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Global generic richness and distribution: new maps of the world of ants with examples of their use in the context of Asia

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ABSTRACT. Knowledge of the biogeographic distribution of ants is central to our understanding of ant ecology, evolution, taxonomy and conservation. Here, we introduce a novel global biogeographic database for ant genera and an associated website with maps showing the known distribution of all extant ant genera. We use this database to consider knowledge of the distribution of ant genera in Asia, a hotspot of ant diversity and biological diversity more generally. We find that, although ant systematists and ecologists are now active in Asia, much remains to be learned about the distribution of Asian ant genera. We highlight areas where additional research would be particularly useful.

In Asia, as elsewhere, ants are ecologically dominant and conspicuous actors in most ecosystems: as predators (Steghaus-Kovac & Maschwitz 1993; Berghoff *et al.* 2002), mutualist partners with other insects (Way 1963; Maschwitz & Hänel 1985; Pierce *et al.* 2002; Pfeiffer & Linsenmair 2007) or plants (Fiala *et al.* 1994; Federle *et al.* 1998; Itioka *et al.* 2000; Kaufmann & Maschwitz 2006; Webber *et al.* 2007), seed-dispersers (Pfeiffer *et al.* 2004, 2006), herbivores (Woods & Elliott 2004; Pfeiffer *et al.* 2006), and mycophages (Witte & Maschwitz 2008). Like other taxa, ants include both rare and common lineages. The life histories of some ant species predispose them to endangerment and extinction (Wilson 1963; Buschinger 1985; Espadaler & López-Soria 1991). On the other hand, several ant species have become invasive, with some species present in more than a hundred countries (McGlynn 1999; Wetterer & Porter 2003; Roura-Pascual *et al.* 2004; Wetterer 2008, 2009). In recent years, major advances have been made in ant systematics (Brady *et al.* 2006; Moreau *et al.* 2006; Ward 2007), yet recorded distribution of ant lineages, particularly in the tropics, has major gaps, as indicated, for example, by the recent discovery of a new ant subfamily (Rabeling *et al.* 2008). A first step towards filling these gaps is to understand the biogeographic distribution of extant ant lineages.

In this article, we describe briefly a new resource for myrmecologists: online maps of the known distribution of all extant ant genera. We focus, in this first paper, on Asia, because it is not only a region of very active ant research and high generic richness (Fisher 2009), but also because tropical Asia has recently been a hotspot for new discoveries of genera of ants (Xu 2000; Fernandez 2003; Dubovikoff 2005; Eguchi & Bui 2007; Yamane *et al.* 2008). In sum, the combination of diverse regions sampled to varying extents, and an active community of ant biologists, suggested that it was Asia where our maps might be most useful and, simultaneously, where additional feedback from myrmecologists might most rapidly improve our collective knowledge of distribution patterns. We provide examples of several maps and present estimates of the known richness of ant genera at island- or country-level and, in some cases, finer-grain geopolitical regions (e.g., provinces). We present this work as an invitation to further contributions from myrmecologists working in Asia and to highlight areas where additional sampling is most likely to be rewarded.

WHY GENERA?

Much of the understanding of the global distribution of species, areas of conservation priority and areas where future discoveries are

likely is based on knowledge of vertebrates (Orme *et al*. 2005; Buckley & Jetz 2007; Schipper *et al*. 2008) and plants (Francis & Currie 2003; Jansson & Davies 2008). We are aware of just a handful of studies at the global scale of coarse-grain patterns in richness of terrestrial insect taxa, including those on tiger beetles (Pearson & Cassola 1992), termites (Eggleton *et al*. 1994), and mosquitoes (Foley *et al*. 2007). A key next step is to assess not only patterns of diversity in other taxa, but also the underlying biogeographic distributions of lineages that lead to these patterns. Ants, while only modestly diverse when compared to groups such as the order of beetles (Grimaldi & Engel 2005), are diverse enough to present a challenge, yet well-enough-known to justify an attempt at global distribution maps. Progress has already been made in understanding the local diversity of species of ants at the global level (Kaspari *et al*. 2004, Dunn *et al*. 2007, Dunn *et al*. 2009a). Ultimately though, one would like to know the global distribution of genera or even species, not just how many species overlap in local assemblages. While one might hope to generate global distributional maps on the basis of species (as has been done for mammals, for example), the reality is that naming, much less knowing the distribution, of all ant species (or the species of any diverse insect taxon) is many years—perhaps many decades—off. Ant genera, on the other hand, are considered to be relatively stable taxonomically (Ward 2007) and potential misidentifications are less likely at the genus level than at the species level. In addition, the number of ant genera is strongly correlated with the number of ant species in the regions considered to date (Andersen 1995; Dunn *et al*. 2009b). Finally, much of the variation in ant life history is between rather than within genera (Brown 2000), such that knowing which genera are present in a region may also allow some inference as to which ant-mediated processes are also present.

WHY GEOPOLITICAL REGIONS?

Geopolitical regions differ in their size and configuration. For posing ecological questions, these spatial references—consequences of politics and history—are problematic. Yet, while myrmecologists can now record the exact position of each of their samples with handheld GPS units (or even with their phones), for most of the long history of myrmecology, this has not been the case. Many hundreds of articles have been published in which specimen data are recorded only to the level of geopolitical region, such as island, country or province. Similarly many, perhaps most, specimen labels in museums record only the geopolitical region of collection. For these reasons (and so as to include as many data as possible), we have chosen to use geopolitical entities as the geographic units at which to compile our data and to inform our maps. As data accumulate, however, we will be able to refine maps, with the ultimate goal of producing maps of ant genera with a finer and more regular scale of sampling.

RESULTS TO DATE FOR ASIA

To date, maps of 295 genera from 372 geopolitical regions have been created and are available online: http://www.antmacroecology.org/ant_genera/index.html (references used for each record are available online at: http://www.antmacroecology.org/godb_data_V1.0.txt.zip). Maps were generated by compiling published records of genera, by consulting ant systematists and ant biologists working in the field, and extracting data from museum and personal collections. Geopolitical regions were islands (e.g., Borneo, New Guinea), countries (e.g., Sri Lanka, Armenia) or, where data permitted, subnational units of large countries such as provinces in China (e.g., Guangxi, Yunnan). As examples of the product of our efforts, we present two maps of genera present in Asia: *Bannapone*, which is known from only one geopolitical region, and *Camponotus*, which is known from essentially all geopolitical regions in Asia (Fig. 1). These two genera frame the range of distributions we have documented in compiling the maps. In Asia, most genera are found in many geopolitical regions, but several tens of genera are still known from just one or a few geopolitical regions (Fig. 2). Based on our knowledge to date, many Asian genera have very narrow modern geographic distributions. Examples include *Ancyridris* (New Guinea), *Aneuretus* (Sri Lanka), *Aulacopone* (Armenia and Azerbaijan), *Bannapone* (Yunnan), *Bregmatomyrma* (Borneo),

Chimaeridris (Borneo and Sulawesi), *Dacatria* (Guangxi and South Korea), *Indomyrma* (Karnataka and Kerala), *Ishakidris* (Borneo), *Lasiomyrma* (Borneo, Java and Vietnam), *Loweriella* (Borneo and Peninsular Malaysia), *Noonilla* (Philippines), *Opamyrma* (Vietnam), *Overbeckia* (Philippines and Singapore), *Parvimyrma* (Vietnam), *Phaulomyrma* (Java, Myanmar and Thailand), *Propodilobus* (Borneo), *Rostromyrmex* (Peninsular Malaysia), *Rotastruma* (Borneo, Hunan, Guangdong and Peninsular Malaysia), *Secostruma* (Borneo and Sulawesi), *Tetheamyrma* (Borneo), *Tricytarus* (New Guinea), *Tyrannomyrmex* (Kerala, Philippines, Sri Lanka and Peninsular Malaysia) and *Yavnella* (Israel, Kerala and Yemen).

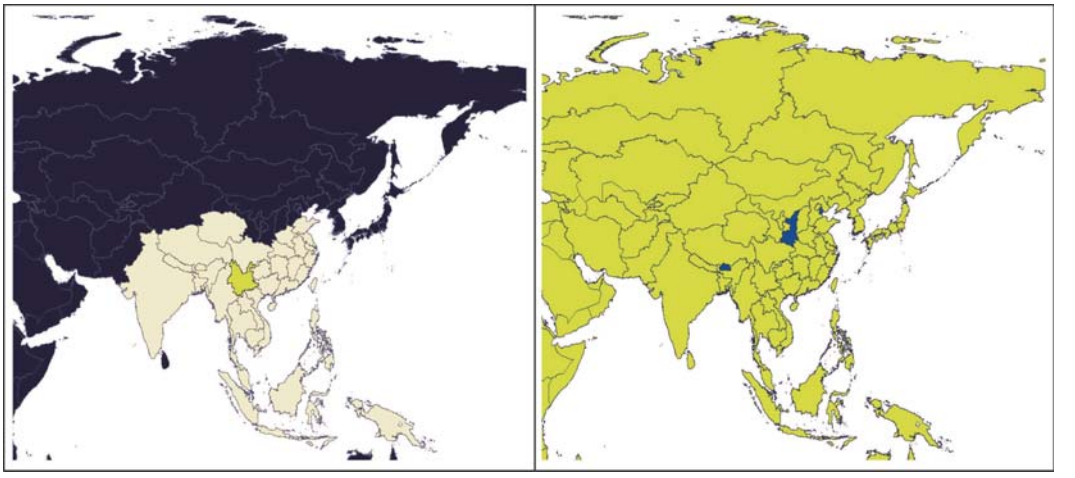

Fig. 1. Maps of a narrowly distributed (*Bannapone* – left) and a widespread (*Camponotus* – right) genus in Asia. Regions where each genus has been recorded are in green; areas where the genus is likely to occur, based on interpolation, are blue. Absences (presence of genus unlikely) are in black and uncertainties (presence of genus possible, but no supportive data available) are in beige.

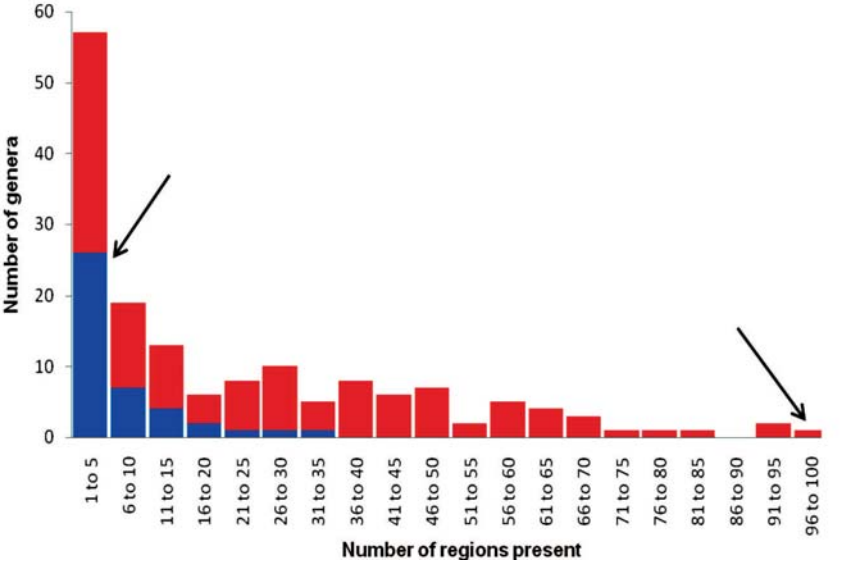

Fig. 2. Histogram of the number of Asian geopolitical regions from which a genus is known. Genera currently considered to be endemic to Asia are in blue; genera with distributions encompassing areas outside Asia are in red.

WHAT ARE WE MISSING?

Regions differ in the completeness of their sampling. It is inevitable that in every part of the world, some regions are more poorly sampled than others. Knowing which regions, countries or states are poorly sampled is not always straightforward. Under-recorded regions may include those where particular genera occur but have not been detected, and those where the records have simply not been made publicly available. With regard to the latter, we have certainly missed records from individual collections and publications to which we have not had access. On the basis of their personal collections, myrmecologists often know of records in regions that are not yet known by the broader community. Such records are very important to understanding the range boundaries of genera and lineages. We therefore invite myrmecologists to consult our online maps and participate in improving them, by notifying us of new, incorrect or missing records.

The maps for the ant genera of Asia may change more in the future than those of any other region. Myrmecologists in Asia are actively updating knowledge of distribution, systematics and diversity of the regional fauna. Since 2000, six genera have been described or resurrected from Asia, *Bannapone* (Xu 2000), *Tyrannomyrmex* (Fernandez 2003), *Chronoxenus* (Dubovikoff 2005), *Parvimyrma* (Eguchi & Bui 2007), *Opamyrma* (Yamane *et al*. 2008), and *Propodilobus* (Branstetter 2009). It is inevitable that more genera await discovery and description. In addition to the discoveries of new genera to science, new records of known genera are likely to be common in the coming years in Asia for some regions. Fig. 3 shows the known generic richness of different geopolitical regions. Light-coloured (low-richness) areas surrounded by dark (high-richness) areas seem likely to be regions where many future discoveries will occur, though a more formal analysis of the number of genera predicted for these regions (on the basis, perhaps, of their climate) would be useful. The ant

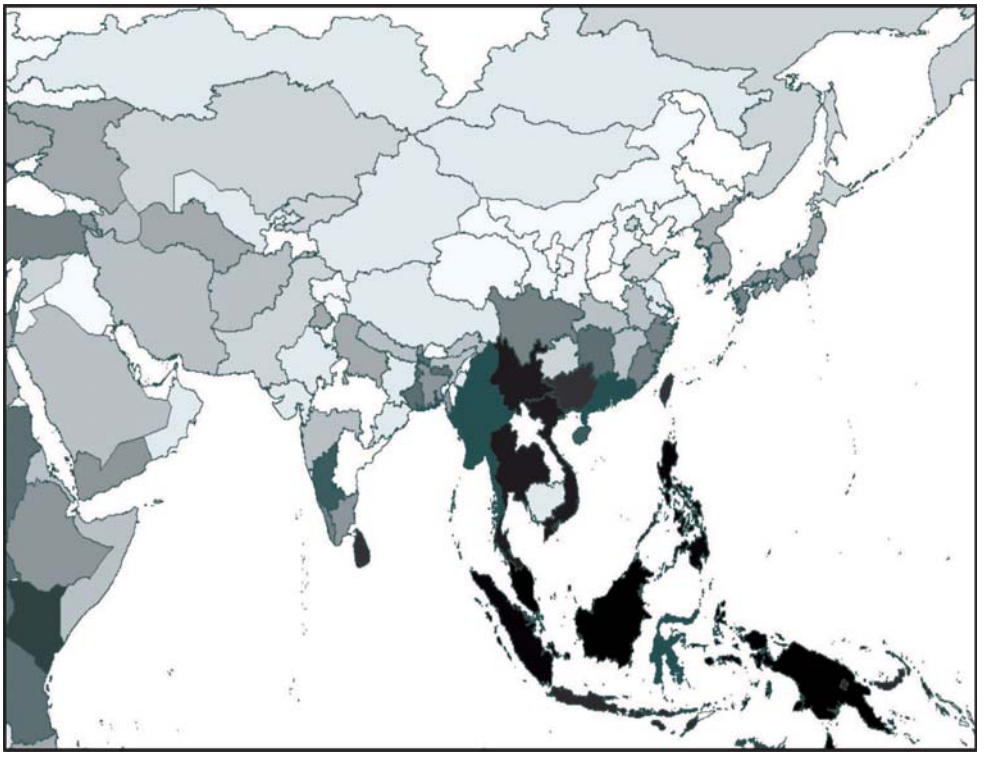

Fig. 3. Map of the known generic richness patterns of ants in Asia, by geopolitical region. Shades indicate the number of genera, from low (light grey) to high (darker colours).

Table 1. Number of genera known from each of the regions of India (list of references used is presented in electronic Appendix 1).

Region of India	Number of known genera
Andaman and Nicobar islands	22
Andhra Pradesh	8
Arunachal Pradesh	28
Assam	38
Bihar + Jharkhand	18
Chandigarh	19
Dadra and Nagar Haveli	0
Daman & Diu	1
Delhi	9
Goa	11
Gujarat	20
Haryana	12
Himachal Pradesh	23
Jammu & Kashmir	13
Karnataka	53
Kerala	46
Lakshadweep	0
Madhya Pradesh + Chhattisgarh	12
Maharashtra	35
Manipur	18
Meghalaya	49
Mizoram	0
Nagaland	0
Orissa	26
Pondicherry	4
Punjab	34
Rajasthan	18
Sikkim	38
Tamil Nadu	40
Tripura	12
Uttar Pradesh + Uttarakhand	37
West Bengal	51

fauna of Laos, for example, remains virtually unknown, at least to Western science.

Perhaps the biggest gap in our map of ant genera is for India, a large country that has large latitudinal and altitudinal gradients that create different ecosystems conducive to a rich diversity of ant genera. India represents the southern limit for species of some Holarctic genera such *Formica*, *Lasius*, *Leptothorax*, *Myrmica* and *Temnothorax* and the northwestern limit for Oriental genera such *Diacamma*, *Dilobocondyla*, *Gesomyrmex*, *Harpegnathos*, *Iridomyrmex*, *Kartidris*, *Lophomyrmex*, *Myopopone*, *Myrmoteras*, *Odontoponera*, *Paratopula*, *Philidris*, *Recurvidris*, *Tyrannomyrmex*, *Vollenhovia* and *Vombisidris*. Yet, while we were able to gather presence records for a total of 86 genera for India, we were unable to find comprehensive information for states. In Fig. 3, we have divided India into 31 different regions (mostly based on states), and among these we find the highest richness of ant genera in the states of Karnataka (53 genera) and West Bengal (51 genera). On the other hand, seven states have fewer than ten recorded genera (ten being, for context, the number of genera recorded in Norway), probably due to a lack of published data. Nine states have between 11 and 20 recorded genera (Montana, USA, and Quebec, Canada, also have generic richness within this range). Four states have between 21 and 30 genera (30 genera can be found even in Austria or Kansas, USA), and eight states have between 31 and 49 genera (Table 1). These numbers are very low in comparison to well-sampled areas with similar climate such as Thailand (67 genera), Yunnan (79 genera) or

Peninsular Malaysia (87 genera) or even less-sampled areas such Myanmar (59 genera). We hope that additional sampling, along with further communication with Indian myrmecologists, will help refine our knowledge of the distribution of genera in India.

We suspect and hope that the present publication will quickly elicit communication of many records we have missed. That would, in our minds, be a wonderful consequence of having published the maps online. Other regions, however, will stay little-known even once myrmecologists working in Asia have consulted their collections. For those regions, we hope that our maps and their "light spots" will serve as a challenge, and that some myrmecologist, young or old, might add, for example, tens of new genus records to Punjab. They are, we are almost certain, there.

Asia remains an auspicious frontier with regard to our understanding of the distribution of ants as of other taxa, such as amphibians (Kohler *et al*. 2005). On the one hand, our relative ignorance about some regions of Asia is exciting and offers the possibility of future discoveries for myrmecologists. On the other hand, Asia and in particular tropical Asia faces a greater conservation threat than anywhere else on Earth (Brook *et al.* 2003; Sodhi *et al.* 2004). Some of the geopolitical regions in which few ant genera are known are largely deforested (Achard *et al*. 2002). It is possible that some genera in these regions are now locally extinct. Considering that other insect taxa are more poorly known than ants, the genera of ants that remain to be found and recorded represent only a fraction of future discoveries. While conservationists often discuss the need to conserve species that are not yet discovered, our maps make this unknown variable more visually apparent. The regionally little-known genera (and within those genera, species) may include not only those of conservation concern, but also those with the potential for positive economic impacts. Before they are recorded, we have no way of knowing.

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