary forest and oil palm plantation or between logged forest and oil palm plantation (Fig. 2).

NUMBER OF COLONIES - Some genera were overall much more prevalent than others, with *Plagiolepis* colonies being found vastly more often than any other Genus, with over 75 colonies found while 11 other genera were only found once each (Fig. 1).

The Generalised Linear Model investigating how the percentage of searched twigs that were colonised per plot was affected by the measured environmental factors did not find any of the tested environmental variables to have a significant effect (Table 2).

SPECIES COMPOSITION - The NMDS ordination shows a great deal of similarity and overlap in species composition between the forest areas, with the least overlap being seen between oil palm plantation and primary forest (Fig. 3). Most notably however, the ordination also shows slight differentiation between the observed and artificial communities, particularly for primary forest.

COLONISATION DETECTION EXPERIMENT - The Chi-Squared test showed significant similarities between the colonisation status determined through the non-invasive monitoring method and the true colonisations status determined through the destructive method ($\chi^2 = 41.88$, df = 1, p = $9.707e^{-11}$). Artificial twigs were correctly judged to not be colonised 792 times and 17 artificial twigs were correctly judged to be colonised, but 50 artificial twigs were falsely judged to be colonised, and 39 were falsely judged to be empty.

DISCUSSION

REPLICABILITY OF SPECIES RICHNESS - The fact that only seven out of 26 genera were found in both observed and artificial twigs and that there were 11 genera found only in natural twigs suggests that the artificial twigs did not provide a suitable nest for many genera and therefore are not effective in attracting communities made up of the same genera as those in a natural, observed community. The fact that there were so many genera that were only found once in either twig type counters this, however, and suggests that the most likely explanation is that sample sizes may simply have been too small to truly reflect the twig type preferences of many of the genera.

It is of note that the genera found in oil palm plantation in this study differed significantly from those in another study on species richness in oil palm plantations in Sabah. Brühl & Eltz (2010) found that the aggressive invasive yellow crazy ant *Anoplolepis gracilipes*, which is not a specialist twig-nesting species (Drescher *et al*. 2011), was the most common species in this forest type, while this study most frequently found *Plagiolepis,* a genus that Brühl & Eltz (2010) did not report finding even once. *Plagiolepis alluardi* is thought to originate in Madagascar and surrounding islands (Wetterer 2013) and is the only species of the genus in Borneo (Pfeiffer *et al*. 2011). While records are not entirely conclusive, they are known to be an invasive species across much of the world, probably including Borneo (Wetterer 2013). That Bruhl and Eltz (2010) did not find them is potentially because *P. alluardi* did not exist at the sites in which they were working, but it is also possible that their tuna-bait method was less effective for this specific genus than the methods employed in this study. If this is the case, it is possible that this would hold true for a number of different genera, not just *P. alluardi*. The fact that this study shows *P. alluardi* takes so readily to artificial twig nests could be a particularly useful outcome of this study for conservation research.

The significantly lower species richness per plot found in primary forest compared to logged forest, as well as fewer genera found overall than in logged forest (but more overall than in oil palm) is in contrast to results reached by Woodcock *et al*. (2011), who found that logged forest had 20 percent lower species diversity for ants (including non-twig-dwelling species). One potential reason for this is that during this study, there was a major El Niño drought. This almost certainly biased the study significantly. During the time that the survey of natural communities observations were made and the artificial twigs were placed down, the forest was experiencing an increasingly severe drought. The drought began to break around 2.5 mos after the first artificial twigs were placed in the forest, and around 1.5 mos before the artificial twigs were opened. This is likely to have strongly affected the genera that were prevalent for both surveys. There is evidence to suggest that species living in hotter conditions adapt greater thermal tolerances (Kaspari *et al*. 2015). As such it is likely that the genera living in logged forest were ones with greater tolerances for hot, dry conditions and therefore were less affected than the genera in primary forest. It is possible that a portion of the genera living in the primary forest may have been killed in large numbers and become locally rare during and following the drought.

REPLICABILITY OF NUMBER OF COLONIES – The fact that no significant difference was found between the percentage of twigs occupied and the type of twig, and the fact that there was no significant interaction found between twig type and forest type for the mean percentage of occupied twigs suggests that in terms of quantity of colonies, the artificial twigs can provide comparable results to natural twigs.

Byrne (1994) found that for one m square plots with ten artificial twigs placed, 18 percent of the twigs would be colonised after 60 ds. This study found lower colonisation rates, with only 6.2 percent of artificial twigs colonised. This could be due to a number of factors such as the longer time the twigs were in the field, the drought, the location, or the material the artificial twigs were made from.

Woodcock *et al*. (2013) found very different results in terms of ant abundance in different forest types and found 20 percent fewer ants (including non-twig-dwelling species) in logged forest than in primary forest. Again, the most likely explanation for this is that the drought disproportionately affected ants in primary forest compared to ants in logged forest. Another caveat to the lack of significant difference in numbers of ants found between areas is that the presence of such huge numbers of *P. alluardi*, a species not frequently found by Woodcock *et al*. (2013), in the disturbed habitats but not primary forest, is likely to have disproportionately affected the results. In an area without *P. alluardi* the findings may have been very different.

REPLICABILITY OF SPECIES COMPOSITION - The overall picture of species composition that was painted by the ordination is that the colonies living in the artificial twigs and the observed communities have overlap with one another, but also show some differences. Logged forest and oil palm plantation also show more overlap than primary forest. This pattern is found to an extent across all three forest areas, but particularly noticeably in primary forest. This is an important result, as it shows that the artificial twig method does not necessarily produce comparable results equally across all forest types.

The differences between the twig types for all forest areas is likely due to the fact that while there were nine genera that both twig types had in common, there were also 17 genera which endemic to only one of the communities. The fact that the primary forest showed more differentiation compared to the other forest areas again is likely to be due to the fact that logged forest and oil palm plantation contained such a preponderance of *P. alluardi* colonies compared to primary forest. This may also have caused the greater mismatch between twig types in primary forest. In logged forest and oil palm plantation the overwhelming numbers of *P. alluardi* (which was found to readily inhabit both twig types) likely buffered the effects of other genera. Primary forest did not have as many *P. alluardi*, and therefore reflected the preferences of other, native, genera more strongly than did the other areas. *Crematogaster* is particularly likely to have exacerbated this effect, as it was the most common genus in primary forest, but was only found in natural twigs.

The material the twigs were made from may also have had an impact on the success and accuracy of replication between the different areas. The oil palm fronds were used as they were locally available and inexpensive, but they were not the ideal material. The fact they are found in large quantities in one forest area but not the others introduces bias, as the ants in oil palm plantations are more likely to be genera that have a propensity for living in oil palm fronds, since they constitute one of the only twig nest materials in that environment. It would also have been better to use a different type of twig than oil palm fronds, as once the drought ended, their disintegration proceeded much more quickly, with disproportionately greater speed in wetter areas with more leaf litter, such as primary forest.

Armbrecht *et al*. (2004) found that although no ants appeared to show a preference for twigs from any particular tree species, using twigs made from wood from a diversity of different tree species in a plot encouraged greater species richness in Colombian coffee plantations. Ideally this would be tried in a repeat of this experiment, as it could create very different results regarding species richness and community structure. The presence of a variety of native species of twig could have encouraged a more normal selection of genera in the artificial twigs.

CONCLUSIONS ON COMMUNITY REPLICABILITY –The results found here on species richness, colony numbers and species composition suggest that while it is possible to replicate a community with a similar species richness and number of colonies to the natural community in artificial twigs, the actual species composition of the community is likely to be somewhat different, particularly for primary forest. The findings here have some major caveats however, particularly as a drought took place during the course of the study, and it is likely that in normal conditions the results would have been drastically different for virtually every aspect investigated.

COLONISATION DETECTION EXPERIMENT - The chi-squared test shows that there was a positive and significant relationship between the predictions made by the colonisation monitoring method trialled and the destructive method. However, the significance of the result was skewed by the fact there were many more empty twigs, which were correctly identified much more frequently, than colonised twigs. It is therefore concluded that the method employed was not an accurate way to monitor colonisation patterns.

Byrne (1994), from whom the methods of this experiment were adapted, reported that in their experiment 84 twigs were correctly assessed as empty through watching them, while only three were incorrectly assessed as empty. This colonisation monitoring experiment may have produced more accurate results if fewer twigs were watched at a time, as with Byrne's methodology. However sample size would then have to be decreased due to time limits and manpower constraints, which would limit the utility of this technique for large-scale experiments. The fact that the colonisation status was already known in Byrne's experiment likely assisted in its accuracy, as the way the twigs were found in the first place (by following the ants back to the nest from tuna bait) probably selected for large, active colonies which will have been easier to assess. There is also the possibility that Byrne's experiment was not quite as accurate as thought. While the twigs were checked for false abandonment results, there was not a check for whether the twigs had in some cases been abandoned earlier than thought, and, as with the twigs in this experiment, the researchers were simply seeing ants entering the twigs while foraging.

The choice of artificial twig material may also have played a role in this part of the study by making the monitoring less successful. As the twigs aged they also became more internally hollow and fibrous. This may have provided additional nesting choices to ants looking to colonise the twig, but it also made it much more difficult to monitor the nesting holes, as there were more possible entrances to each twig than there would have been if an artificial twig made out of hardwood had been used.

IN CONCLUSION – The accuracy of artificial twigs for replicating communities in different logging scenarios has overall been proven to be good by this study. The trial method for unobtrusively monitoring large numbers of artificial twigs over time for ant colonisation and abandonment has, however, been found to be inaccurate, putting great limitation on the versatility of twig-dwelling ants as an effective experimental subject for studying the potential future impacts of deforestation and climate change on ant communities. Methods that involve destruction of nest twigs for data collection as have been used in previous studies, while more restrictive, should provide much more robust evidence on the threats posed to ants and the ecosystem services which they provide.

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LITERATURE CITED

ARMBRECHT, I., I. PERFECTO, AND J. VANDERMEER, 2004. Enigmatic biodiversity correlations: ant diversity responds to diverse resources. Science 304: p.284–286.

BRÜHL, C.A., AND T. ELTZ, 2010. Fuelling the biodiversity crisis: species loss of ground-dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo). Biodivers Conservation 19: p.519–529.

BYRNE, M.M., 1994. Ecology of Twig-Dwelling Ants in a Wet Lowland Tropical Forest. Biotropica 26: p.61.

CHAVE, J., M. REJOU-MECHAIN , A. BURQUEZ, E. CHIDUMAYU, M.S. COLGAN, W.B.C. DELITTI, A. DUQUE, T. EID, P.M. FEARNSIDE, R.C. GOODMAN, M. HENRY, A. MARTINEZ-YRIZAR, W.A. MUGASHA, H. C. MULLERLAND, M. MENCUCCINI, B.W. NELSON, A. NGOMANDA, E.M. NOGUEIRAS, E. ORTIZ-MALAVASSI, R.P ELISSIER, P. PLOTON, C.M. RYAN, J.G. SALDARRIAGA AND G. VIEILLEDENT, 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Global change biology 20: p.3177–3190.

CRIST, 2009. Biodiversity, species interactions, and functional roles of ants (Hymenoptera: Formicidae) in fragmented landscapes: a review. Myrmecological News 12: p.3-13.

DORNHAUS, FRANKS, HAWKINS, AND SHERE, 2004. Ants move to improve: colonies of Leptothorax albipennis. Animal Behaviour, 67.

DRESCHER, J., H. FELDHAAR, AND N. UTHGEN, 2011. Interspecific Aggression and Resource Monopolization of the Invasive Ant *Anoplolepis gracilipes* in Malaysian Borneo. Biotropica, 43(1): p.93–99.

EWERS, R.M., R.K. DIDHAM, L. FAHRIG, G. FERRAZ, A. HECTOR, R.D. HOLT, V. KAPOS, G. REYNOLDS, W. SINUN, J.L. SNADDON, AND E.C. TURNER, 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. Philos Trans R Soc Lond, B, Biol Sci 366: p.3292–3302.

FAYLE, TOM M., unpubl. data. Key to the workers of the 100 ant genera and 12 ant subfamilies of Borneo in English and Malay. Unpublished.

HARDWICK, S.R., R. TOUMI, M. PFEIFER, E.C. TURNER, R. NILUS, AND R.M. EWERS, 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. Agricultural and Forest Meteorology 201: p.187–195.

HOLWAY, D.A., L. LACH, A.V. SUAREZ, N.D. TSUTSUI, AND T.J. CASE, 2002. The causes and consequenses of ant invasions. Annu Rev Ecol Syst 33: p.181–233.

KASPARI, M., N.A. CLAY, J. LUCAS, S.P. YANOVIAK, AND A. KAY, 2015. Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. Global change biology 21: p.1092–1102.

KELLER, L. AND GORDON, E., 2009. The Lives of Ants. First edition. Great Clarendon Street, Oxford, OX 6DP, Oxford University Press.

LEVINGS, S., 1983. Tropical Forest: Some Causes of Patchy Species Distributions. Ecological Monographs, 53: 435–455. doi:10.2307/1942647

MIETTINEN, J., C. SHI, AND S.C. LIEW, 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. Global change biology 17: p.2261–2270.

OKSANEN, J.F., G. BLANCHET, M. FRIENDLY, R. KINDT, P. LEGENDRE, D. MCGLINN, P.R. MIN CHIN, R. B. O'HARA, G.L. SIMPSON, P. SOLYMOS, M.H.H. STEVENS, E. SZOECS AND H. WAGNER, 2016. vegan: Community Ecology Package. R package version 2.4-0. http://CRAN.R-project.org/package=vegan

Pfeiffer, M., D. Mezger, S. Hosoishi, B. Yahya, and A. Kohout, 2011. The Formicidae of Borneo (Insecta: Hymenoptera): a preliminary species list. Asian Myrmecology, 4: p.9–58.

Philpott, S.M., and P.F. Foster, 2005. Nest-site limitation in coffee agroecosystems: artificial nests maintain diversity of arboreal ants. Ecol Appl 15: p.1478–1485.

Pizo, M.A., 2007. The Use of Seeds by a Twig-Dwelling Ant on the Floor of a Tropical Rain Forest. Biotropica 0: p.070507065322003

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Sagata, K., A.L. Mack, D.D. Wright, and P.J. Lester, 2010. The influence of nest availability on the abundance and diversity of twig-dwelling ants in a Papua New Guinea forest. Insectes Soc 57: p.333–341.

Sunday, J.M., A.E. Bates, M.R. Kearney, R.K. Colwell, N.K. Dulvy, J.T. Longino, and R.B. Huey, 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc Natl Acad Sci U S A 111: p.5610–5615.

Wetterer, J.K., 2013. Worldwide spread of Alluaud's little yellow ant, Plagiolepis alluaudi (Hymenoptera: Formicidae). Myrmecological News, 19: p53-59.

Woodcock, P., D.P. Edwards, T.M. Fayle, R.J. Newton, C.V. Khen, S.H. Bottrell, and K.C. Hamer, 2011. The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. Philos Trans R Soc Lond, B, Biol Sci 366: p.3256–3264.

Woodcock, P., D.P. Edwards, R.J. Newton, C. Vun Khen, S.H. Bottrell, and K.C. Hamer, 2013. Impacts of intensive logging on the trophic organisation of ant communities in a biodiversity hotspot. PLoS ONE 8: p.e60756.

TABLES

	estimate	2.50 %	97.50%	statistic	p.value
(Intercept)	-5.79	-18.881	7.166	-0.877	0.381
Above Ground Biomass (Mg / 0.0625 ha)	2.208	-0.028	4.455	1.938	0.053
Air Temperature (°C)	0.291	-0.099	0.698	1.444	0.149
Surface Temperature (°C)	-0.016	-0.273	0.238	-0.12	0.904
Humidity (%)	-0.01	-0.048	0.028	-0.494	0.622
Light Levels (Lux)	-0.001	-0.003	0	-1.638	0.101
Twig Type	-0.302	-0.752	0.138	-1.337	0.181
Forest area (Oil Palm Plantation)	-0.416	-1.769	0.936	-0.606	0.545
Forest area (Primary Forest)	-2.955	-5.334	-1.032	-2.719	0.007
Above Ground Biomass with Air Temperature	-0.071	-0.148	0.007	-1.799	0.072

Table 1. Results of a GLM with Poisson error structure examining the effects of forest area, twig type and various environmental variables on the species richness of twig-dwelling ants found per plot.

	estimate	2.50 %	97.50 %	statistic	p.value
(Intercept)	4.531	-22.302	31.876	0.332	0.743
Above Ground Biomass (Mg / 0.0625 ha)	-5.56	-11.758	-0.401	-1.952	0.063
Air Temperature (°C)	0.287	-0.671	1.273	0.583	0.565
Humidity (%)	-0.061	-0.15	0.016	-1.497	0.148
Surface Temperature (°C)	-0.362	-0.875	0.118	-1.448	0.161
Light Levels (Lux)	-0.002	-0.007	0.002	-0.913	0.371
Twig Type	-0.494	-2.015	1.35	-0.601	0.553
Forest Area (Oil Palm Plantation)	0.556	-2.336	3.638	0.372	0.714
Forest Area (Primary Forest)	-3.625	-8.281	0.076	-1.757	0.092
Above Ground Biomass with Air Temperature	0.203	0.023	0.421	2.038	0.053
Twig Type with Forest Area (Oil Palm Plantation)	0.481	-1.993	2.747	0.406	0.689
Twig Type with Forest Area (Primary Forest)	2.145	-0.43	5.458	1.553	0.134

Table 2. Results of a GLM with quasibinomial error structure examining the effects of forest area, twig type and various environmental variables on the percentage twigs colonised by twig-dwelling ants per plot.

FIGURES

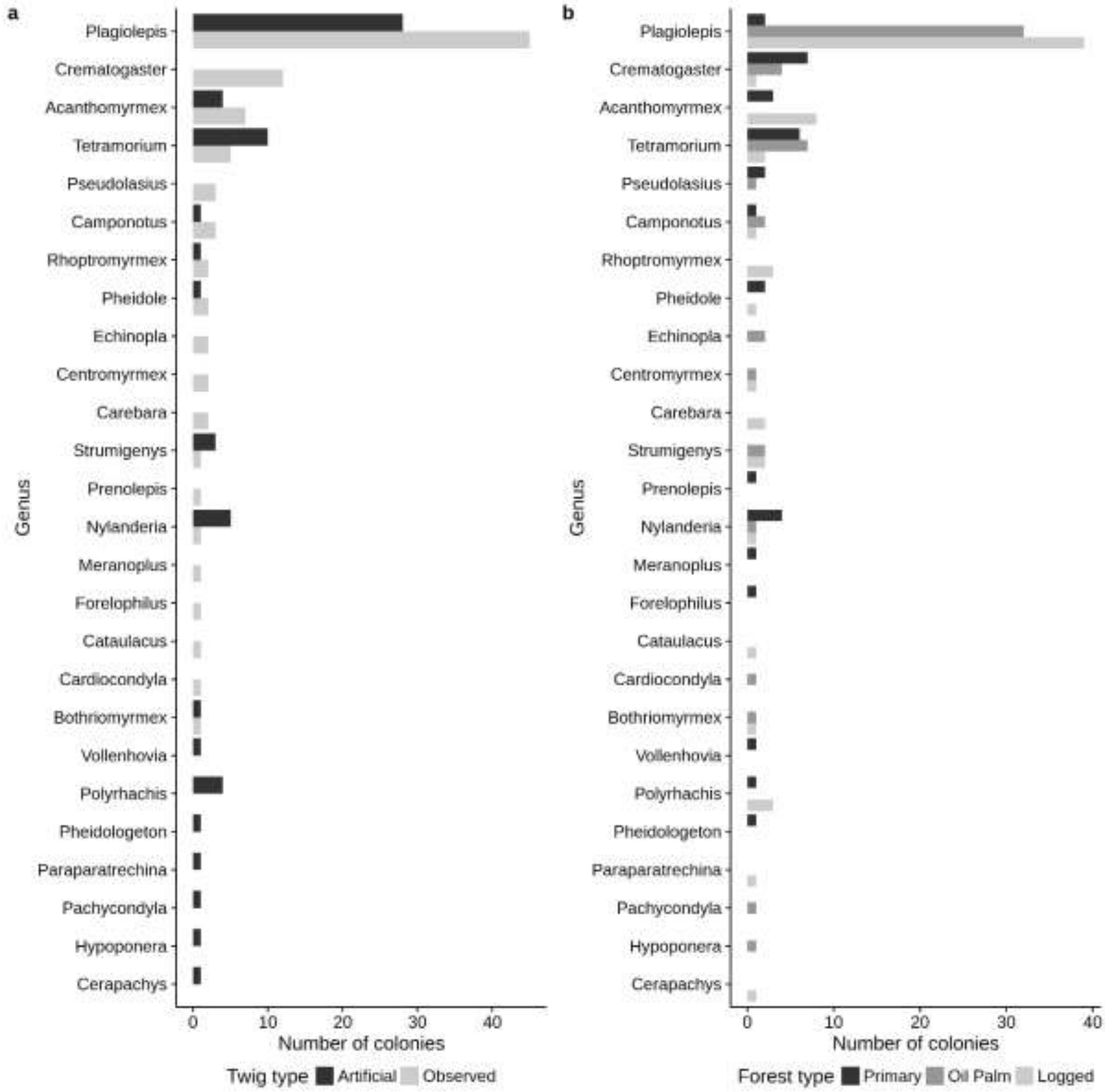

Figure 1. The number of colonies of each genus found (a) by twig type and (b) by forest area.

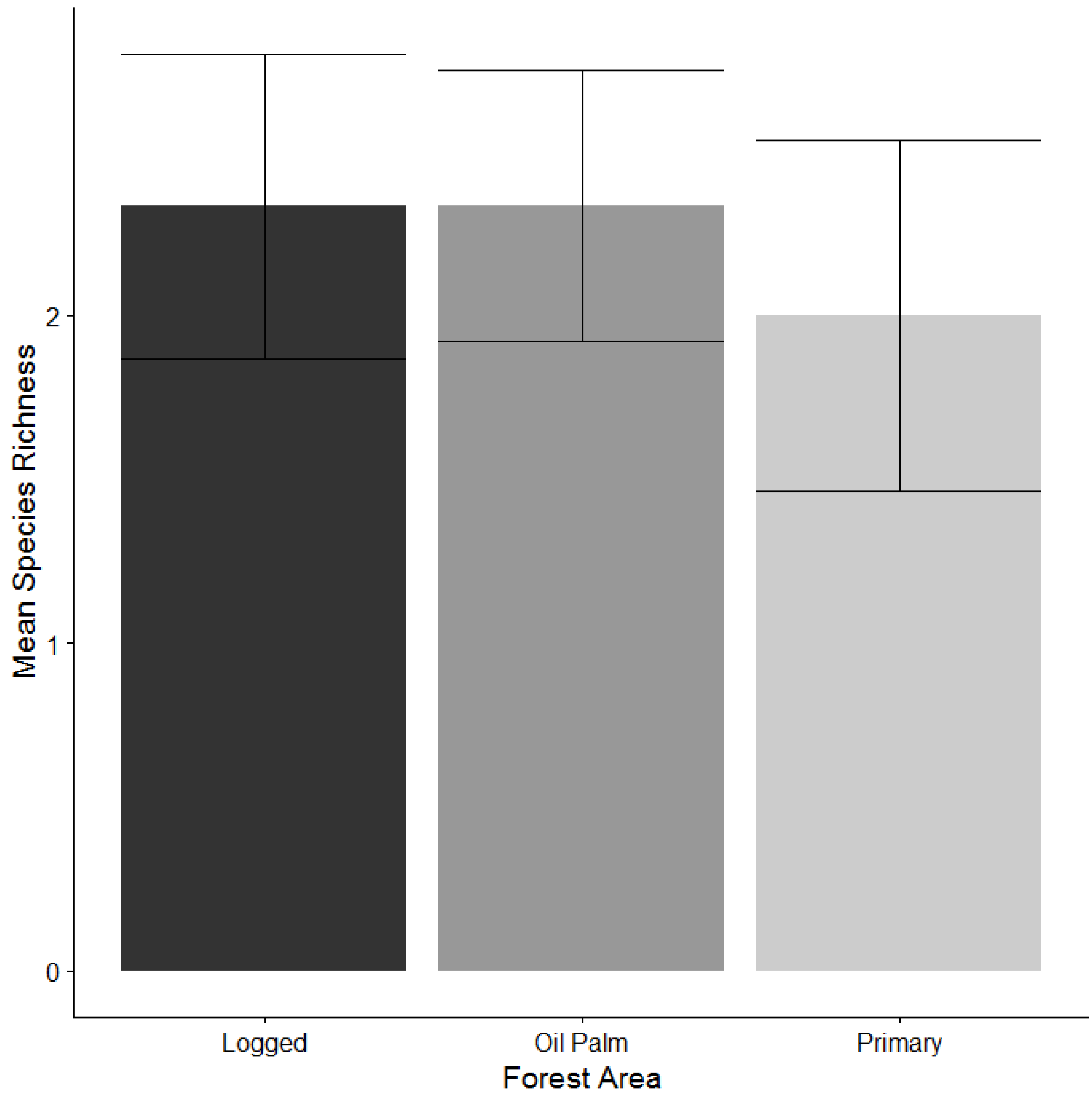

Figure 2. Mean species richness of twig-dwelling ants per plot in logged forest, primary forest and oil palm. Bars indicate standard error.

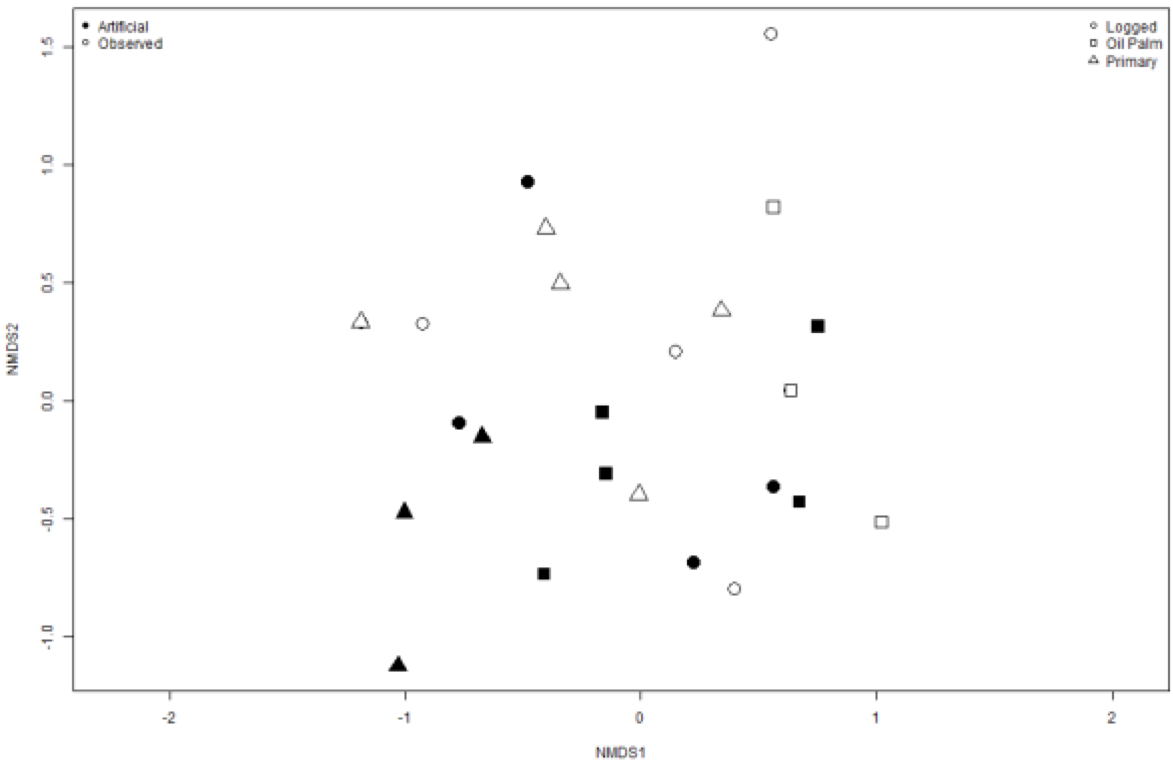

Figure 3. An ordination of species composition found per plot in observed and artificial twigs in primary forest, logged forest and oil palm plantation.