*Bulletin of Entomological Research* (2018) **108**, 792–799
© Cambridge University Press 2018

doi:10.1017/S000748531800010X

# Temporal changes in arthropod activity in tropical anthropogenic forests

**G.-J. Brandon-Mong[1,2], J.E. Littlefair[3,4], K.-W. Sing[5], Y.-P. Lee[6,7], H.-M. Gan[6,7,8], E.L. Clare[3] and J.-J. Wilson[9,10,11]***

[1]Institute of Biological Sciences, Faculty of Science, University of Malaya, 50603 Kuala Lumpur, Malaysia: [2]Biodiversity Research Center, Academia Sinica, No. 28, Lane 70, Section 2, Yanjiuyuan Road, Nangang District, Taipei City, 115, Taiwan: [3]School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Rd., London, E1 4NS, UK: [4]Department of Biology, McGill University, 1205 Docteur Penfield, Montréal, Québec H3A 1B1, Canada: [5]South China DNA Barcoding Center, Kunming Institute of Zoology, Chinese Academy of Sciences, 32 Jiaochang Donglu, 650223 Kunming, Yunnan, P. R. China: [6]School of Science, Monash University Malaysia, Jalan Lagoon Selatan, Bandar Sunway, 47500 Petaling Jaya, Selangor, Malaysia: [7]Monash University Malaysia Genomics Facility, Monash University Malaysia, Jalan Lagoon Selatan, Bandar Sunway 47500 Petaling Jaya, Selangor, Malaysia: [8]Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Geelong, Victoria 3220, Australia: [9]International College Beijing, China Agricultural University, Beijing, 100083, P. R. China: [10]School of Applied Sciences, Faculty of Computing, Engineering and Science, University of South Wales, Pontypridd, CF37 4DB, United Kingdom: [11]Department of Microbiology and Parasitology, Faculty of Medical Science, Naresuan University, Phitsanulok 65000, Thailand

## Abstract

Arthropod communities in the tropics are increasingly impacted by rapid changes in land use. Because species showing distinct seasonal patterns of activity are thought to be at higher risk of climate-related extirpation, global warming is generally considered a lower threat to arthropod biodiversity in the tropics than in temperate regions. To examine changes associated with land use and weather variables in tropical arthropod communities, we deployed Malaise traps at three major anthropogenic forests (secondary reserve forest, oil palm forest, and urban ornamental forest (UOF)) in Peninsular Malaysia and collected arthropods continuously for 12 months. We used metabarcoding protocols to characterize the diversity within weekly samples. We found that changes in the composition of arthropod communities were significantly associated with maximum temperature in all the three forests, but shifts were reversed in the UOF compared with the other forests. This suggests arthropods in forests in Peninsular Malaysia face a double threat: community shifts and biodiversity loss due to exploitation and disturbance of forests which consequently put species at further risk related to global warming. We highlight the positive feedback mechanism of land use and temperature, which pose threats to the arthropod communities and further implicates ecosystem functioning and human well-being. Consequently, conservation and mitigation plans are urgently needed.

---

*Author for correspondence
Phone: +447456690249
E-mail: wilso04@gmail.com; johnjameswilson@qq.com

**Keywords:** Insects, biodiversity, global warming, land-use, Malaise trap, metabarcoding

(Accepted 19 December 2017; First published online 14 February 2018)

## Introduction

Biodiversity in the tropics is increasingly affected by rapid changes in land use. For example, 318,000 ha of natural forest was converted to oil palm plantations in Peninsular Malaysia between 1990 and 2010 (Gunarso *et al.*, 2013) with oil palm 'forests' now accounting for 45% (2.6 million ha) of the forested land (MPOB, 2016) in the peninsula. Forested land in total, accounts for 44% (5.80 million ha) of land in Peninsular Malaysia, including 1.92 million ha of protected forest (Forestry Department Peninsular Malaysia, 2016), while urban land accounts for around 6% (0.8 million ha) (National Physical Plan-2, 2010). The proportion of urban land will continue to increase across Tropical East Asia (Schneider *et al.*, 2015), and in Peninsular Malaysia specifically, the land around Kuala Lumpur, known as the Klang Valley conurbation, is experiencing rapid urban sprawl (Sing *et al.*, 2016a). Urban parks and gardens with substantial vegetation, 'ornamental forests', could help to retain biodiversity in tropical urban areas where little natural habitat remains (Alvey, 2006; Sing *et al.*, 2016*a*, *b*).

In addition to land use changes, the global average temperature has increased by 0.16 °C over the past decade (NASA, 2015), with impacts on terrestrial and marine species worldwide (Pacifici *et al.*, 2015). For example, activity patterns of terrestrial arthropods, poikilothermic animals with vital ecosystem roles (e.g. pollinators, seed dispersers, scavengers, decomposers, trophic intermediaries; Foottit & Adler, 2009) are dictated by climate. Changes in atmospheric temperatures influence arthropod activity both directly - temperature increases result in uncoordinated locomotion, increased metabolic expenditure, an accelerated life cycle, 'heat coma', and death (Piyaphongkul *et al.*, 2012; Jaworski & Hilszczański, 2013), and indirectly - through plant phenology, food quality, and parasitoid, predator and pathogen abundances (Colinet *et al.*, 2015). In temperate regions, activity in a wide range of arthropod orders is influenced by changes in temperature and precipitation between seasons (Jaworski & Hilszczański, 2013). However, in tropical regions, where annual changes in temperature and precipitation are much less pronounced, arthropod activity is generally assumed to be aseasonal (Anu *et al.*, 2009). Consequently, global warming may be considered a lower threat to arthropod biodiversity in tropical than in temperate regions because species showing patterns of activity influenced by fluctuations in temperature and precipitation are thought to be at higher risk of climate-related extirpation (Piyaphongkul *et al.*, 2012). Conversely, tropical arthropods, already living at the limit of their narrow temperature range, may be less tolerant of temperature fluctuations compared with their temperate relatives (Bale & Hayward, 2010; Corlett, 2011; Andrew *et al.*, 2013). Tropical arthropods will experience historically unprecedented climates within the next decade because the tropics will be among the regions of the world first affected by global climate change (Mora *et al.*, 2013).

Our objective was to characterize changes in tropical arthropod activity, corresponding to changes in temperature and precipitation, across three major tropical anthropogenic forest types: secondary reserve forest (SRF), oil palm forest (OPF), and urban ornamental forest (UOF). We collected weekly Malaise trap samples at each forest type over 12 months and used DNA metabarcoding (Brandon-Mong *et al.*, 2015) to examine shifts in arthropod activity.

## Materials and methods

### *Anthropogenic forest sites and climate data*

Malaise traps were deployed for 1 year (from October 2014 to October 2015) at three anthropogenic forest sites in Peninsular Malaysia representing typical examples of the major anthropogenic forest types found in the peninsular.

The first site was Ulu Gombak Forest Reserve, a 17,000 ha SRF in Selangor. Ulu Gombak Forest Reserve represents a typical secondary forest reserve found in the west of Peninsular Malaysia comprising logged, mixed, dipterocarp forest and has been intensively studied since the establishment of a Field Studies Centre in 1966 (Sing *et al.*, 2013). The second site was Rimba Ilmu, an 82 ha UOF located at the University of Malaya main campus at the western boundary of the Federal Territory of Kuala Lumpur. Rimba Ilmu (http://rimba.um.edu.my) represents a typical urban park found in Peninsular Malaysia; Rimba Ilmu is open to the public, comprises a mixture of old trees, hedges (shrubs), flowerbeds, and small 'unmanaged' areas with early successional species (e.g. grasses) (Sing *et al.*, 2016*a*), and is surrounded by residential and commercial land use. The third site was OPF in Perak. The Malaise trap at OPF was originally sited at Teluk Intan, Perak, but was stolen in December 2014. A new Malaise trap was then immediately deployed at Parit, Perak, 60 km away from the original location. Both OPF locations were part of a large contiguous area of oil palm plantations in Perak and represent typical OPF in Peninsular Malaysia comprising a monoculture of *Elaies guineensis* × *Elaies oleifera*. It is common practice to remove weeds in the understory but some early successional species (notably non-native species; Teuscher *et al.*, 2016) may persist, especially at forest edges.

Peninsular Malaysia, situated at the centre of hyperdiverse, tropical, Southeast Asia has almost no variability in the annual temperature (26°C ± 2°C), with high humidity (79–90%) and high rainfall (2400 mm per year) year-round (Akhiri & Yong, 2011). Mild annual changes result from two monsoon seasons; drier conditions are experienced during southwest monsoon (May–August) compared with the northeast monsoon (November–February), known as the 'rainy' season (Hafezatul Rasyidah, 2010; Akhiri & Yong, 2011; Tangang *et al.*, 2012). These monsoons are increasingly unpredictable. The southwest monsoon is starting earlier and lasting longer, resulting in a significant increase in mean precipitation (8% increase across South Asia; Tangang *et al.*, 2012), whereas the northeast monsoon is getting drier (Tangang *et al.*, 2012). The interacting effects of El Niño Modoki have resulted in increased droughts and heat waves, while interacting effects of the Borneo Vortex have caused major floods, and a rare typhoon, during the northeast monsoon (Tangang *et al.*, 2012). The average annual temperature in Peninsular Malaysia is expected to increase 3–5°C to 29–30°C by the end of the century (Tangang *et al.*, 2012).

Weather data (daily mean rainfall, maximum and minimum temperature) for each site was obtained from the Malaysian Meteorological Department: (1) SRF from the station located at 'Jabatan Kemajuan Orang Asli' (JAKOA) Gombak; (2) UOF from the station located in Petaling Jaya; (3) OPF at Teluk Intan from Accuweather (http://www.accuweather.com/en/my/teluk-intan/229685/weather-forecast/229685); (4) OPF at Parit from the station at Pusat Pertanian Titi Gantong; defective data from this station (due to either malfunctioning of the instrument, maintenance, or failure to pass quality control steps) was replaced with either data obtained from the station at Hospital Kampar or from Accuweather (http://www.accuweather.com/en/my/parit/229765/weather-forecast/229765). Daily mean data were averaged to produce a single mean temperature for each week (Saturday to Friday because collection bottles were changed on Fridays).

### *Sample sorting and DNA extraction*

The collection bottles of the Malaise traps were collected weekly and replaced with new bottles containing 150 ml ethanol. The collected samples were stored in a −20°C freezer prior to sample sorting and DNA extraction. Weekly samples were individually placed in previously sterilized Petri dishes (10% Chlorox) using forceps. Two legs from arthropod specimens, equal to or larger in size than a honeybee, and whole bodies of smaller specimens were placed in a 15 ml sterile tube. Specimens were oven-dried for 1 week and the mass of the weekly sample was recorded. Based on the mass, 8.0 ml of T1 lysis buffer, 1.1 ml of proteinase K, 8.8 ml of B3 lysis buffer, and 9.3 ml of absolute ethanol per 1.0 g were added to the tube. Genomic DNA was extracted using a NucleoSpin Tissue kit (Macherey-Nagel, Germany), using a single column per weekly sample, and otherwise following the manufacturer's instructions.

### *Polymerase chain reaction (PCR) and sequencing*

Partial Illumina adapter sequences were incorporated into primers mlColintF and HCO2198 (Folmer et al., 1994; Leray et al., 2013; Supplementary Table 1). The bulk DNA extracts were used for PCR following the protocol described for [V3] mlColintF/[MID96]HCO2198 by Brandon-Mong *et al.* (2015) with an expected amplicon length of 313 bp. Five independent amplicons were pooled and were purified and size-selected using 0.8× volume ratio of AMPure XP® beads (Beckman Coulter Inc., USA). The purified amplicons were used as templates for the second round of PCR to generate amplicons containing full Illumina adaptors and unique dual-index tags (following Lee *et al.*, 2016). The library was quantified using KAPA library quantification kit (KAPA Biosystems, South Africa), normalized, and pooled. Sequencing was performed on an Illumina MiSeq Sequencer (2 × 250 bp paired-end read setting) at the Monash University Malaysia Genomics Facility.

Sequencing was initially performed in two runs corresponding to weekly samples from October to March and April to September. Reads were demultiplexed and adapter trimmed onboard the MiSeq using the MiSeq Reporter software. The number of reads produced per weekly sample ranged from 146 to 389,750. Thirty-one weekly samples which produced ≤90,000 reads in the first run were repeated. The number of reads per weekly sample in the second run ranged from 11,892 to 143,180. Six samples which produced ≤15,000 reads in the second run were repeated. If a weekly sample was subjected to multiple runs, all reads were pooled for analysis. FASTQ files related to this study are available in the NCBI SRA under accession SRR5179085 (weekly samples from October to March) and SRR5181818 (weekly samples from April to September).

### *Bioinformatics analysis*

The output FASTQ files were dereplicated and quality-filtered using the online PRINSEQ (Schmieder & Edwards, 2011). The PRINSEQ output data (in FASTA format) was further filtered manually in CodonCode Aligner (CondonCode Corp., USA) following the protocol described by Brandon-Mong *et al.* (2015). The resulting metabarcodes (final Operational Taxonomic Units; OTU) were uploaded to the Barcode of Life Datasystems (BOLD) (Ratnasingham & Hebert, 2007) and are available in the public dataset DS-MTISA (http://www.boldsystems.org/index.php/MAS_Management_OpenDataset?datasetcode=DS-MTISA).

### *Order assignment*

Order names were assigned to the OTU based on matches obtained from the (full) BOLD identification engine. Names were assigned to OTU when the closest matching database sequence in BOLD shared >85.9% similarity (following Zeale *et al.*, 2011). 91.0% of OTU were assigned an order name. Due to incompleteness of DNA barcode reference libraries available for the region (Wong *et al.*, 2015; Wilson *et al.*, 2016), we did not systematically assign more precise taxonomic names to the OTU.

### *Statistical analyses*

To avoid biases in diversity estimates caused by unavoidable inconsistencies in the number of reads produced across independent samples by high-throughput sequencers (Leray & Knowlton, 2016), high-throughput sequencing data are commonly analyzed using proportions or rarefraction (Beng *et al.*, 2016). Due to the problem of 'lost data' associated with rarefaction (McMurdie & Holmes, 2014), we opted to calculate the proportion of OTU representing each of the five most abundant arthropod orders in each weekly sample. The proportions were arcsine-transformed prior to statistical analysis (arcsine transformation is recommended to normalize proportions; Lachin, 1981).

Multiple linear regressions were fitted to examine the effect of weather variables on the proportion of the top five most abundant insect orders throughout the year. For each insect order (Diptera, Lepidoptera, Coleoptera, Hemiptera, and Hymenoptera), a multiple linear regression was performed with the following terms added as initial fixed effects: weekly maximum temperature (°C), weekly minimum temperature (°C), weekly mean rainfall (mm), and the second order interaction of each weather variable with forest type. Higher order interactions and other second-order interactions were not included to avoid over-parameterizing the models. Models were simplified using deletion tests based on partial F tests (using the base R function drop1), and non-significant terms were removed until minimal adequate models were achieved (Crawley, 2012). Explanatory variables with a $P$ value of <0.05 were retained in the minimal adequate models. Model validation plots were examined for deviations from the assumptions of a linear model.

## Results

We detected 8387 OTU across all sites (several overlapped multiple sites) and sampling weeks: 2603 from UOF, 3341 from OPF, and 4296 from SRF. In total, 7635 OTU were assigned to 28 arthropod orders. The orders containing the most OTU were Diptera (4672 OTU; 56%), Lepidoptera (1108 OTU; 13%), Coleoptera (778 OTU; 9%), Hemiptera (427 OTU; 5%), and Hymenoptera (199 OTU; 2%). Other arthropod orders were detected but with fewer OTU (<2%; Supplementary Table 2). Non-arthropod orders (mostly bacterial or fungal in origin) contributed 14% (1196) of the OTU detected.

The proportion of Diptera was significantly affected by the interaction between forest type and maximum temperature (fig. 1a, $F_{2,\,149} = 8.63$, $P < 0.001$). This relationship was strongly positive in the UOF ($y = 2.17x - 6.47$), and negative in both the oil palm ($y = -0.829x + 77.5$) and SRFs ($y = -1.31x + 93.6$).

The proportion of Coleoptera was also significantly affected by the interaction between forest type and maximum temperature (fig. 1b, $F_{2,\,149} = 7.85$, $P < 0.001$). This relationship was slightly positive in both the oil palm ($y = 0.706x - 6.43$) and SRFs ($y = 0.695x - 4.69$), and negative in the UOF ($y = -1.11x + 46.4$).

The proportion of Lepidoptera was also significantly affected by the interaction between forest type and maximum temperature (fig. 1c, $F_{2,\,149} = 4.28$, $P = 0.0156$). This relationship was strongly positive in the SRF ($y = 1.18x - 15.9$), slightly positive in the OPF ($y = 0.257x + 11.7$), and negative in the UOF ($y = -0.676x + 37.5$).

The proportion of Hemiptera was significantly affected by forest type only (fig. 1d, $F_{2,\,152} = 37.2$, $P < 0.001$). The proportion of Hymenoptera was not affected by the forest type or any weather variables, with the model producing non-significant results for all variables.

## Discussion

Although seasons across Southeast Asia are mostly characterized by heavy rainfall (i.e., the monsoons), the arthropod communities detected in this study did not show shifts significantly related to rainfall. Conversely, the arthropod communities detected in this study did show shifts which were significantly related to maximum temperature in various ways. These changes were compounded by differences in forest types, and similar to previous studies, we found substantially lower species richnesses of arthropods in oil palm plantations (Fitzherbert *et al.*, 2008; Koh, 2008; Fayle *et al.*, 2010; Senior *et al.*, 2013) and urban green spaces (Uno *et al.*, 2010; Syaripuddin *et al.*, 2015) compared with more natural forests. Consequently, tropical arthropod biodiversity may face a cumulative threat with the impact of climate change being felt more strongly in intensely human-modified ecosystems which already support reduced levels of arthropod activity in comparison with more natural forests. Crucial ecosystem functions are performed by forest arthropods, such as the decomposition of vertebrate carcasses (Sugiura *et al.*, 2013) and plant biomass (Price *et al.*, 2011), pollination (Vanbergen, 2013), and seed dispersal (Nichols *et al.*, 2008), and such ecosystem functions will be impacted by changes in arthropod activity (Weisser & Siemann, 2004).

Interestingly, responses to maximum temperature differed by arthropod order as well as forest type. The proportion of Coleoptera was significantly affected by the interaction between forest type and maximum temperature. The relationship was slightly positive in both the OPF and SRF, but negative in the UOF. Other studies have also reported significant correlations between beetle diversity and temperature (Pinheiro *et al.*, 2002; Sittichaya *et al.*, 2013; Aneni *et al.*, 2014), for example, Pinheiro and colleagues (2002) showed the abundance of beetles in Brazilian Cerrado was significantly positively correlated with delayed maximum temperature (maximum temperature of the previous month). Most beetles are nocturnal or remain hidden during daylight (when the maximum temperature is most likely to occur), move slowly and rarely fly, and are unlikely to thermoregulate (Lease *et al.*, 2014). However, some beetles, such as dung beetles, do thermoregulate and remain active at high temperature (Verdú *et al.*, 2004, 2012). Interestingly, beetles in the family Bostrichidae, which includes serious insect pests of forests and agriculture (Sittichaya *et al.*, 2013), appeared in the OPF (based on BOLD database matches sharing >95% similarity) in February (end of northeast monsoon) and July 2016 (end of southeast monsoon), however, the abundance of Bostrichidae in mixed crop plantations in Thailand was reported to fluctuate without any prominent peaks (Sittichaya *et al.*, 2013).

Similarly to Coleoptera, the proportion of Lepidoptera was significantly affected by the interaction between forest type and maximum temperature. Likewise, the relationship was positive in the SRF and OPF, but negative in the UOF. The lowest maximum temperatures were reported for the SRF, and the highest maximum temperatures for the OPF. OPFs have generally been reported to be hotter (+2.84°C) and drier than both primary and secondary forest reserves (Luskin & Potts, 2011), but this will be dependent on the age of trees in the oil palm plantation. Roberts *et al.* (2000) suggested the higher density of canopy trees in the less-disturbed forest could provide shade and lower the atmospheric temperature (Liow *et al.*, 2001), which presumably buffers arthropod communities from changes in temperature (Pincebourde *et al.*, 2007). Urban forests generally have fewer trees in the over-storey compared with forest reserves and plantations, effectively providing less shade (Porter *et al.*, 2001) which may account for the different patterns observed between these forest types.

The dominance of dipterans in Malaise trap samples across the three anthropogenic forests was similar to previous findings, for example, Zhang *et al.* (2016) reported that the collections from traps deployed in a tropical forest in southern mainland China comprised 43% dipterans ($n = 848$). Similarly to Coleoptera and Lepidoptera, the proportion of Diptera was significantly affected by the interaction between forest type and maximum temperature. However, in contrast to both Coleoptera and Lepidoptera, the relationship for Diptera was strongly positive in the UOF but negative in both the OPF and SRF. Nazareth *et al.* (2016) suggested that warmer temperatures (between the upper and lower limits) may increase the development rate of certain mosquito species, and some blood-feeding dipterans, such as mosquitoes, can thermoregulate during feeding (Benoit & Denlinger, 2010; Lahondère & Lazzari, 2012). However, considering Diptera comprised the majority of OTU across all the samples

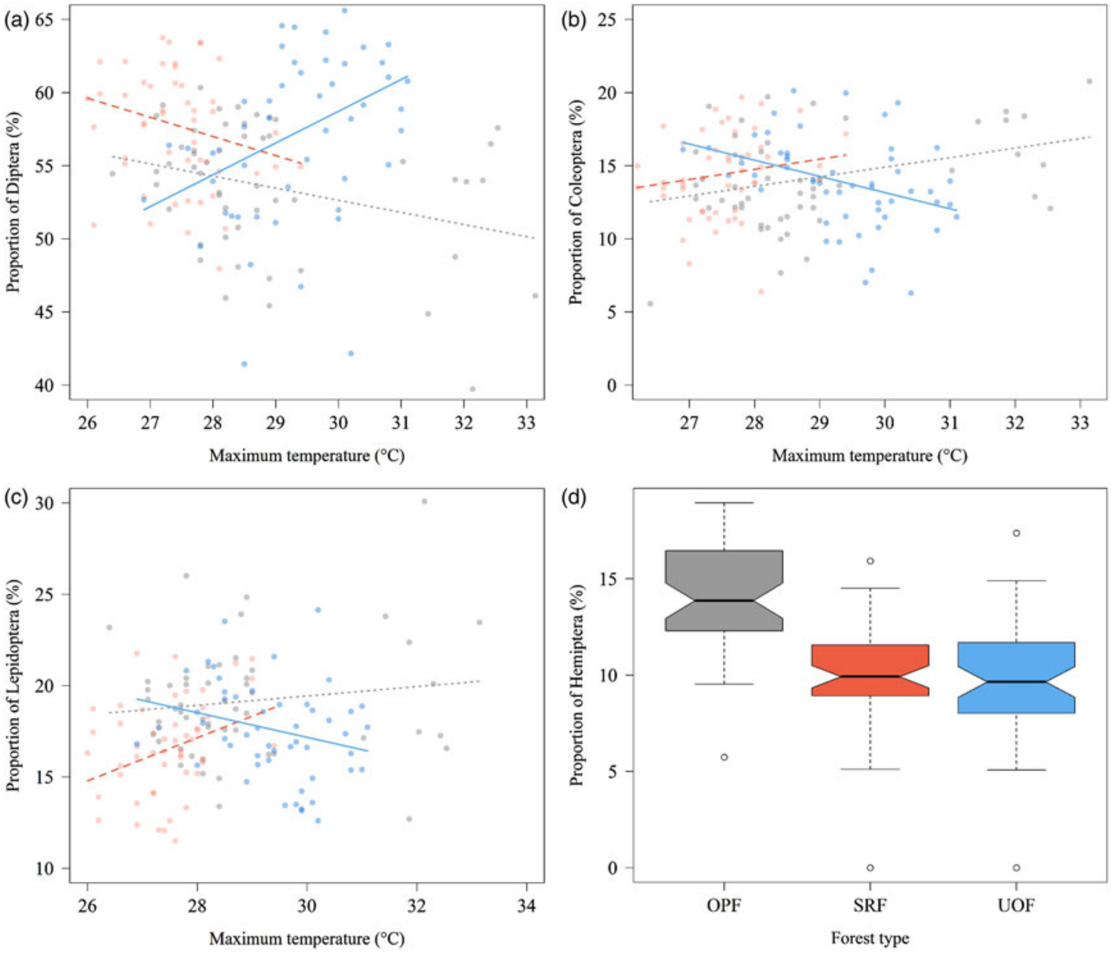

Fig. 1. Number of operational taxonomic units collected in weekly samples over 1 year at three anthropogenic forests in Peninsular Malaysia.

(fig. 2), the increase in the proportion of Diptera could actually represent a decrease in other arthropod orders which are responding negatively to warmer temperatures in the UOF. Nevertheless, peak activities observed in OTU from the superfamily Empidoidea (based on BOLD database matches sharing >91% similarity), for example, corresponded closely with those reported in a previous study from Thailand (Plant *et al.*, 2011), with *Iteaphila* recorded between April and July, and *Syndyas* recorded between December and February.

The proportion of Hemiptera was significantly affected by forest type only whereas the proportion of Hymenoptera was not affected by any of the weather variables or the forest type. The OPF had a significantly greater proportion of Hemiptera OTU (14.1%; of the top five orders), whereas the SRF and UOF had more similar proportions (10.1% and 9.68% respectively). Hemiptera in OPFs includes pest species such as *Recilia mica* (Delphacidae) (a vector of blast disease) and *Leptopharsa gibbicarina* (Tingidae) (a vector of *Pestalotiopsis*; Corley & Tinker, 2016). Delphacidae and Tingidae were detected in the OPF (based on database matches sharing >91% similarity), but not the SRF or UOF. Throughout a year-long study across different tropical forest ecosystems we have shown that changes in weather have stronger, and often opposite, impacts on arthropod activity found in highly modified forests (particularly UOFs) compared with more natural secondary forest. Changes in ecosystem functioning in anthropogenic forests, as a result of changes in arthropod activity, can have significant links to human well-being, including physical (e.g., food resources, protection from environmental hazards, and medicines) and psychological health (e.g., leisure and recreation) (Haines-Young & Potschin, 2010). Several recommendations have been put forward for the conservation of biodiversity, including arthropods, in anthropogenic forests: limiting the development of new oil palm plantations to non-forested lands (Austin *et al.*, 2015); use of reduced-impact logging methods, including appropriate directional logging, and careful planning of roads and trails to avoid collateral damage (Putz *et al.*, 2008); less-intensive logging and maintenance of canopy closure to ensure suitable habitat for shade-requiring species (Putz *et al.*, 2008); preservation of trees in urban areas to provide shade and planting drought-tolerant species (Gill *et al.*, 2007); green corridors and retaining habitat connectivity (Wilby & Perry, 2006). Considering that responses to maximum temperature differed by arthropod order as well as forest type, management of tropical biodiversity should also consider taxonomic specific differences when developing conservation strategies.

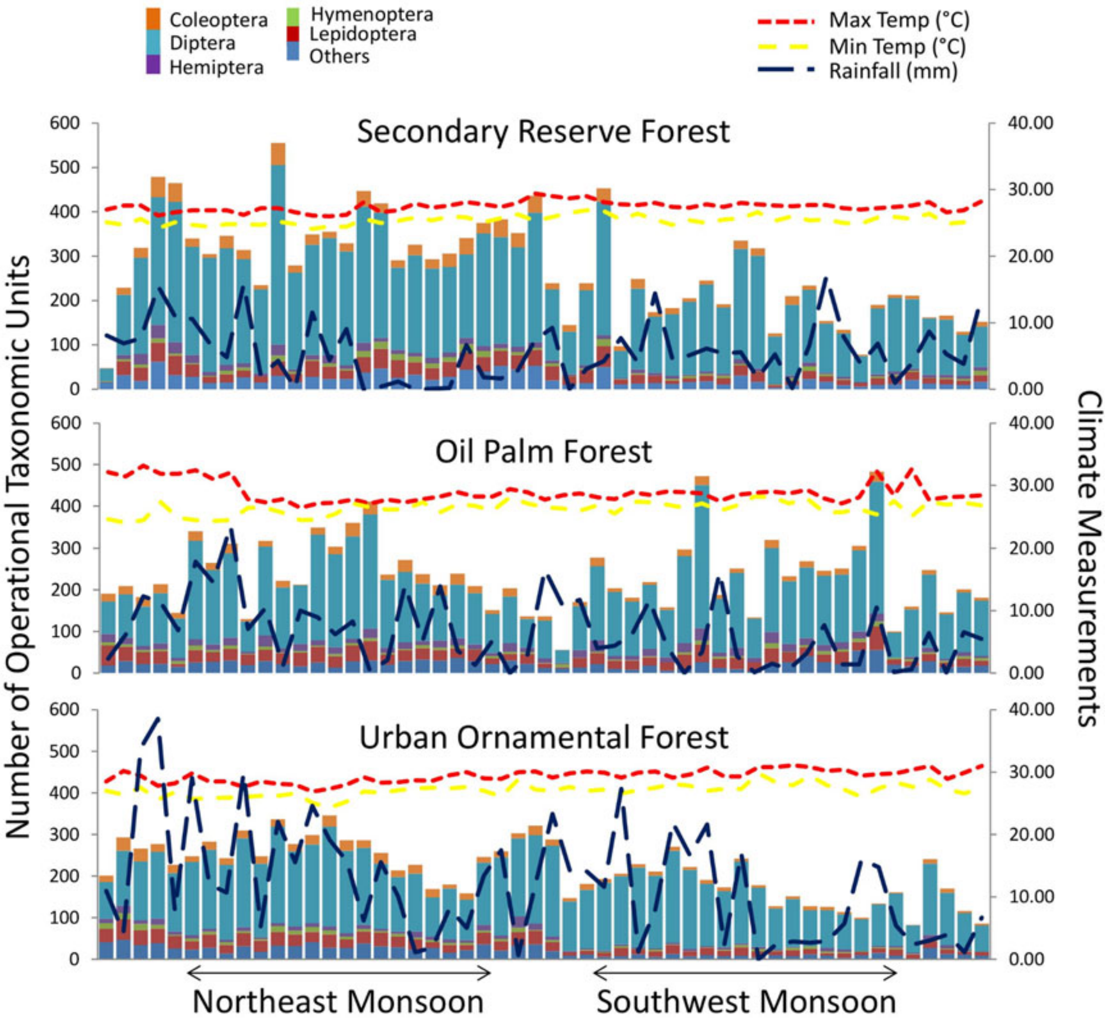

Fig. 2. Multiple linear regressions indicate the interaction between different anthropogenic forest types (grey = Oil Palm Forest, red = Secondary Reserve Forest, blue = Urban Ornamental Forest) and weather variables.

## Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S000748531800010X

## Acknowledgements

The authors thank the staff at Ulu Gombak Field Studies Centre and other helpers (Mono, Leong Sow Woon, John Mong Guo An, Yee Yoke Pei Narong Jaturas, Cheah Yih Horng, Daniel Kong Wye Lup, Lim Aik Hean) for insect collections from Malaise traps. M. Sugumaran (coordinator of Rimba Ilmu Botanic Garden), Rosli Hashim (coordinator Ulu Gombak Field Studies Centre) and the owners of the oil palm estates (Got Tuan Tek and Lee Kwu Li) provided permission to deploy the Malaise traps. This work was initiated when BMGJ, KWS, and JJW were at the Institute of Biological Sciences, Faculty of Science, University of Malaya (UM) and was supported by a High Impact Research Grant (Chancellery) from UM to JJW and Lim Phaik Eem. The collaboration between UM and Queen Mary University of London was supported through a Newton-Ungku Omar Institutional Links Grant to ELC and JJW. The collaboration between UM and Monash University Malaysia was coordinated under an MOA.

## Competing financial interests

The authors declare no competing financial interests.

## References

**Akhiri, M.F.M. & Yong, J.C.** (2011) Seasonal variation of water characteristics during inter-monsoon along the east coast of Johor. *Journal of Sustainability Science and Management* **6**, 206–214.

**Alvey, A.A.** (2006) Promoting and preserving biodiversity in the urban forest. *Urban Forestry and Urban Greening* **5**, 195–201.

**Andrew, N.R., Hart, R.A., Jung, M.P., Hemmings, Z. & Terblanche, J.S.** (2013) Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, *Iridomyrmex purpureus* (Formicidae), with potential climate change. *Journal of Insect Physiology* **59**, 870–880.

**Aneni, T.I., Aisagbonhi, C.I., Iloba, B.N., Adaigbe, V.C. & Ogbebor, C.O.** (2014) Influence of weather factors on seasonal population dynamics of *Coelaenomenodera elaeidis* (Coleoptera: Chrysomelidae) and its natural enemies in NIFOR, Nigeria. *American Journal of Plant Sciences* **5**, 42–47.

**Anu, A., Sabu, T.K. & Vineesh, P.J.** (2009) Seasonality of litter insects and relationship with rainfall in a wet evergreen forest in South Western Ghats. *Journal of Insect Science* **9**, 46.

**Austin, K.G., Kasibhatla, P.S., Urban, D.L., Stolle, F. & Vincent, J.** (2015) Reconciling oil palm expansion and climate change mitigation in Kalimantan, Indonesia. *PLoS ONE* **10**, e0127963.

**Bale, J.S. & Hayward, S.A.** (2010) Insect overwintering in a changing climate. *The Journal of Experimental Biology* **213**, 980–994.

**Beng, K.C., Tomlinson, K.W., Shen, X.H., Surget-Groba, Y., Hughes, A.C., Corlett, R.T. & Slik, J.W.** (2016) The utility of DNA metabarcoding for studying the response of arthropod diversity and composition to land-use change in the tropics. *Scientific Reports* **6**, 24965.

**Benoit, J.B. & Denlinger, D.L.** (2010) Meeting the challenges of on-host and off-host water balance in blood-feeding arthropods. *Journal of Insect Physiology* **56**, 1366–1376.

**Brandon-Mong, G.J., Gan, H.M., Sing, K.W., Lee, P.S., Lim, P.E. & Wilson, J.J.** (2015) DNA metabarcoding of insects and allies: an evaluation of primers and pipelines. *Bulletin of Entomological Research* **105**, 717–727.

**Colinet, H., Sinclair, B.J., Vernon, P. & Renault, D.** (2015) Insects in fluctuating thermal environments. *Annual Review of Entomology* **60**, 123–140.

**Corlett, R.T.** (2011) Impacts of warming on tropical lowland rainforests. *Trends in Ecology and Evolution* **26**, 606–613.

**Corley, R.H.V. & Tinker, P.B.H.** (2016) *The oil Palm*. 5th edn. Chapter 14. p. 458. UK, John Wiley & Sons, Ltd.

**Crawley, M.J.** (2012) *The R Book*. 2nd edn. Chapter 9, p. 393. UK, John Wiley & Sons, Ltd.

**Fayle, T.M., Turner, E.C., Snaddon, J.L., Chey, V.K., Chung, A.Y. C., Eggleton, P. & Foster, W.A.** (2010) Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic and Applied Ecology* **11**, 337–345.

**Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P. F. & Phalan, B.** (2008) How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution* **23**, 538–545.

**Foottit, R.G. & Adler, P.H.** (2009) *Insect Biodiversity Science and Society*. Chapter 2. p. 8. UK, John Wiley & Sons Ltd.

**Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R.** (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.

**Forestry Department Peninsular Malaysia, Kuala Lumpur, Malaysia**. (2016) Forestry Statistics Peninsular Malaysia 2014. Link: http://www.forestry.gov.my/jpsm/index.php/my/pusat-sumber/2016-06-07-03-12-29 (accessed 11 January 2017).

**Gill, S.E., Handley, J.F., Ennos, A.R. & Pauleit, S.** (2007) Adapting cities for climate change: the role of the green infrastructure. *Built Environment* **33**, 115–133.

**Gunarso, P., Hartoyo, M.E., Agus, F. & Killeen, T.J.** (2013) Oil palm and land use change in Indonesia, Malaysia and Papua New Guinea. pp. 65–88. *in* Killeen, T. J. & Goon, J. (*Eds*) *Reports From the Technical Panels of the Second RSPO GHG Working Group, Roundtable for Sustainable Palm Oil – RSPO*. Kuala Lumpur. The Netherlands: Tropenbos International.

**Hafezatul Rasyidah, O.** (2010) *Wind environment evaluation on major town of Malaysia*. (Unpublished bachelor's thesis). Faculty of civil engineering & earth resources, Universiti Malaysia Pahang, Pahang, Malaysia.

**Haines-Young, R. & Potschin, M.** (2010) The links between biodiversity, ecosystem services and human well-being. Chapter 6. pp. 1–31. *in* Raffaelli, D. & Frid, C. (*Eds*) *Ecosystem Ecology: A New Synthesis. BES Ecological Reviews Series*. Cambridge, CUP, in press.

**Jaworski, T. & Hilszczański, J.** (2013) The effect of temperature and humidity changes on insects development their impact on forest ecosystems in the expected climate change. *Forest Research Papers* **74**, 345–355.

**Koh, L.P.** (2008) Can oil palm plantations be made more hospitable for forest butterflies and birds? *Journal Applied Ecology* **45**, 1002–1009.

**Lachin, J.M.** (1981) Introduction to sample size determination and power analysis for clinical trials. *Controlled Clinical Trials* **2**, 93–113.

**Lahondère, C. & Lazzari, C.R.** (2012) Mosquitoes cool down during blood feeding to avoid overheating. *Current Biology* **22**, 40–45.

**Lease, H.M., Goelst, K., Seely, M.K. & Mitchell, D.** (2014) Evidence of temperature-independent metabolic rates in diurnal Namib Desert tenebrionid beetles. *Physiological Entomology* **39**, 254–262.

**Lee, P.S., Gan, H.M., Clements, G.R. & Wilson, J.J.** (2016) Field calibration of blowfly-derived DNA against traditional methods for assessing mammal diversity in tropical forests. *Genome* **59**, 1008–1022.

**Leray, M. & Knowlton, N.** (2016) Visualizing patterns of marine eukaryotic diversity from metabarcoding data using QIIME. *Methods in Molecular Biology* **1452**, 219–235.

**Leray, M., Yang, J.Y., Meyer, C.P., Mills, S.C., Agudelo, N., Ranwez, V., Boehm, J.T. & Machida, R.J.** (2013) A new versatile primer set targeting a short fragment of the mitochondrial COI region for metabarcoding metazoan diversity: application for characterizing coral reef fish gut contents. *Frontiers in Zoology* **10**, 34.

**Liow, L.H., Sodhi, N. S. & Elmqvist, T.** (2001) Bee diversity along a disturbance gradient in tropical lowland forests of South-East Asia. *Journal of Applied Ecology* **38**, 180–192.

**Luskin, M.S. & Potts, M.D.** (2011) Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology* **12**, 540–551.

**McMurdie, P.J. & Holmes, S.** (2014) Waste not, want not: why rarefying microbiome data is inadmissible. *PLoS Computational Biology* **10**, e1003531.

**Mora, C., Frazier, A.G., Longman, R.J., Dacks, R.S., Walton, M. M., Tong, E.J., Sanchez, J.J., Kaiser, L.R., Stender, Y.O., Anderson, J.M., Ambrosino, C.M., Fernandez-Silva, I., Giuseffi, L.M. & Giambelluca, T.W.** (2013) The projected timing of climate departure from recent variability. *Nature* **502**, 183–187.

**MPOB** (2016) Malaysia: Distribution of oil palm planted area by state and sector in 2014. Link: http://www.data.gov.my/data/en_US/dataset/malaysia-distribution-of-oil-palm-planted-area-by-state-and-sector-in-2014/resource/9b6fcd3b-f361-42c2-ae6f-e668f4efcf11 (accessed 11 January 2017).

**NASA**. Link: http://climate.nasa.gov/vital-signs/global-temperature/ (accessed 7 April 2015).

**National Physical Plan-2** (2010) Federal Department of Town and Country Planning. Ministry of Housing and Local Government. Link: http://www.townplan.gov.my/download/National%20Physical%20Plan(kecik).pdf (accessed 27 January 2017).

**Nazareth, T., Seixas, G. & Sousa, C.A.** (2016) *Climate Change and Mosquito-Borne Diseases. Part of the Series Climate Change Management*. pp. 187–199. Switzerland: Springer International Publishing.

**Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S. & Favila, M.E. & The Scarabaeinae Research Network.** (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* **141**, 1461–1474.

**Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., Corlett, R.T., Huntley, B., Bickford, D., Carr, J.A., Hoffmann, A.A., Midgley, G.F., Pearce-Kelly, P., Pearson, R.G., Williams, S.E., Willis, S.G. & Young, B. & Rondinini, C.** (2015) Assessing species vulnerability to climate change. *Nature Climate Change* **5**, 215–224.

**Pincebourde, S., Sinoquet, H., Combes, D. & Casas, J.** (2007) Regional climate modulates the canopy mosaic of favourable and risky microclimates for insects. *Journal of Animal Ecology* **76**, 424–438.

**Pinheiro, F., Diniz, I.R., Coelho, D. & Bandeira, M.P.S.** (2002) Seasonal pattern of insect abundance in the Brazilian cerrado. *Austral Ecology* **27**, 132–136.

**Piyaphongkul, J., Pritchard, J. & Bale, J.** (2012) Can tropical insects stand the heat? A case study with the brown planthopper *Nilaparvata lugens* (Stål). *PLoS ONE* **7**, e29409.

**Plant, A.R., Surin, C., Saokhod, R. & Srisuka, W.** (2011). Higher taxon diversity, abundance and community structure of Empididae, Hybotidae and Brachystomatidae (Diptera: Empidoidea) in tropical forests - results of mass sampling in Thailand. *Studia dipterologica* **18**, 121–149.

**Porter, E.E., Forschner, B.R. & Blair, R.B.** (2001) Woody vegetation and canopy fragmentation along a forest-to-urban gradient. *Urban Ecosystem* **5**, 131–151.

**Price, P.W., Denno, R.F., Eubanks, M.D., Finke, D.L. & Kaplan, I.** (2011) *Ecosystem Processes. Chapter 1.7. In: Insect Ecology: Behavior, Populations and Communities*. UK: Cambridge University Press.

**Putz, F.E., Zuidema, P.A., Pinard, M.A., Boot, R.G., Sayer, J.A., Sheil, D., Sist, P., Elias & Vanclay, J.K.** (2008) Improved tropical forest management for carbon retention. *PLoS Biology* **6**, e166.

**Ratnasingham, S. & Hebert, P.D.N.** (2007) BOLD: the Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes* **7**, 355–364.

**Roberts, D.L., Cooper, R.J. & Petit, L.J.** (2000) Use of premontane moist forest and shade coffee agroecosystems by army ants in western Panama. *Conservation Biology* **14**, 192–199.

**Schmieder, R. & Edwards, R.** (2011) Quality control and preprocessing of metagenomic datasets. *Bioinformatics* **27**, 863–864.

**Schneider, A., Mertes, C.M., Tatem, A.J., Tan, B., Sulla-Menashe, D., Graves, S.J., Patel, N.N., Horton, J.A., Gaughan, A.E. & Rollo, J.T.** (2015) A new urban landscape in East–Southeast Asia, 2000-2010. *Environmental Research Letters* **10**, 3.

**Senior, M.J.M., Hamer, K.C., Bottrell, S., Edwards, D.P., Fayle, T. M., Lucey, J.M., Mayhew, P.J., Newton, R., Peh, K.S.H., Sheldon, F.H., Stewart, C., Styring, A.R., Thom, M.D.F., Woodcock, P. & Hill, J.K.** (2013) Trait-dependent declines of species following conversion of rain forest to oil palm plantations. *Biodiversity and Conservation* **22**, 253–268.

**Sing, K.W., Syaripuddin, K. & Wilson, J.J.** (2013) Changing perspectives on the diversity of bats (Chiroptera) at Ulu Gombak since the establishment of the Field Studies Centre in 1965. *Raffles Bulletin of Zoology* **S29**, 211–217.

**Sing, K.W., Jusoh, W.F.A., Hashim, N.R. & Wilson, J.J.** (2016a) Urban parks: refuges for tropical butterflies in Southeast Asia? *Urban Ecosystems* **19**, 1131–1147.

**Sing, K.W., Dong, H., Wang, W.Z. & Wilson, J.J.** (2016b) Can butterflies cope with city life? Butterfly diversity in a young megacity in southern China. *Genome* **59**, 751–761.

**Sittichaya, W., Thaochan, N. & Tasen, W.** (2013) Powderpost beetle communities (Coleoptera: Bostrichidae) in durian-based agricultural areas in southern Thailand. *Kasetsart Journal: Natural Science* **47**, 374–386.

**Sugiura, S., Tanaka, R., Taki, H. & Kanzaki, N.** (2013) Differential responses of scavenging arthropods and vertebrates to forest loss maintain ecosystem function in a heterogeneous landscape. *Biological Conservation* **159**, 206–213.

**Syaripuddin, K., Sing, K.W. & Wilson, J.J.** (2015) Comparison of butterflies, bats and beetles as bioindicators based on four key criteria and DNA barcodes. *Tropical Conservation Science* **8**, 138–149.

**Tangang, F.T., Liew, J., Salimun, E., Kwan, M.S., Loh, J.L. & Muhamad, H.** (2012) Climate change and variability over Malaysia: gaps in science and research information. *Sains Malaysiana* **41**, 1355–1366.

**Teuscher, M., Gérard, A., Brose, U., Buchori, D., Clough, Y., Ehbrecht, M., Hölscher, D., Irawan, B., Sundawati, L., Wollni, M. & Kreft, H.** (2016) Experimental biodiversity enrichment in Oil-palm-dominated landscapes in Indonesia. *Frontiers in Plant Science* **7**, 1538.

**Uno, S., Cotton, J. & Philpott, S.M.** (2010) Diversity, abundance, and species composition of ants in urban green spaces. *Urban Ecosystems* **13**, 425–441.

**Vanbergen, A. J.** (2013) Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment* **5**, 251–259.

**Verdú, J.R., Díaz, A. & Galante, E.** (2004) Thermoregulatory strategies in two closely related sympatric Scarabaeus species (Coleoptera: Scarabaeinae). *Physiological Entomology* **29**, 32–38.

**Verdú, J.R., Alba-Tercedor, J. & Jiménez-Manrique, M.** (2012) Evidence of different thermoregulatory mechanisms between two sympatric Scarabaeus species using infrared thermography and micro-computer tomography. *PLoS ONE* **7**, e33914.

**Weisser, W.W. & Siemann, E.** (2004) The various effects of insects on ecosystem functioning. pp. 3–24. *in Insects and Ecosystem Function*. Berlin Heidelberg, Springer.

**Wilby, R.L. & Perry, G.L.W.** (2006) Climate change, biodiversity and the urban environment: a critical review based on London, UK. *Progress in Physical Geography* **30**, 73–98.

**Wilson, J.J., Sing, K.W., Lee, P.S. & Wee, A.K.** (2016) Application of DNA barcodes in wildlife conservation in tropical East Asia. *Conservation Biology* **30**, 982–989.

**Wong, M.M., Lim, C.L. & Wilson, J.J.** (2015) DNA barcoding implicates 23 species and four orders as potential pollinators of Chinese knotweed (*Persicaria chinensis*) in Peninsular Malaysia. *Bulletin of Entomological Research* **105**, 515–520.

**Zeale, M.R.K., Butlin, R.K., Barker, G.L.A., Lees, D.C. & Jones, G.** (2011) Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. *Molecular Ecology Resources* **11**, 236–244.

**Zhang, K., Lin, S.L., Ji, Y.Q., Yang, C.X., Wang, X.Y., Yang, C.Y., Wang, H., Jiang, H., Harrison, R.D. & Yu, D.W.** (2016) Plant diversity accurately predicts insect diversity in two tropical landscapes. *Molecular Ecology* **25**, 4407–4419.