Research Article

An elevational gradient in litter-dwelling ant communities in Imbak Canyon, Sabah, Malaysia

Kalsum Mohd Yusah^{1,2*}, Edgar Clive Turner^{2,3}, Bakhtiar Effendi Yahya¹ and Tom Maurice Fayle⁴

¹Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Locked Bag 2073, 88999 Kota Kinabalu, Sabah, Malaysia. *email:kalsum.myusah@gmail.com

²Forest Ecology and Conservation Group, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, SL5 7PY, UK.

³Insect Ecology Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.

⁴Laboratory of Tropical Ecology, Faculty of Science, University of South Bohemia, Branišovská 31, CZ-37005 České Budějovice, Czech Republic.

ABSTRACT. The predicted effect of climate change across a range of taxa is currently a hotly debated topic. There is a pressing need to learn more about how animals and plants respond to climatic change in their surrounding habitats. A commonly used approach is to link changes in the taxon of interest to elevational gradients, where communities under a range of climatic conditions can be sampled in a small area. We conducted an elevational study of ant communities in the Imbak Canyon Conservation Area. The objective of the study was to investigate changes in ant species richness, abundance and composition along an elevational gradient from 300 m to 1,100 m a.s.l. with sampling points spaced at 100 m elevational intervals. We also measured litter depth to assess whether this factor affected ant communities within each elevational band. Over a total of 1,296 trap-hours, we collected 1,002 individual ants from 41 genera and 116 species. Ant species richness decreased with increasing elevation, as has been found for other invertebrates. However, there were no changes in ant abundance or species

composition along the elevational gradient. Our results indicate that the ant communities within this area may be relatively robust to increasing temperatures. Further studies in similar habitats and environments should be carried out in order to reveal the consistency of these results across the region and to investigate changes in ant contribution to ecosystem functions at different elevations.

Keywords: Formicidae, climate change, rainforest, heath forest, pitfall trap, elevational gradients.

INTRODUCTION

Climate change is one of the most pressing threats to biodiversity on Earth, potentially affecting a wide range of taxa across many geographical regions (Bellard *et al.*, 2012; Chown *et al.*, 2010). This is especially true in the tropics, where animals and plants are closer to their thermal limits than in temperate zones (Deutsch *et al.*, 2008; Ghalambor *et al.*, 2006). The fact that tropical rainforests are highly

diverse makes it even more urgent to document the effects of changes in climate.

There has been extensive work using latitudinal and elevational gradients in animal and plant composition to predict the effects of climate change on biotic communities (Condamine et al., 2012; Deutsch et al., 2008; Tewksbury et al., 2008). The general conclusion of this research has been that there are more species in lower latitudes than higher latitudes, and that these species are more vulnerable to climate warming, even once other factors such as phylogenetic history and ecological traits have been taken into account (Diamond et al., 2012). Comparably, higher elevations also tend to contain fewer species than lower elevations (Beck & Kitching, 2009: Kumar et al., 2009; Hillebrand, 2004). While the drivers of these diversity patterns are not yet entirely clear, gradients in climate are very likely to play a role, hence the use of latitudinal and elevational gradients as surrogates for climate change through time (Botes et al., 2006; Taylor et al., 1999).

Ants have been among the most successful groups of animals since they began to expand and diversify in the Late Cretaceous and Early Eocene: a period that coincided with the rise of the angiosperms and the major groups of herbivorous insects (Moreau et al., 2006). They occur in nearly all terrestrial habitats, occupy a wide range of ecological niches and consequently play important roles in providing ecosystem services and maintaining ecosystem stability (Wilson, 1987).

Because of their importance to the stability of ecosystems, it is imperative that ant distributions across gradients of latitude and elevation are known. This will allow for the assessment of the vulnerability of ant communities to climate change. In particular, it is vital to discover whether ants are still able to maintain the ecosystem services that they provide in a changing climate. Ants are generally thermophilic (Dunn et al., 2007), with diversity declining further away from the

equator (Dunn et al., 2009), and with increasing elevation (e.g. Bruhl et al., 1999). According to a recent study by Diamond et al. (2011), ants at lower elevations have a smaller thermal buffer, making them more sensitive to climate warming. Lowland tropical species are therefore likely to be most sensitive to climate change.

To date, there has been relatively little research carried out in Sabah on elevational changes in ant communities, apart from work by Bruhl (1999); Malsch et al. (2008) and Mohamed (1998). All these studies have been conducted at a single site: Mount Kinabalu. With increasing elevation, they found a monotonic decrease in species richness. Whether this pattern is consistent across other mountains in the same region or whether the more commonly found mid-elevational peak in species richness seen in many other taxa (Stevens, 1992; Colwell & Lee, 2000; Cardelus et al., 2006) is present, is not currently known.

Here we present data from an expedition to Imbak Canyon, Sabah, Malaysia, on ant species diversity and composition along an elevational gradient. The area surrounding the canyon is newly explored and there have been only two previous expeditions to the area (in 2004 and 2010). Our study was the first to record ant diversity and elevational changes among ant communities within this area.

MATERIALS AND METHODS

Fieldwork was carried out in the forest near Gunung Kuli Research Station, Imbak Canyon, Sabah, Malaysia (5.04N, 117.06E) between 13 and 20 June 2011. The Imbak Canyon Conservation Area covers an area of 30,000 hectares and is a Class I (Protection) Forest Reserve, conserved as a watershed and for the maintenance of stability of essential climatic and other environmental factors. Sampling was carried out along the "Ridge trail" which follows the main ridge to the west of the research station. The trail is approximately 10 km long and passes through a lowland mixed dipterocarp forest before entering the lower

montane heath forest above 1,000 m a.s.l. The climate in the interior of Sabah in mainly aseasonal, with an average annual rainfall of 2,669 mm and average annual temperature of 26.7°C recorded at the lowland dipterocarp rainforest at the nearby Danum Valley Field Centre (Walsh & Newbery, 1999).

Pitfall trapping for ants was conducted at intervals of 100 m elevation from 300 m to 1,100 m a.s.l. (nine different elevations). At each point, two pitfall traps were placed at a horizontal distance of 56 m from each other with the trail as the middle point (the total number of pitfall traps per elevation was limited by the length of the expedition). A total of 18 pitfall traps (nine pairs) were put in place for 72 hours (1,296 trap-hours).

The pitfall traps used in this research comprised a 500 ml bottle, a funnel of 19.5 cm diameter, and four wooden sticks of approximately 30 cm in length, to which a plastic cover was tied to shelter the trap from rain (Figure 1). A hole was dug and the bottle, with c. 150 ml of 70% alcohol added, was placed in the hole and the funnel was inserted into it such that the funnel rim was level to the ground. Earth was packed around the gap between the funnel edge and the ground to

increase trapping efficiency. The four sticks supporting a plastic cover were then stuck into the ground to cover the funnel. This pitfall trap design is identical to those that are being used in the nearby Stability of Altered Forest Ecosystems project (SAFE), one of the largest forest fragmentation experiments in the world (Ewers et al., 2011).

Litter depth (cm) was measured in three different locations at approximately 30 cm distance from each other, with the pitfall trap as the centre point. An average was taken to represent litter depth for each site.

Changes in species richness and abundance across different elevations and litter depths were tested using General Linear Models. The effects of elevation and litter depth on species composition were measured using Canonical Correspondence Analysis. Analyses were carried out in R Statistical Analysis Packages (R Development Core Team 2010) and CANOCO 4.5.

RESULTS

A total of 1,002 ants from 10 subfamilies (41 genera, 116 species) were collected (Table 1). The sub-family Myrmicinae represented



Figure 1. A pitfall trap showing the funnel, plastic sheet and four wooden sticks. A bottle containing alcohol was placed under the funnel. Note the hole cutter (candak) that was used to dig the pitfall trap.

51.7% of the total species, followed by Ponerinae (18.1%), Dolichoderinae (12.9%) and Formicinae (8.6%). The remaining subfamilies accounted for 6.9% of the total species number.

Ant species richness decreased with increasing elevation, but did not change with litter depth (Elevation: T=-2.47, P=0.026; Litter depth: T=-0.025, P=0.803). Ant abundance was not affected by either elevation or litter depth (Elevation: T=-0.57, P=0.575; Litter depth: T=-0.32, P=0.752; Figure 2). There was also no effect of either elevation or litter depth on species composition (Elevation: F=1.164, P=0.185; Litter depth: F=0.964, P=0.446; Figure 3).

DISCUSSION

The number of ant species declined as elevation increased from 300 m to 1,100 m a.s.l. Based on fitted values from the linear regression, mean species richness decreased from 16.4 to 8.9 (-46%) per pitfall trap from the lowest to the highest elevation. This represents a loss of 0.9 species per 100 m increase in

elevation. However, there was no change in abundance or species composition. This pattern of negative relationship between species richness and elevation is consistent with that found in many other studies on insects (McCoy, 1990; Beck & Kitching, 2009; Kumar et al., 2009; Machac et al., 2011).

There is no evidence of a mid-elevational peak in species richness in this study. The same results are shown by Bruhl (1999) and Malsch et al. (2008) who conducted studies in Mount Kinabalu from elevations of 560 m to 2,600 m a.s.l. (Bruhl, 1999) and 580 m to 1,520 m a.s.l. (Malsch et al., 2008) despite the existence of a mid-elevational peak in diversity of vascular plants within the same sampling area (Grytnes & Beaman, 2006). In an elevational study carried out by Samson et al. (1997), a midelevational peak of ant species richness was found at 400 m a.s.l. However, this result may have been due to the lower elevation site (200 m) being in a different location to the rest of the sampling points. Mid-elevational peaks of insect diversity are often associated with short-term, and therefore incomplete, sampling with one proposed explanation being that

Table 1. Species of ants collected from Imbak Canyon at nine different elevations (300m a.s.l to 1100 m a.s.l). Numbers in brackets denote species richness for the specified genera.

Subfamilies	Genus
Aenictinae	Aenictus (1)
Amblyoponinae	Prionopelta (1)
Cerapachynae	Cerapachys (2)
Dolichoderinae	Dolichoderus (6), Euprenolepis (2), Loweriella (2), Nylanderia (5)
Ectatomminae	Gnamptogenys (3)
Formicinae	Acropyga (1), Camponotus (3), Oecophylla (1), Prenolepis (1), Pseudolasius (4)
Leptanillinae	Leptanilla (1)
Myrmicinae	Cardiocondyla (1), Carebara (4), Cataulacus (1), Crematogaster (3),
	Lophomyrmex (2), Monomorium (2), Myrmecina (1), Myrmicaria (1),
	Pheidole (18), Pheidologeton (2), Proatta (1), Pyramica (3), Rhopalomastix
	(1), Solenopsis (1), Strumigenys (6), Technomyrmex (2), Tetramorium (7),
Ponerinae	Cryptopone (1), Diacamma (1), Harpegnathos (1), Hypoponera (2),
	Leptogenys (7), Odontoponera (1), Pachycondyla (4), Ponera (4)
Proceratiinae	Discothyrea (2)

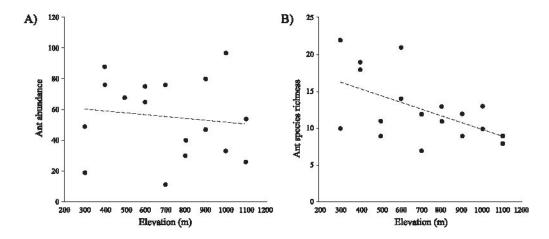


Figure 2. Ant abundance did not change with elevation (A), whereas ant species richness decreased (B). Neither abundance or species richness changed with litter depth (data not plotted).

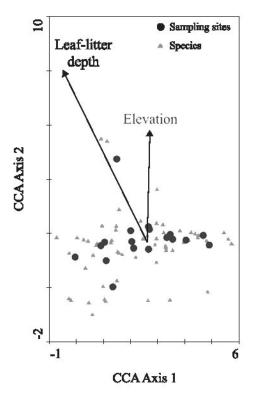


Figure 3. There was no effect of elevation or leaf litter depth on species composition, (CCA, 1000 permutations for environmental variables).

turnover in space or time is higher at lower elevations. This could result in species pools being incompletely sampled at lower elevations (McCoy, 1990). If this is the case, it would indicate that our sampling was sufficiently intensive for a representative species assemblage to be collected at each elevation.

One reason for the decline of species richness in this study is probably the change in vegetation from a lowland mixed dipterocarp forest to a heath forest. A study previously conducted by Andersen (1986), although not carried out along an elevational gradient, showed that there were twice as many ant species in a Eucalyptus forest than in a heath forest. This is probably due to lack of nesting sites and food resources in the heath forest (Malsch et al., 2008). Another factor that may influence changes in species richness we observed was the microclimate, in this case mainly lower temperature and higher humidity at higher elevations (Bruhl, 1999). The same patterns of species richness declining with elevation caused by changes in temperature has been shown by Machac et al. (2011) in three different mountainous areas in North America with elevation ranging from 379 m to 2,600 m a.s.l.

Despite changes in species richness, there

was no change in abundance of ants from low to high elevations within our study area. This indicates that the colony size is larger at higher elevations (Machac et al., 2011). Such a result is in accordance with Bergman's rule, which states that at higher latitudes or elevations, animals evolve larger body sizes in order to be able to more closely thermoregulate their body temperature (Blackburn et al., 1999). A study carried out by Kaspari & Vargo (1995) showed that colony size (being the measure of "body size" for a whole ant colony) follows Bergmann's rule. They found that ant colony sizes increase by an order of magnitude from the tropics to temperate areas. However, Geraghty et al. (2007) found that although ant species with higher latitudinal ranges can tolerate higher elevations, there was no evidence for Bergmann's rule. An alternative explanation might be that climate limits the number of species able to survive at higher elevations, and therefore the remaining species are released from competition and are able to produce more workers.

There was no significant change in species composition with elevation, meaning that very few species are unique to particular elevations, indicating that the ant communities at this site will cope reasonably well with any changes in climate. This is despite the prediction that ants in tropical forests are at the highest risk of going extinct compared to those in colder regions (Diamond et al., 2011). This might also be the case if lower elevations become uninhabitable from clear cutting, logging and the expansion of oil palm plantations (Achard et al., 2002; Sodhi et al., 2010; Turner et al., 2009, Fayle et al., 2010). However, more subtle differences in community composition with elevation might not have been detected using our sampling protocol, since only two pitfall traps were used at every elevation. Furthermore, because a shift of climatic bands up the side of the canyon would result in smaller population sizes for the ant species present (since there is a lower density of species at higher elevations), it is possible that there are longer term extinction risks for some of the rarer species.

In conclusion, ant species richness

decreases monotonically with increasing elevation, although there is no change in abundance and species composition. This result suggests that ant communities within this area will be relatively robust to increasing temperatures, although possibly will become more vulnerable due to smaller population sizes in the future, either from climate change or from habitat alteration and degradation. There is a need to sample across wider geographical and elevational ranges in order to reveal the generality of these patterns. Moreover, there is also a pressing need to determine changes in ant contribution to ecosystem functions in relation to changes in community structure with elevation.

ACKNOWLEDGEMENTS

We thank Yayasan Sabah for the permission given to the Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah to carry out the expedition into the Imbak Canyon Conservation Area. We are also grateful to Dr. Mahadimenakbar Dawood and Assoc. Prof. Abdul Hamid Ahmad for organising the expedition. Financial support was provided by the Sime Darby Foundation (KMY and TMF) and the project Biodiversity of forest ecosystems CZ.1.07/2.3.00/20.0064 cofinanced by the European Social Fund and the state budget of the Czech Republic (TMF). Finally, for his tireless assistance in the field, we are very grateful to Awang.

REFERENCES

Achard, F., H.D. Eva, H.-J. Stibig Mayaux, P. Gallego, J. Richards & J.-P. Malingreau. 2002. Determination of deforestation rates of the world's humid tropical forests. Science 297: 999-1002.

Andersen, A.N. 1986. Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in South-Eastern Australia. Australian Journal of Zoology 34: 53-64.

Beck, J. & I.J. Kitching. 2009. Drivers of moth species richness on tropical altitudinal gradients: a cross-regional comparison. Global Ecology and Biogeography 18: 361-

Bellard, C., C. Bertelsmeier, P. Leadley,

- W.Thuiller & F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15 (4): 365-377.
- Blackburn, T., K. Gaston & N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity* and Distributions 5: 165-174.
- Botes, A., M.A. McGeoch, H.G. Robertson, A. Niekerk, H.P. Davids & S.L. Chown. 2006.
 Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* 33: 71-90.
- Brühl, C.A., M. Mohamed & K.E. Linsenmair. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* 15: 265–277.
- Cardelus, C.L., R.K. Colwell &J.E. Watkins. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology* 94: 144-156.
- Chown, S., A. Hoffmann, T. Kristensen, M.Angilletta, N. Stenseth & C. Pertoldi. 2010. Adapting to climate change: a perspective from evolutionary physiology. Climate Research 43: 3-15.
- Colwell, R.K. & D.C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution* 15: 70-76.
- Condamine, F.L., F.A.H. Sperling, N. Wahlberg, J.-Y. Rasplus & G.J. Kergoat. 2012. What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. *Ecology Letters* 15(3): 267-277.
- Deutsch, C.A., J.J. Tewksbury, R.B. Huey, K.S. Sheldon, C.K. Ghalambor, D.C. Haak & P.R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences of the United States of America 105: 6668-6672.
- Diamond, S.E., D.M. Sorger, J. Hulcr, S.L. Pelini, I.D. Toro, C. Hirsch, E. Oberg & R.R. Dunn. 2012. Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. Global Change Biology 18: 448-456.
- Dunn, R.R., D. Agosti, A.N. Andersen, X. Arnan, C.A. Bruhl, X. Cerda, A.M. Ellison, B.L. Fisher, MC. Fitzpatrick, H. Gibb, N.J. Gotelli, A.D. Gove, B. Guenard, M. Janda, M. Kaspari, E.J. Laurent, J.-P. Lessard, J. T. Longino, J.D. Majer, S.B. Menke, T.P.

- McGlynn, C.L. Parr, S.M.Philpott, M. Pfeiffer, J. Retana, A.V. Suarez, H.L. Vasconcelos, M.D. Weiser & N.J. Sanders. 2009. Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters* 12: 324-333.
- Dunn, R.R., C.R. Parker & N.J. Sanders 2007.

 Temporal patterns of diversity: assessing the biotic and abiotic controls on ant assemblages. Biological Journal of the Linnean Society 91: 191-201.
- Ewers, R.M., R.K. Didham, L. Fahrig, G. Ferraz, A. Hector, R.D. Holt, V. Kapos, G. Reynolds, W. Sinun, J.L. Snaddon & E.C. Turner. 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. Philosophical Transactions of the Royal Society B-Biological Sciences 366: 3292-3302.
- Fayle, T.M., E.C. Turner, J.L. Snaddon, V.K. Chey, A.Y.C. Chung, P. Eggleton & W.A. Foster. 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic and Applied Ecology* 11: 337-345.
- Geraghty, M., R. Dunn & N.J. Sanders. 2007.

 Body size, colony size, and range size in ants (Hymenoptera: Formicidae): are patterns along elevational and latitudinal gradients consistent with Bergmann's Rule?

 Myrmecological News 10: 51-58.
- Ghalambor, C.K., R.B. Huey, P.R. Martin, J.J. Tewksbury & G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integrative and Comparative Biology 46: 5-17.
- Grytnes, J.A. & J.H. Beaman. 2006. Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. *Journal of Biogeography* 33:1838-1849.
- **Hillebrand, H. 2004.** On the generality of the latitudinal diversity gradient. *American Naturalist* 163:192-211.
- Kaspari, M. & E.L. Vargo. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. American Naturalist 145: 610-632.
- Kumar, A., J.T. Longino, R.K. Colwell & S.O. Donnell. 2009. Elevational patterns of diversity and abundance of eusocial paper wasps (Vespidae) in Costa Rica. *Biotropica* 41: 338-347.
- Machac, A., M. Janda, R.R. Dunn & N.J. Sanders. 2011. Elevational gradients in phylogenetic structure of ant communities

- reveal the interplay of biotic and abiotic constraints on diversity. *Ecography* 34: 364-371.
- Malsch, A.K.F., B. Fiala, U. Maschwitz, M., Mohamed, J. Nais & K.E. Linsenmair. 2008. An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo. Asian Myrmecology 2: 33-49.
- Mccoy, E.D. 1990. The distribution of insects along elevational gradients. *Oikos* 58: 313-322.
- Mohamed, M. 1998. Terrestrial ants (Formicidae: Hymnoptera) of Sayap-Kinabalu Park, Sabah. ASEAN Review of Biodiversity and Environmental Conservation 6:1-16.
- Moreau, C.S., C.D. Bell, R. Vila, S.B. Archibald & N.E. Pierce. 2006. Phylogeny of the Ants: Diversification in the age of angiosperms. *Science* 312: 101-104.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.
- Samson D.A., E.A. Rickart & P.C. Gonzales. 1997. Ant diversity and abundance along an elevational gradient in the Philippines. *Biotropica* 29: 349–363.
- Sodhi, N.S., L.P.Koh, R. Clements, T.C. Wanger, J.K. Hill, K.C. Hamer, Y. Clough, T.,

- **Tscharntke, M.R.C. Posa & T.M. Lee. 2010.** Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biological Conservation* 143: 2375-2384.
- Stevens, G.C. 1992. The Elevational gradient in altitudinal range: An extension of Rapoport's Latitudinal Rule to altitude. *American Naturalist*140: 893-911.
- Taylor, D., P. Saksena, P.G. Sanderson & K. Kucera. 1999. Environmental change and rain forests on the Sunda shelf of Southeast Asia: drought, fire and the biological cooling of biodiversity hotspots. Biodiversity and Conservation 8: 1159-1177.
- Tewksbury, J.J., R.B. Huey & C.A. Deutsch. 2008. Putting the heat on tropical animals. *Science* 320: 1296-1297.
- Turner, E.C. & W.A. Foster. 2009. The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. *Journal of Tropical Ecology* 25: 23-30.
- Walsh, R.P.D. & D.M. Newbery. 1999. The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions:* Biological Sciences 354: 1868-1883
- Wilson, E.O. 1987. Causes of ecological success: The case of the ants. *Journal of Animal Ecology* 56:1-9.