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Understanding the ecological and evolutionary processes shaping ant biodiversity across spatiotemporal scales

by

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Declaration of Original and Sole Authorship

I, Cong Liu, declare that this thesis entitled "Understanding the ecological and evolutionary processes shaping ant biodiversity across spatiotemporal scales" and the data presented in it are original and my own work.

I confirm that:

- No part of this work has previously been submitted for a degree at this or any other university.

- References to the work of others have been clearly acknowledged. Quotations from the work of others have been clearly indicated, and attributed to them.

- In cases where others have contributed to part of this work, such contribution has been clearly acknowledged and distinguished from my own work.

- None of this work has been previously published elsewhere, with the exception of the following: (*Corresponding author)

> **Liu C***, Dudley KL, Xu ZH, Economo EP. (2017). Mountain metacommunities: climate and spatial connectivity shape ant diversity in a complex landscape. *Ecography*. DOI: 10.1111/ecog.03067.
>
> **Liu C***, Guénard B, Blanchard B, Peng YQ, Economo EP. (2016) Reorganization of taxonomic, functional, and phylogenetic ant biodiversity patterns after conversion to rubber plantation in Southeast Asia. *Ecological Monographs.* 86(2): 215-227.
>
> **Liu C***, Hita Garcia F, Peng YQ, Economo EP. (2015) *Aenictus yangi* sp. n. – a new species of the *A. ceylonicus* species group (Hymenoptera, Formicidae, Dorylinae) from Yunnan, China. *Journal of Hymenoptera Research* 42: 33-45.
>
> **Liu C***, Guénard B, Hita Garcia F, Yamane SK, Blanchard B, Economo EP (2015) New records of ant species from Yunnan, China. *Zookeys* 477: 17-68.

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Understanding the ecological and evolutionary processes shaping ant biodiversity across spatiotemporal scales

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Cong Liu

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Abstract

Ecological and historical evolutionary processes together generate biodiversity patterns across geographies and across the tree of life. However, understanding the relative importance of, and the interplay between ecological mechanisms and evolutionary processes in shaping biodiversity patterns is still a challenge due to the different spatiotemporal scales on which they are operating. Therefore, a fundamental goal of biodiversity research is to use different research approaches to investigate how the ecological processes (dispersal, competition, and environmental filtering), as well as long-term evolutionary processes (adaptation and speciation), contribute to the community assembly and biodiversity patterns. In this thesis, I investigate ant biodiversity patterns and underlying eco-evolutionary processes across multiple systems (tropical agroecosystem, complex mountainous landscape, and Pacific archipelago), providing a comparative framework to understand the eco-evolutionary processes driving biodiversity patterns. I first present results from an ant biodiversity survey in Xishuangbanna, Yunnan, China, where I found 213 species/morphospecies of ants from 10 subfamilies and 61 genera. Forty species represent new records for Yunnan province and 17 species are newly recorded for China. In addition, I describe one new species, *Aenictus yangi*. When examining the changes in taxonomic, functional, and phylogenetic ant biodiversity after conversion to rubber plantation, I found a sharp decline of species richness in rubber plantation with lower than expected taxonomic and functional beta diversity. This suggested a strong environmental filtering driving ant biodiversity in the rubber plantation. I then investigate the variation in taxonomic and phylogenetic ant diversity patterns along a geographic transect spanning 5000m in elevational range in the Hengduan mountains, where environmental gradients and spatial connectivity are intertwined as a complex process that might shape biodiversity patterns. I found that environmental gradients dominate variation in both alpha and beta diversity in this landscape, with alpha diversity strongly declining with elevation and beta diversity driven by elevational differences. Finally, I apply a comparative phylogeographic framework to examine the evolution of the hyperdiverse ant genus *Strumigenys* in Fiji archipelago using RAD sequencing. My results revealed the history of *Strumigenys* species that colonized to Fiji archipelagoes in Miocene (10.5-7.5 Ma), following by two independent radiations across the whole archipelago, leading to the emergence of 11 endemic species. The population structure and demographic history of each endemic species consistently support the idea of deterministic macroevolutionary processes that drive the diversity dynamic of ants in Fiji archipelago. Together, this study highlights the need for a pluralistic framework that integrates different approaches to understanding the eco-evolutionary drivers of biodiversity patterns across scales.

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I would like to thank my advisor Evan Economo, for providing fantastic resources, absolute freedom, sound advice, and support throughout my PhD study. I thank my collaborator, Benoit Guénard, for opening the door of myrmecological study, and for teaching me ant sampling and subsequent biodiversity analyses. I also thank my collaborators, Eli Sarnat, Francisco Hita Garcia, Georg Fischer, Masashi Yoshimura, and Seiki Yamane, for their help with ant identification and for teaching me ant taxonomy and systematics. Many thanks to Nick Friedman, Clive Darwell, and Nao Takashina for the insightful discussions in multiple projects as well as their suggestions in pursuing an academic career. Thank Nick Friedman again for his valuable and constructive comments on the first draft. I would like to thank our lab technicians for their supports during my graduate study: Kenneth Dudley for his help with GIS analyses; Nitish Narula, for his help with programming; Julia Janicki, for her help with databasing; and Masako Ogasawara, for her help with ant sorting and mounting. I thank Benjamin Blanchard for his help with the ant biodiversity survey in China as well as the ant specimen sorting and mounting. I appreciate the supports from our lab administrator Chisa Oshiro, as well as the supports from OIST student support section. I would like to thank my Chinese collaborators, Yang Da-Rong, Peng Yan-Qiong, and Xu Zhen-Hui, for their supports and assistance with ant biodiversity survey and data providing. Finally, I would like to thank OIST and JSPS for the research funding.

List of Abbreviations

BQ	Beqa
CI	Cephalic index
DEM	Digital elevational map
EDF	Effective degree of freedom
EL	Eye length
FD	Functional alpha diversity
FL	Femur length
GA	Gau
GAM	Generalized additive models
HL	Head length
HW	Maximum head width
ICE	Incidence-based coverage estimator
KR	Koro
KV	Kadavu
LA	Ovalau
MCMC	Markov chain Monte Carlo
ML	Mesosomal length
ML	Moala
MNTD	Mean nearest taxon distance
MPD	Mean pairwise distance
NMDS	Nonparametric multidimensional scaling
PBD	Phylogenetic beta diversity
PCA	Principal component analyse
PD	Phylogenetic alpha diversity
PL	Petiole length
RADseq	Restriction site associated DNA sequencing
SES	Standardized effect sizes
SI	Scape index
SL	Scape length
SNP	Single-nucleotide polymorphism
SRTM	Shuttle Radar Topography Mission
TA	Taveuni
TBD	Taxonomic beta diversity
TIN	Triangulated irregular network
TL	Tibal length
UTM	Universal Transverse Mercator
VL	Viti Levu
VN	Vanua Levu
WL	Weber’s length
XTBG	Xishuangbanna Tropical Botanical Garden

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1. Introduction

Historical evolutionary processes interact with ecological processes to generate current biodiversity patterns across geographies and the tree of life. However, understanding the relative importance of, and the interplay between ecological processes and evolutionary mechanisms in shaping biodiversity patterns is still challenging due to the multiple spatiotemporal scales at which they are operating (Lessard et al. 2012). Therefore, a fundamental goal of biodiversity research is to place different research approaches within a dynamic framework to investigate how the ecological processes (migration, competition, and environmental filtering) incorporate with long-term evolutionary processes (adaptation and speciation) contribute to the community assembly and structure (Gillespie 2016).

Community assembly can be driven by ecological processes which involving the dispersal of species from regional species pool followed by environmental filtering and species interaction (Figure 1.1, Process I). The extent to which ecological communities are structured by stochastic factors such as dispersal and ecological drift (Hubbell 2001), or more deterministic assembly forces such as species sorting and competition (Chase and Leibold 2003) has long been a contentious debate. If stochastic factors largely shape community assembly, species differences (e.g., functional and phylogenetic relationship) will not be important in determining which species occupy which communities, leading to random species composition communities. In contrast, under deterministic scenarios, various non-random processes such as competition and species sorting could result in a predictable community structure (Chase and Leibold 2003).

On the other hand, interactions among species within local communities might feedback to influence the evolutionary processes that generate regional species pool through speciation and adaptation (Figure 1.1, Process II; Mittelbach and Schemske 2015). Studying this evolutionary feedback will shed light on the controversy of whether evolution follows deterministic pathways (e.g., Taxon cycle, Wilson 1959, 1961) or is driven by stochastic processes (e.g. random genetic drift, Nei et al. 1975), and will provide insight into the evolutionary processes that influence the community assembly.

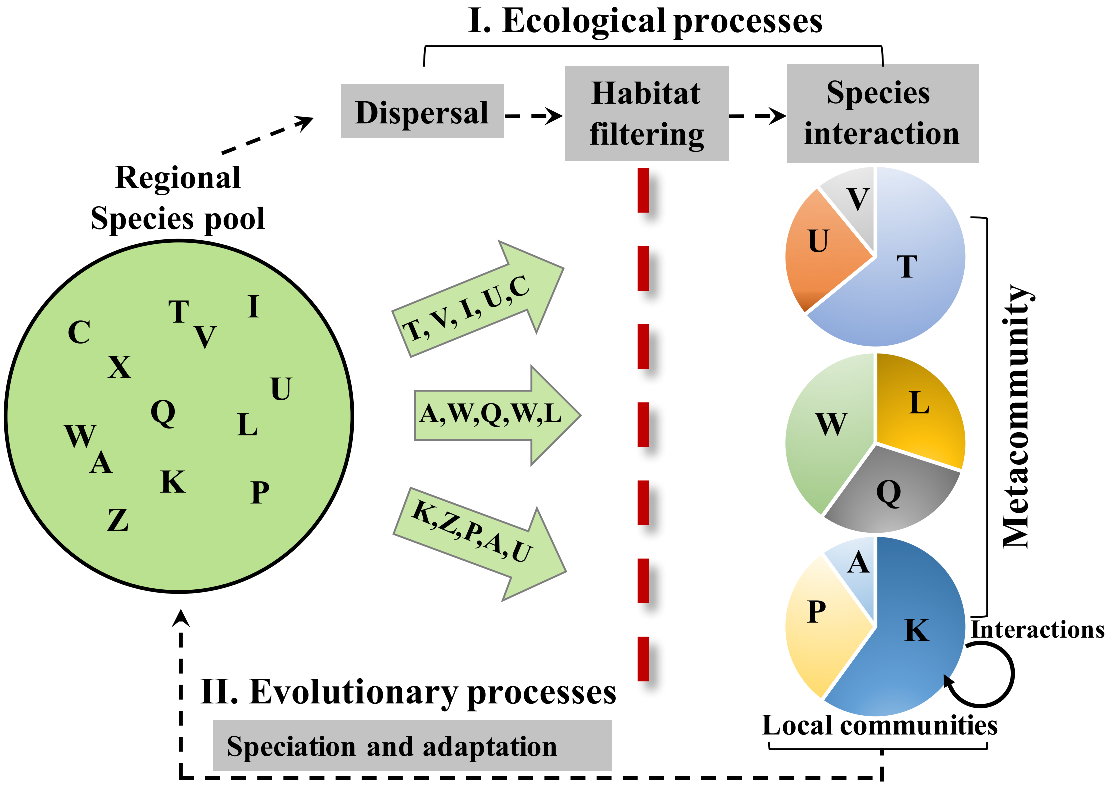

Figure 1.1 I Community assembly through ecological processes (I), and evolutionary processes (II).

These ecological and evolutionary processes are often intertwined, and together shape community assembly dynamics through time. Therefore, to disentangle these processes, it is essential to study how do those eco-evolutionary processes drive the diversity patterns, as well as community structure through time. In this thesis, I investigate ant biodiversity patterns and underlying eco-evolutionary processes across multiple systems including a tropical agroecosystem, a complex mountainous landscape, and a Pacific archipelago. My goal is to provide a comparative framework to understand the eco-evolutionary processes driving biodiversity patterns. In Chapter 1, I present results from ant biodiversity inventory in Xishuangbanna, Yunnan, China. Then, I examine the changes in taxonomic, functional, and phylogenetic ant biodiversity after conversion from natural forest to rubber and test three hypotheses (stochastic, environmental filtering, and biotic interaction) describing community processes underlying changes in biodiversity in the agroecosystem in Chapter 2. In Chapter 3, I evaluate the effects of environmental gradients and spatial factors on ant community patterns in this complex mountainous landscape by investigating the variation in taxonomic and phylogenetic ant diversity patterns along a geographic transect spanning 5000m in elevational range in the Hengduan mountains. Finally, in Chapter 4 I apply a comparative phylogeographic framework using RAD sequencing to examine the evolution of the hyperdiverse ant genus *Strumigenys* in Fiji archipelago and to investigate how such evolution patterns affect ant community assembly through time.

2. Ants biodiversity inventory and taxonomy in Xishuangbanna, Yunnan, China

2.1 Introduction

The understanding of regional and global patterns of insect diversity is limited by our incomplete accounting of Earth's species, especially for tropical regions where species richness peaks in most taxonomic groups. This is also true for Formicidae, an ecologically dominant insect family comprising at least 15,000 described species (Bolton 2014). Despite the ubiquity and ecological importance of ants (Hölldobler and Wilson 1990), many tropical regions remain undersampled even at the generic level (Guénard and Dunn 2012). Compiling and curating complete and accurate species checklists for all regions of the world should be a priority in biodiversity research, especially for diverse insect groups.

Towards that end, here I present the results of an ant survey conducted during the summer of 2013 in the area of Xishuangbanna, Yunnan Province, in the south of China. In particular, our goal here is to document new records of ant species detected in Yunnan, and some new records for China as a whole. The geographic location of Yunnan (ranging from 21.15°N to 29.20°N of latitude) and its topography (elevation range from < 100m to 6740m) render it the most diverse province of China in terms of ant diversity (406 species) (Guenard and Dunn 2012). The same is true for other taxa, such as plants (Li and Walker 1986, Mutke and Barthlott 2005), tiger beetles (Wu and Shook 2007), butterflies (Xie et al. 2009), or amphibians (Chen and Bi 2007). Xishuangbanna prefecture is located in the tropical southwestern region of Yunnan province, bordering Laos and Myanmar, and has been identified as the most diverse region of Yunnan (Long 1995). The ant fauna of Xishuangbanna has been the subject of three studies (Xu

1998, 1999, 2002) and new species are regularly described from this prefecture (e.g. Guénard et al. 2013, Xu et al. 2014a, b). According to Xu's survey (Xu 2002), the myrmecofauna of Xishuangbanna consists of approximately 262 species, which constitute about 65% of the total number of species recorded for Yunnan province.

While elements of China's ant fauna may be undocumented due to a lack of sampling in certain geographic regions, there are many taxa likely hidden in areas that have been sampled historically. In particular, methods targeting specifically subterranean or leaf litter ants have been rarely used in China, which as a result might bias our detection of ant species from specific strata. One of the most successful sampling techniques for collecting leaf litter ants, Winkler extraction, which is now commonly used for ant fauna surveys all over the world (Olson 1991, Fisher 1999, Delabie et al. 2000, Martelli et al. 2004, Groc et al. 2007, Vasconcelos and Lopes 2008, Ivanov and Keiper 2009), has only been used once in China (Hong Kong in Fellowes 1996) to the best of our knowledge. I used Winkler extraction as a standardized collection technique for the first time in order to survey the leaf litter ant fauna of Xishuangbanna. Based predominantly on this highly successful sampling technique, my diversity survey revealed 40 new species records for Yunnan including 17 new records for China. Here I present those new records, as well as their known global distributions by using data information aggregated by the Global Ant BioInformatics project (GABI, Guénard et al. 2017).

I also describe a new *Aenictus* species from the *A. ceylonicus* species group. The material was collected during this ant biodiversity survey. Despite being clearly a member of the *A. ceylonicus* group, my detailed morphological analysis did not allow us to fit it to any of the described group members. In addition, the material did not key out with the recent identification key provided by Jaitrong & Yamane (2013) in their revision of the *A. ceylonicus* group.

Consequently, I consider the material as new and describe it herein as *A. yangi* **sp. n.** on the basis of the worker caste. I also integrate it into the taxonomic system created by Jaitrong & Yamane (2011, 2013) by updating their key to species of the *A. ceylonicus* group and providing a diagnostic discussion and high-quality illustrations of important species and morphological characters identification key provided by Jaitrong & Yamane (2013) in their revision of the *A. ceylonicus* group. Consequently, I consider the material as new and describe it herein as *A. yangi* **sp. n.** on the basis of the worker caste. I also integrate it into the taxonomic system created by Jaitrong & Yamane (2011, 2013) by updating their key to species of the *A. ceylonicus* group and providing a diagnostic discussion and high-quality illustrations of important species and morphological characters.

2.2 Methods

2.2.1 Ant collection and specimens processing

Ant specimens were collected from primary forest, secondary forest and rubber plantation habitats near Menglun town, Xishuangbanna Prefecture, Yunnan Province, China during a survey in June 2013. Ants from leaf litter of multiple sites were collected and extracted by mini Winkler extractors for 72 hours using the shuffling method as described in (Guenard and Lucky 2011). Ants were also collected by hand on the ground, lower vegetation, and tree trunks.

Samples were first sorted to morphospecies in alcohol, and up to three representatives of each morphospecies per sample were point-mounted. Each mounted specimen was assigned a unique specimen code, in this case a CASENT number, and traditional locality and collection labels. All mounted and alcohol-preserved ant specimens are currently located in EPE’s lab at the Okinawa Institute of Science and Technology Graduate University. Extended depth of field specimen images were taken with an incorporated Leica DFC400 digital camera mounted on a Leica M205C stereomicroscope through the Leica Application Suite V4 software. All specimens were identified to genus using Bolton's key (Bolton 1994), and then identified to species using available keys (see results section) as well as the digital resources on AntWeb (http://www.antweb.org). All the specimen data are freely available on AntWeb.

Species distributions presented in the following maps are based on records reported here at the country level, or for the larger countries (China, India, Japan), at the first administration level. For large islands (e.g. Borneo, Sumatra, New Guinea) that form natural biogeographic units, I used the island boundary instead of political boundaries similar to a previous study (Guénard and Dunn 2012).

2.2.2 New *Aenictus* species description

All available workers of new *Aenictus* species were mounted, analysed, and measured. Morphological observations and measurements were done with a Leica M165 C stereomicroscope equipped with an orthogonal pair of micrometres at a magnification of 100x. Measurements were recorded in mm to three decimal places and rounded to two decimal places for presentation. The measurements and indices used in this study follow Jaitrong & Yamane (2011, 2013):

CI Cephalic index: HW / HL * 100.

HL Maximum head length in full-face view, measured from the anterior clypeal margin to the midpoint of a line drawn across the posterior margin of the head.

	[Note: the anterior clypeal margin in species on the *A. ceylonicus* group is sometimes concave, which is the case in *A. yangi*, and measuring as defined above reduces the maximum head length].
HW	Maximum head width in full-face view.
ML	Mesosomal length measured from the point at which the pronotum meets the cervical shield to the posterior margin of metapleuron in profile.
PL	Petiole length measured from the anterior margin of the peduncle to the posterior-most point of the tergite.
SI	Scape index: SL / HW * 100.
SL	Scape length, excluding the basal constriction and condylar bulb.
TL	Total length, roughly measured from the anterior margin of head to the tip of the gaster in stretched-out specimens.

In general, the morphological terminology used in this study follows Hölldobler and Wilson (1990), Bolton (1994), and for key characters of the genus *Aenictus* Jaitrong and Yamane (2011).

2.3 Results

2.3.1 Collection effects

Over 20000 specimens from 61 genera and 213 valid species and morphospecies were collected during this ant diversity survey (Appendix Table 8.1). A total of 40 new species records are presented for Yunnan province. Seventeen of these are recorded for the first time from China. The newly detected species belong to 15 genera from eight subfamilies. It is beyond the scope of the current paper to perform a comprehensive review/revision of the ant fauna of Yunnan Province, which would require much more geographically comprehensive sampling. Here, I present species accounts for the described ant species found during our survey that were previously unknown to Yunnan, supplementing other recently published checklists of the myrmecofauna of the region (Guénard and Dunn 2012).

2.3.2 New records

Aenictus artipus **Wilson, 1964** (Figure 2.1)

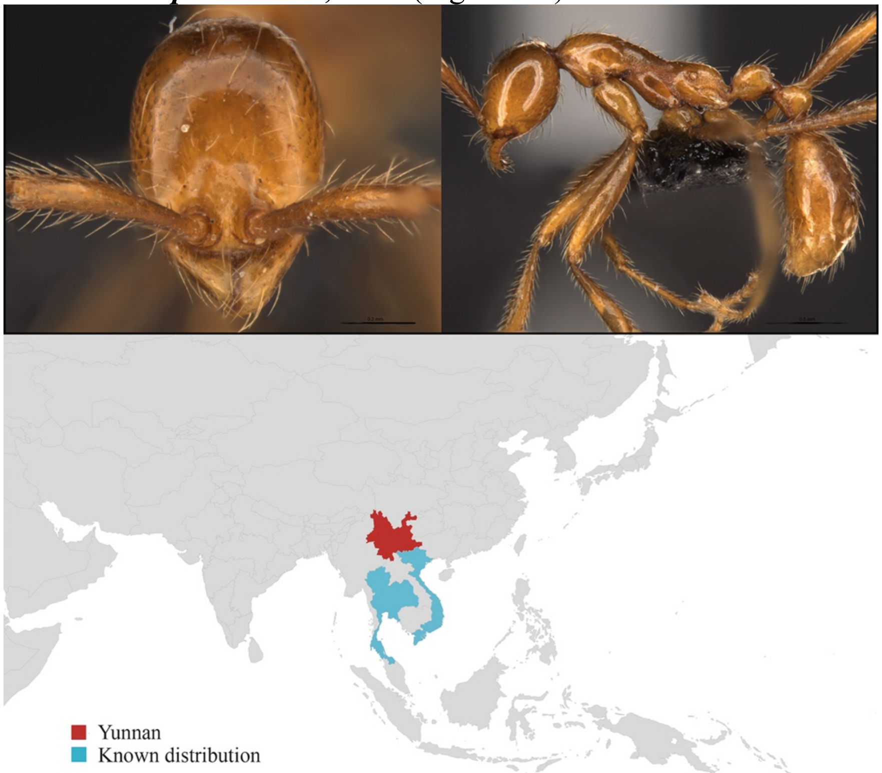

Figure 2.1 | Aenictus artipus.

(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: Man Sai village (21.858° N, 101.277° E), Rubber plantation, 12.vi.2013, 5 workers, 705m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.278° E), Secondary forest, 12.vi.2013, 18 workers, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Yunnan (new record), Vietnam and Thailand (Figure 2.1C). This collection represents the northern-most record of *Aenictus artipus*.

Taxonomic note. *Aenictus artipus* belongs to the *Aenictus wroughtonii* species group and can be easily identified with the identification key provided by Jaitrong et al. (2010).

Natural history. *Aenictus artipus* has been collected from leaf litter in various habitats such as secondary forest and rubber plantation located near natural secondary forest. In addition, *A*. *artipus* has also been found in different habitats such as montane evergreen forest, savanna forest, evergreen forest and disturbed forest (Jaitrong et al. 2010).

***Aenictus hodgsoni* Forel, 1901** (Figure 2.2)

Material examined. CHINA, Yunnan, Xishuangbanna: Xishuangbanna Tropical Botanical Garden (known as 'XTBG') (21.919° N, 101.270° E), Secondary forest, 08.vi.2013, 12 workers, 610m, Hand collection, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Secondary forest, 13.vi.2013, 40 workers, 825m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Widely distributed in the Indo-Malayan subregions (Figure 2.2C).

Taxonomic note. *Aenictus hodgsoni* belongs to the *Aenictus laeviceps*s species group and can be easily identified with the identification key provided by Jaitrong and Yamane (2011).

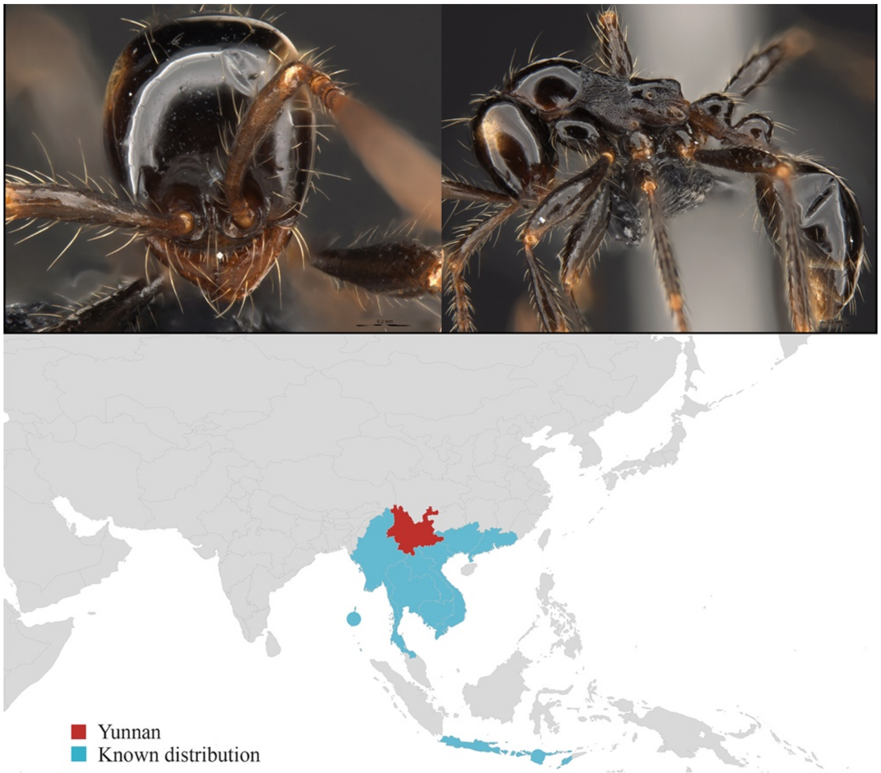

Figure 2.2 I Aenictus hodgsoni ***worker.***

(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Natural history. *Aenictus hodgsoni* has been collected from leaf litter and foraging columns on the forest ground in secondary forest. This species has also been found from lowland to highland in varied forest types (hill evergreen forest, dry evergreen forest, evergreen rain forest, mixed deciduous forest, and savanna) (Jaitrong and Yamane 2011).

Aenictus maneerati **Jaitrong & Yamane, 2013** (Figure 2.3)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.916° N, 101.274° E), Secondary forest, 08.vi.2013, 1 worker, 615m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

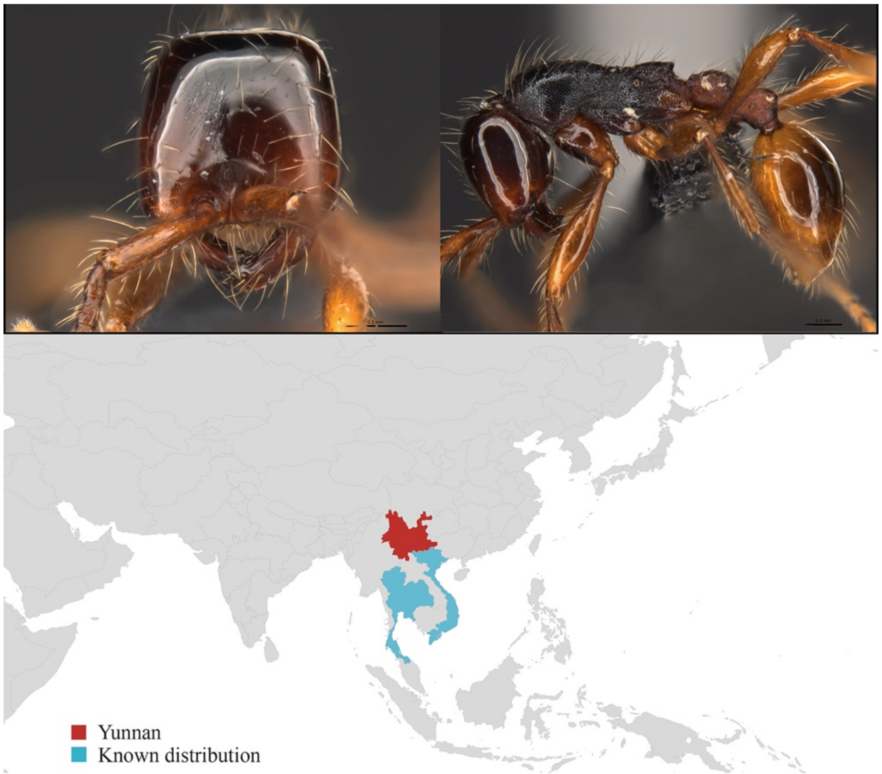

Figure 2.3 | ***Aenictus maneerati*.**
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Distribution. Yunnan (new record), Vietnam and Thailand (Figure 2.3C). Our material represents the northern-most record of *Aenictus hodgsoni*.

Taxonomic note. *Aenictus hodgsoni* belongs to the *Aenictus ceylonicus* species group and can be easily identified with the identification key provided by Jaitrong and Yamane (2013).

Natural history. Little is known about the bionomics of *Aenictus hodgsoni*. Before our survey, it has been only collected from primary forest (Jaitrong and Yamane 2013). I collected it from leaf litter in secondary forest.

Aenictus paradentatus **Jaitrong, Yamane & Tasen, 2012** (Figure 2.4)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.911° N, 101.281° E), Limestone forest, 06.vi.2013, 46 workers, 655m, Hand collection, B. Guénard, B. Blanchard and C. Liu.

Distribution. Yunnan (new record), Vietnam, Laos, and Thailand (Figure 2.4C). This collection represents the northern-most record of *Aenictus paradentatus*.

Taxonomic note. *Aenictus paradentatus* is very similar to *Aenictus dentatus* Forel, 1911, and can be easily identified with the key of Jaitrong et al. (2012).

Natural history. *Aenictus paradentatus* has been collected from foraging columns on the ground in limestone forest, but was also reported to be found in other forest habitats, ranging from primary forest to disturbed forest (Jaitrong et al. 2012).

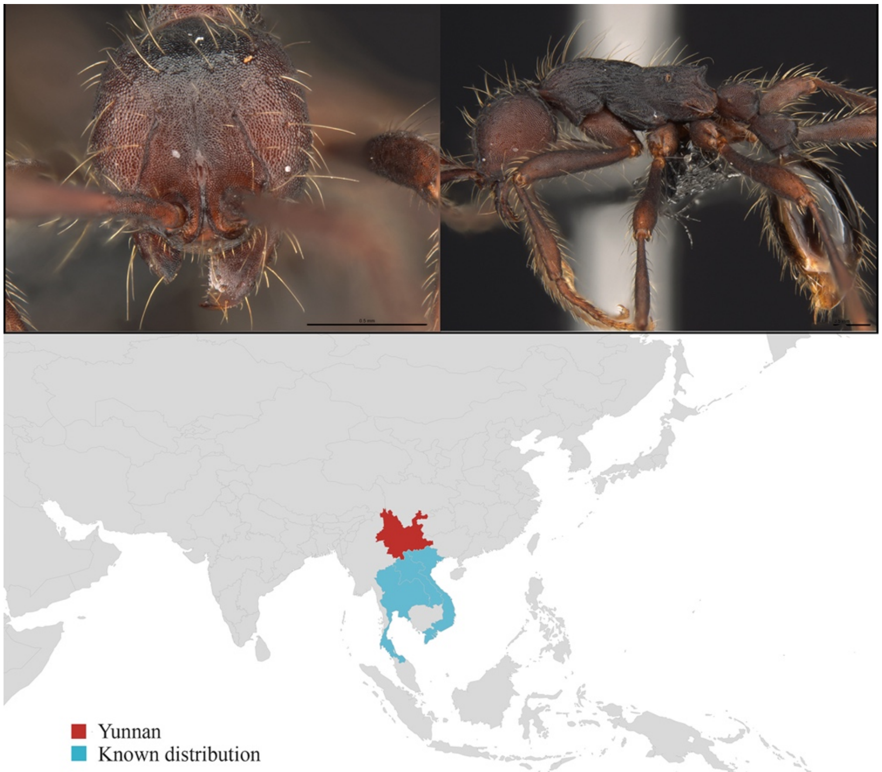

Figure 2.4 | *Aenictus paradentatus.*
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

***Aenictus thailandianus* Terayama & Kubota, 1993** (Figure 2.5)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.274° E), Secondary forest, 11.vi.2013, 19 workers, 590m, Hand collection, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.857° N, 101.277° E), Rubber plantation, 12.vi.2013, 19 workers, 680m, Hand collection, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.857° N, 101.277° E), Rubber plantation, 12.vi.2013, 254 workers, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

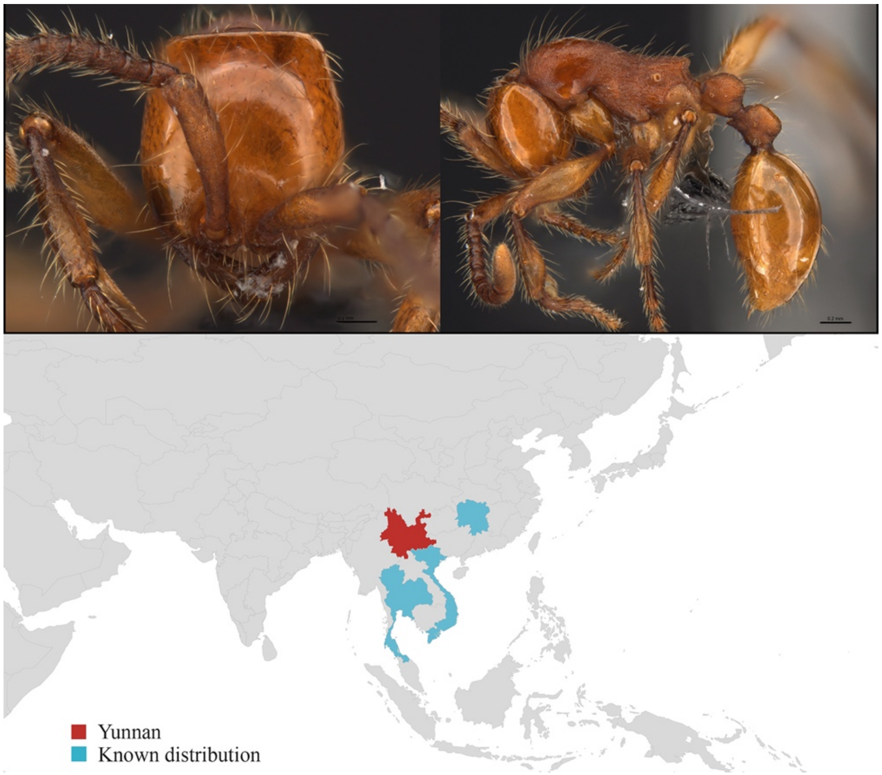

Figure 2.5 | *Aenictus thailandianus*.
(A) Head in front view. **(B)** Mesosoma in profile view. **(C)** Global distribution map.

Distribution. Yunnan (new record), Hunan, Vietnam and Thailand (Figure 2.5C).

Taxonomic note. *Aenictus thailandianus* belongs to the *Aenictus ceylonicus* species group and can be easily identified with the identification key presented by Jaitrong and Yamane (2013).

Natural history. *Aenictus thailandianus* has only been found at higher elevations (1000-1500m) in primary and secondary forest (Jaitrong and Yamane 2013). I collected it from leaf litter and foraging columns on the ground in secondary forest and rubber plantations at lower elevations (under 1000m).

***Stigmatoma scrobiceps* Guénard, Blanchard, Liu, Yang & Economo, 2013** (Figure 2.6)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 2 workers, 550m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

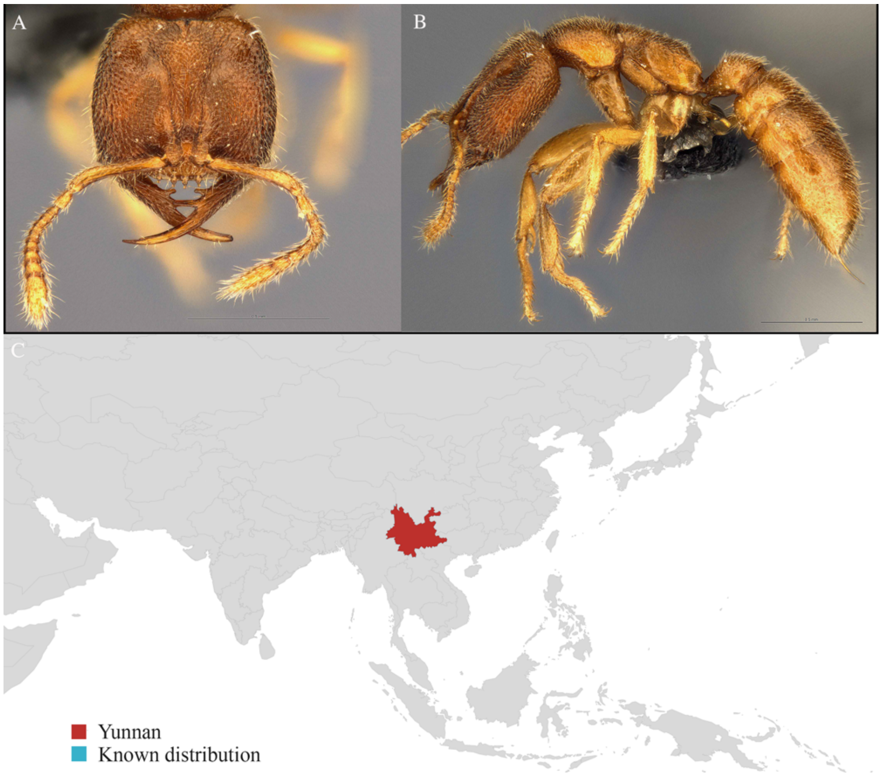

Figure 2.6 | ***Stigmatoma scrobiceps.***
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Distribution. Yunnan (new record) (Figure 2.6C).

Taxonomic note. *Stigmatoma scrobiceps* was described recently (Guénard et al. 2013).

Natural history. Little is known about the bionomics of *Stigmatoma scrobiceps*. The species was collected from leaf litter in secondary forest located at 550 meters elevation (Guénard et al. 2013).

***Carebara melasolena* (Zhou & Zheng, 1997)** (Figure 2.7)

Material examined. CHINA, Yunnan, Xishuangbanna: Kilometer 55 station (21.960° N, 101.199° E), Rain forest, 10.vi.2013, 23 workers, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

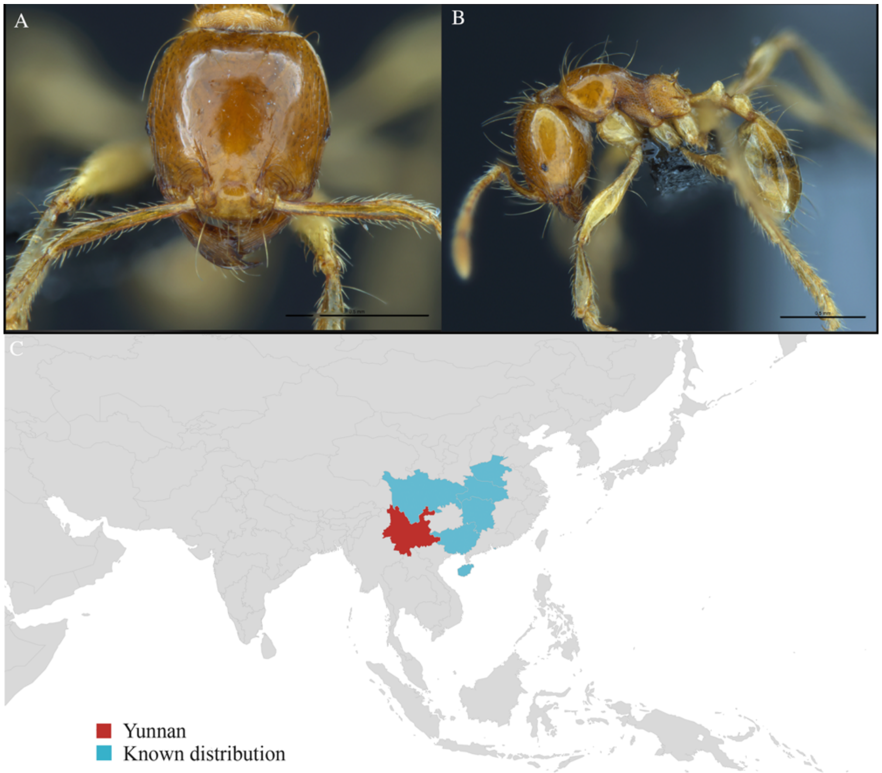

Figure 2.7 | *Carebara melasolena.*
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Distribution. Widely distributed in Middle and South China (Figure 2.7C).

Taxonomic note. *Carebara melasolena* can be identified with the key provided by Zhou and Zheng (1997; treated as *Pheidologeton melasolenus*)

Natural history. *Carebara melasolena* has been collected from leaf litter in primary forest.

***Discothyrea clavicornis* Emery, 1897** (Figure 2.8)

Material examined. CHINA, Yunnan, Xishuangbanna: Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 10.vi.2013, 1 worker, 830m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 13.vi.2013, 8 workers, 805m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.201° E), Rain forest, 13.vi.2013, 1 worker, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.964° N, 101.202° E), Rain forest, 13.vi.2013, 3 workers, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.270° E), Rubber plantation, 09.vi.2013, 12 workers, 645m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 6 worker, 550m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.912° N, 101.285° E), Limestone forest, 06.vi.2013, 3 workers, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.274° E), Limestone forest, 05.vi.2013, 15 workers, 552m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.284° E), Limestone forest, 06.vi.2013, 1 worker, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.918° N, 101.271° E), Rain forest, 05.vi.2013, 3 workers, 581m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.281° E), Limestone forest, 05.vi.2013, 1 worker, 650m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG

(21.916° N, 101.274° E), Rain forest, 08.vi.2013, 3 workers, 615m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.917° N, 101.274° E), Rain forest, 08.vi.2013, 2 workers, 625m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.922° N, 101.268° E), Rubber plantation, 14.vi.2013, 3 workers, 620m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. *Discothyrea clavicornis* is a very widespread and common species encountered throughout most of the Austral-Asian and Indo-Malayan subregions (Figure 2.8C). This new record represents an important extension of the northern range in the distribution of this species.

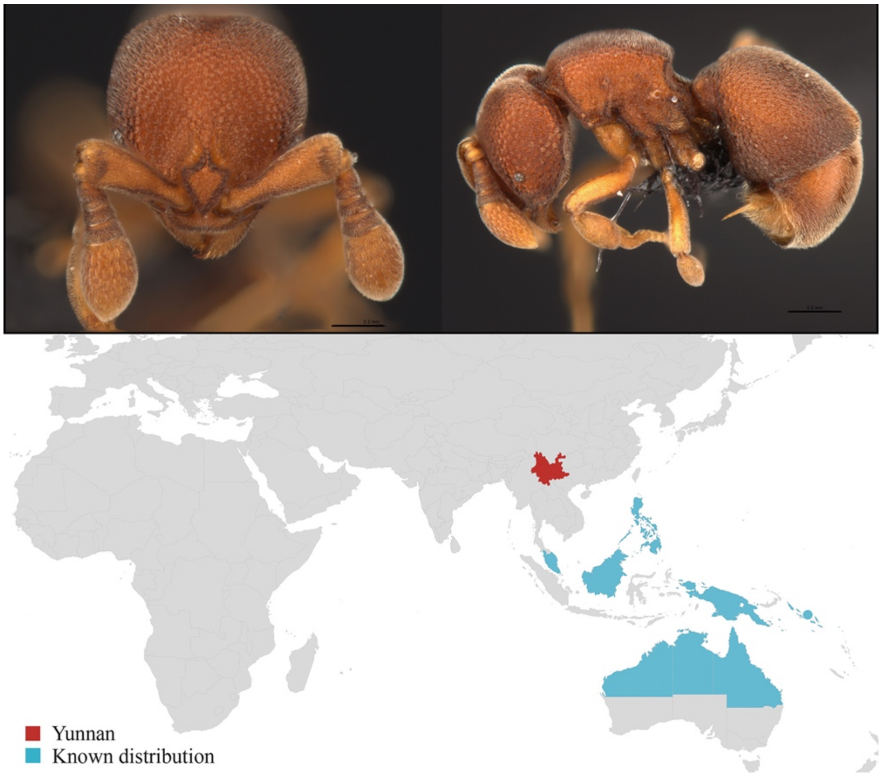

Figure 2.8 | ***Discothyrea clavicornis.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Taxonomic note. There is no available key for *Discothyrea clavicornis*. Our identification is based on the original description (Emery 1897), comparison with reference material, and montage images of the holotype provided by AntWeb.

Natural history. *Discothyrea clavicornis* has been collected from leaf litter in various habitats such as primary forest, limestone forest and rubber plantation.

Discothyrea kamiteta **Kubota & Terayama, 1999** (Figure 2.9)

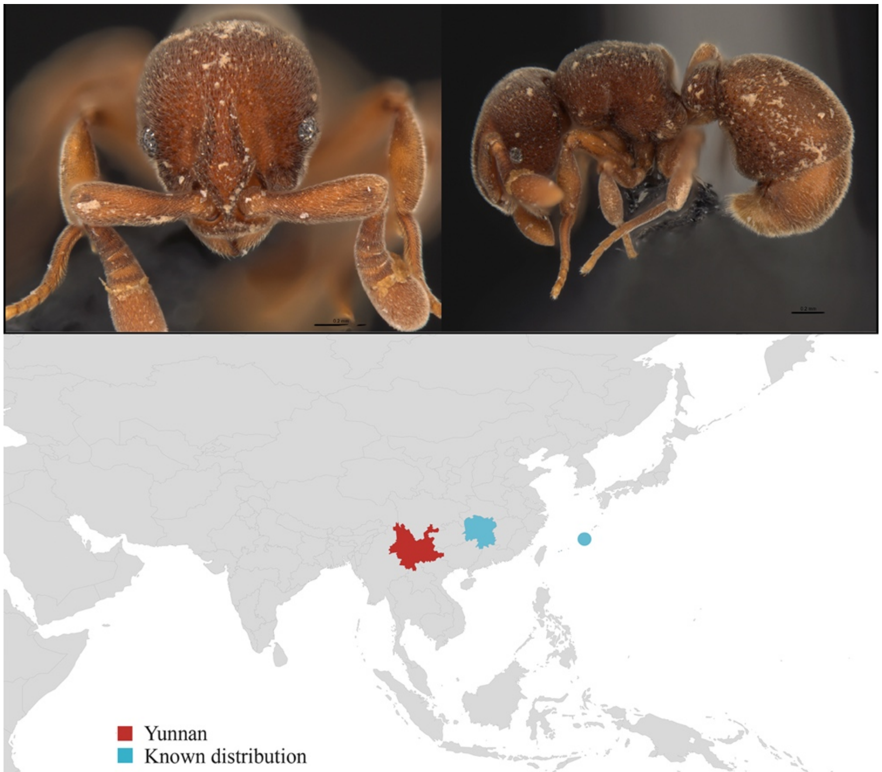

Figure 2.9 | ***Discothyrea kamiteta.***
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: Kilometer 55 station (21.963° N, 101.201° E), Rain forest, 13.vi.2013, 1 worker, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.283° E), Limestone forest, 06.vi.2013, 1 worker, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.917° N, 101.274° E), Secondary forest, 08.vi.2013, 1 worker, 625m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 1 worker, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Yunnan (new record), Hunan, Okinawa (Figure 2.9C). This new record represents an important western-most extension in the known distribution of this species.

Taxonomic note. *Discothyrea kamiteta* is very similar to the recently described *Discothyrea banna* Xu, Burwell & Nakamura, 2014. Both species seem to be very close morphologically, and their separation is based on minor differences, which could also be attributed to intraspecific variation. The identification is based on the original description of *D. kamiteta*, comparison with *D. kamiteta* material from the type locality (Okinawa), and Xu's key (Xu et al. 2014)

Natural history. *Discothyrea kamiteta* has been collected from leaf litter in various habitats, such as primary forest, limestone forest and secondary forest.

Dolichoderus laotius Santschi, 1920 (Figure 2.10)

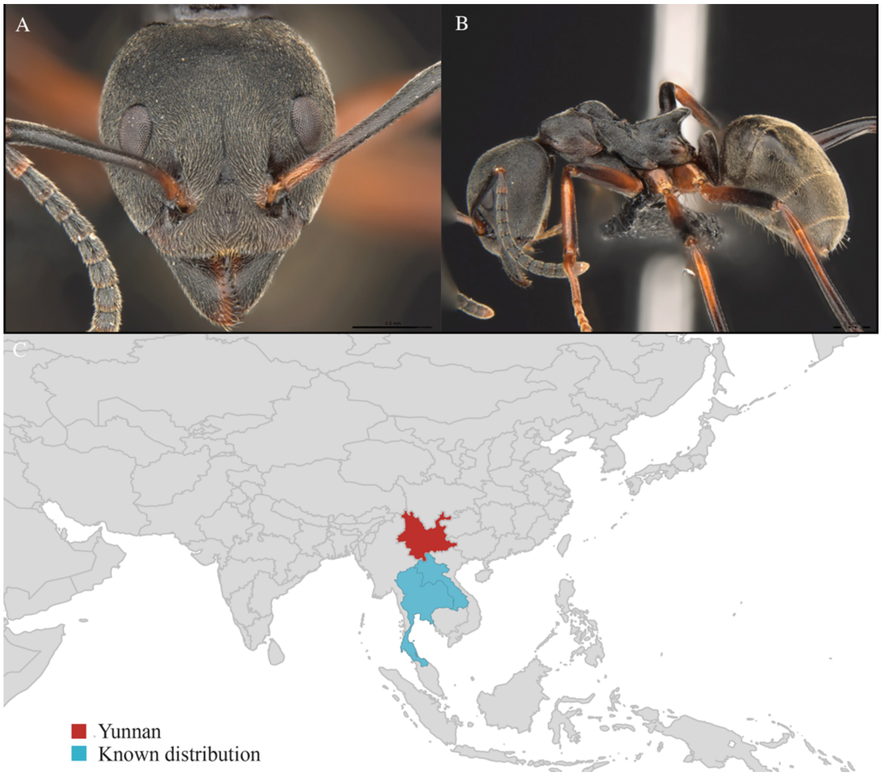

Figure 2.10 | ***Dolichoderus laotius.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 5 worker, 690m, Hand collection, B. Guénard, B. Blanchard and C. Liu.

Distribution. Yunnan (new record), Laos, Thailand (Figure 2.10C). This collection represents the northern-most record of *Dolichoderus laotius*.

Taxonomic note. There is no available key for the genus in the region. Our identification is based on the description provided by Dill et al. (2002).

Natural history. Little is known about the bionomics of *Dolichoderus laotius* . This species has been collected on a tree trunk in secondary forest.

Echinopla cherapunjiensis **Bharti & Gul, 2012** (Figure 2.11)

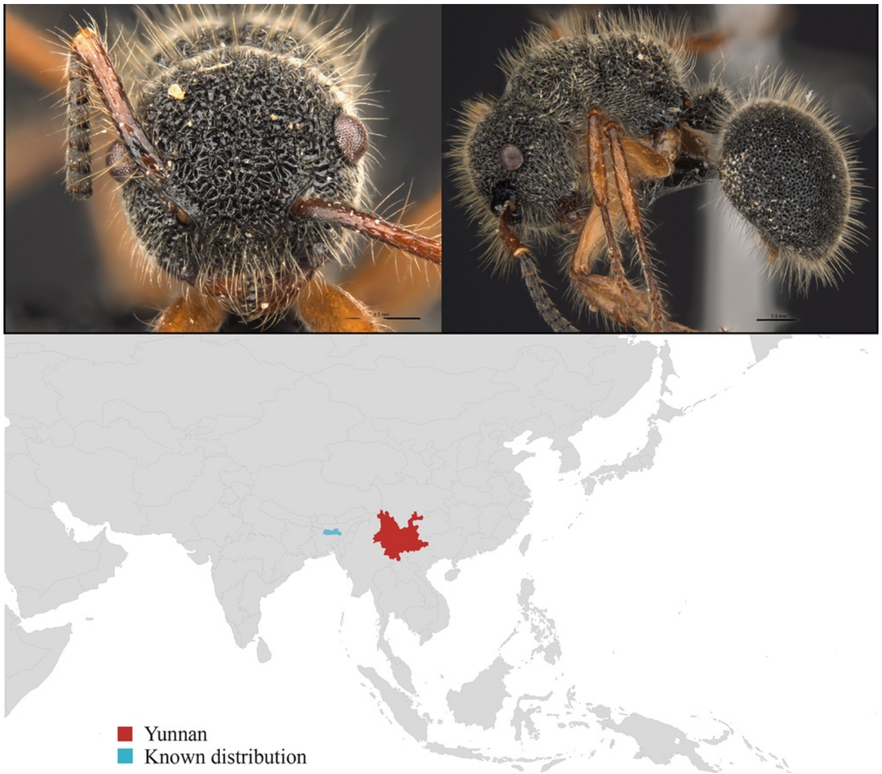

Figure 2.11 | ***Echinopla cherapunjiensis.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.273° E), Secondary forest, 08.vi.2013, 1 worker, 615m, Hand collection, B. Guénard, B. Blanchard and C. Liu.

Distribution. Yunnan (new record) and Meghalaya (Figure 2.11C). This new record represents an important northern and western extension in the distribution of *Echinopla cherapunjiensis*.

Taxonomic note. There is no available key for this genus. Identification is based on the original description (Bharti and Gul 2012).

Natural history. Little is known about the bionomics of *Echinopla cherapunjiensis*. This species has been collected on a tree trunk in secondary forest.

***Gesomyrmex kalshoveni* Wheeler, 1929** (Figure 2.12)

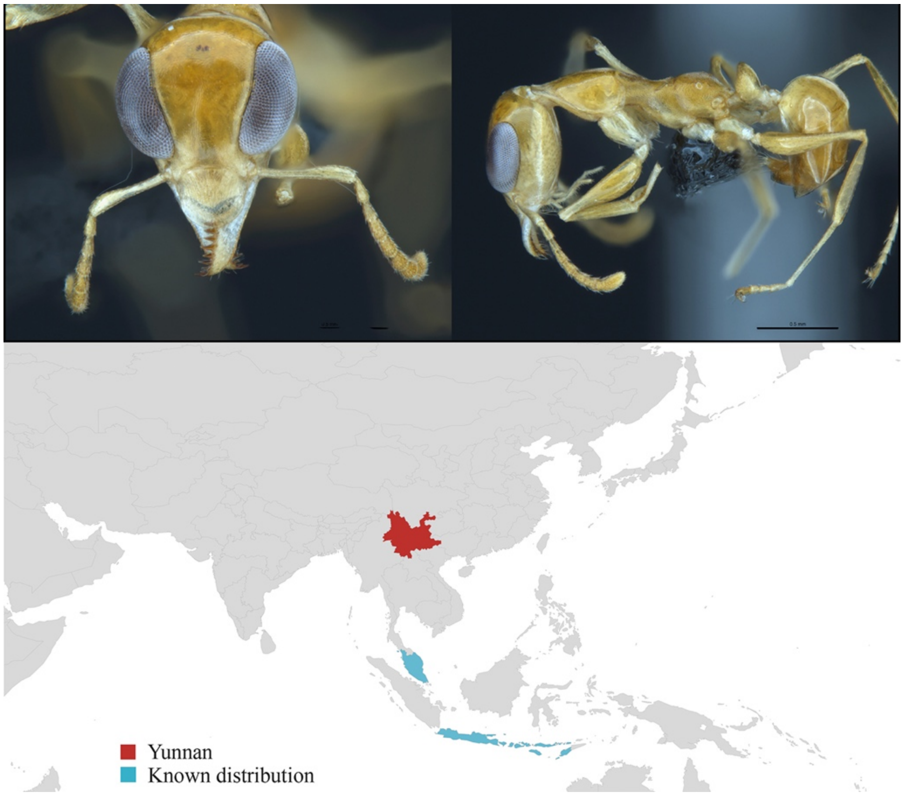

Figure 2.12 | *Gesomyrmex kalshoveni.*
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.925° N, 101.270° E), Forest fragment, 08.vi.2013, 1 worker, 615m, Hand collection, B. Guénard, B. Blanchard and C. Liu.

Distribution. Yunnan (new record), Malaysia and Indonesia (Figure 2.12C). This new record represents an important extension in the northern range of the distribution of this species and the first occurrence of the genus *Gesomyrmex* from Yunnan province.

Taxonomic note. There is no available key for this genus. The identification is based on the original description (Wheeler 1929) and comparison with reference material from Borneo. Identification in *Gesomyrmex* is generally very difficult due to the high degree of worker polymorphism. However, our single specimen is a minor worker and fits the minor workers of *G. kalshoveni* very well.

Natural history. Little is known about the bionomics of *Gesomyrmex kalshoveni*. It has been collected from a small branch of a tree on the side of road.

***Gnamptogenys costata* (Emery, 1889)** (Figure 2.13)

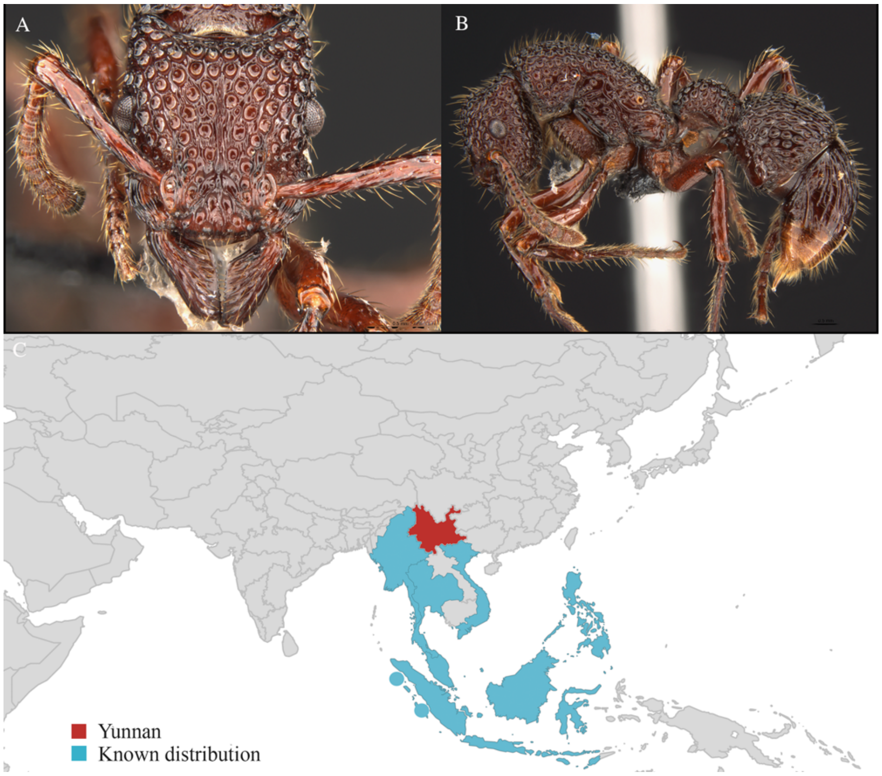

Figure 2.13 | ***Gnamptogenys costata.***
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.911° N, 101.281° E), Limestone forest, 06.vi.2013, 1 worker, 655m, Hand collection, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.274° E), Rain forest, 08.vi.2013, 2 workers, 615m, Hand collection, B. Guénard, B. Blanchard and C. Liu

Distribution. Widely distributed in the Austral-Asian and Indo-Malayan subregions (Figure 2.13C).

Taxonomic note. The identification is based on the key provided by Lattke (2004). The material from Yunnan shows some minor variation in the development of gastral sculpture, which I consider as geographic, intraspecific variation.

Natural history. *Gnamptogenys costata* has been collected from foraging columns on the ground in rain forest and limestone forest.

Gnamptogenys treta **Lattke, 2004** (Figure 2.14)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.912° N, 101.285° E), Limestone forest, 06.vi.2013, 1 worker, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; “Holy Hills” (21.920° N, 101.240° E), Rain forest, 07.vi.2013, 1 worker, 665m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.271° E), Rubber plantation, 09.vi.2013, 7 workers, 645m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.277° E), Secondary forest, 12.vi.2013, 2 workers, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 13.vi.2013, 10 workers, 865m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu

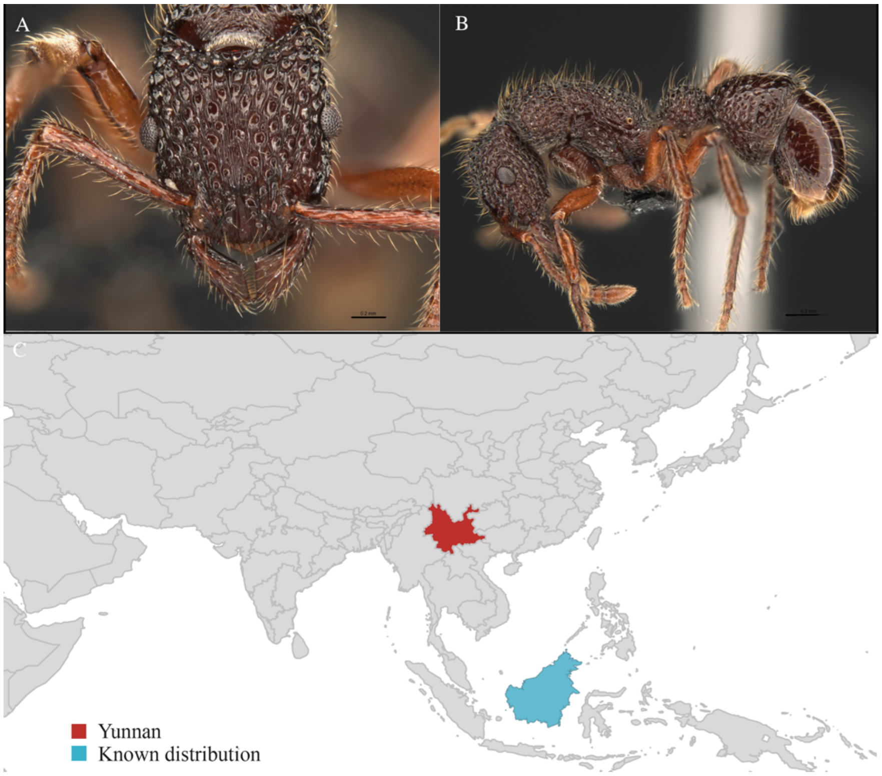

Figure 2.14 | ***Gnamptogenys treta.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Distribution. Known from Yunnan (new record) and Borneo (Figure 2.14C). This collection represents the northern-most record in the distribution of *Gnamptogenys treta*.

Taxonomic note. The identification is based on the key provided by Lattke (2004). Our material fits the holotype very well, except for the shape of the ventral process of the petiole, which is more rectangular in the material from Yunnan, whereas in the material from Borneo it is more triangular. Since this is the only difference I was able to observe, I treat it as intraspecific variation.

Natural history. *Gnamptogenys treta* has been collected from the leaf litter in rain forest, secondary forest and limestone forest and rubber plantation.

***Myrmecina curvispina* Zhou, Huang & Ma L., 2008** (Figure 2.15)

Material examined. CHINA, Yunnan, Xishuangbanna: “Holy Hills” (21.920° N, 101.240° E), Rain forest, 07.vi.2013, 1 worker, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; “Holy Hills” (21.919° N, 101.239° E), Rain forest, 07.vi.2013, 1 worker, 670m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.961° N, 101.200° E), Rain forest, 10.vi.2013, 1 worker, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Secondary forest, 13.vi.2013, 12 workers, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.963° N, 101.201° E), Rain forest, 13.vi.2013, 14 workers, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.277° E), Rubber plantation, 12.vi.2013, 1 worker, 705m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; : Man Sai village (21.907° N, 101.273° E), Rubber plantation, 12.vi.2013, 2 workers, 635m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; : Man Sai village (21.858° N, 101.277° E), Secondary forest, 12.vi.2013, 2 workers, 685m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 3 workers, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.278° E), Secondary forest, 12.vi.2013, 2 workers, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.271° E), Rubber plantation, 09.vi.2013, 3 workers, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

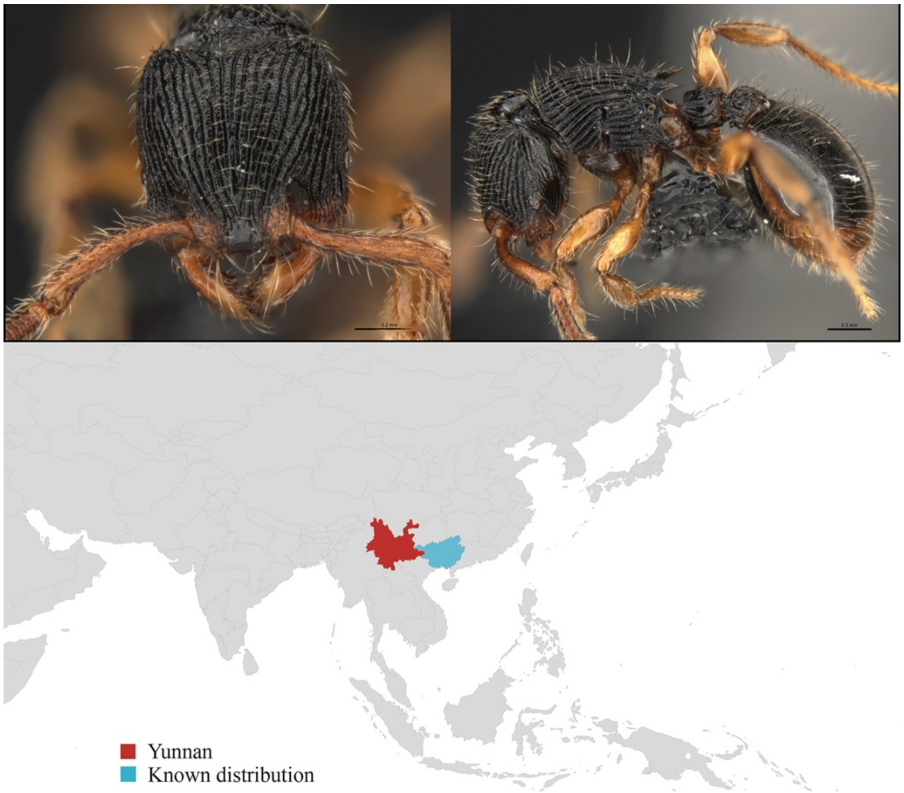

Figure 2.15 | ***Myrmecina curvispina.***
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Distribution. Yunnan (new record) and Guangxi (Figure 2.15C). This new record represents the western-most occurrence in the distribution of *Myrmecina curvispina*.

Taxonomic note. The identification is based on the original description and the identification key given by Zhou et al. (2008).

Natural history. *Myrmecina curvispina* has been collected from the leaf litter of various habitats such as rain forest, secondary forest and rubber plantation.

Myrmecina guangxiensis Zhou, 2001 (Figure 2.16)

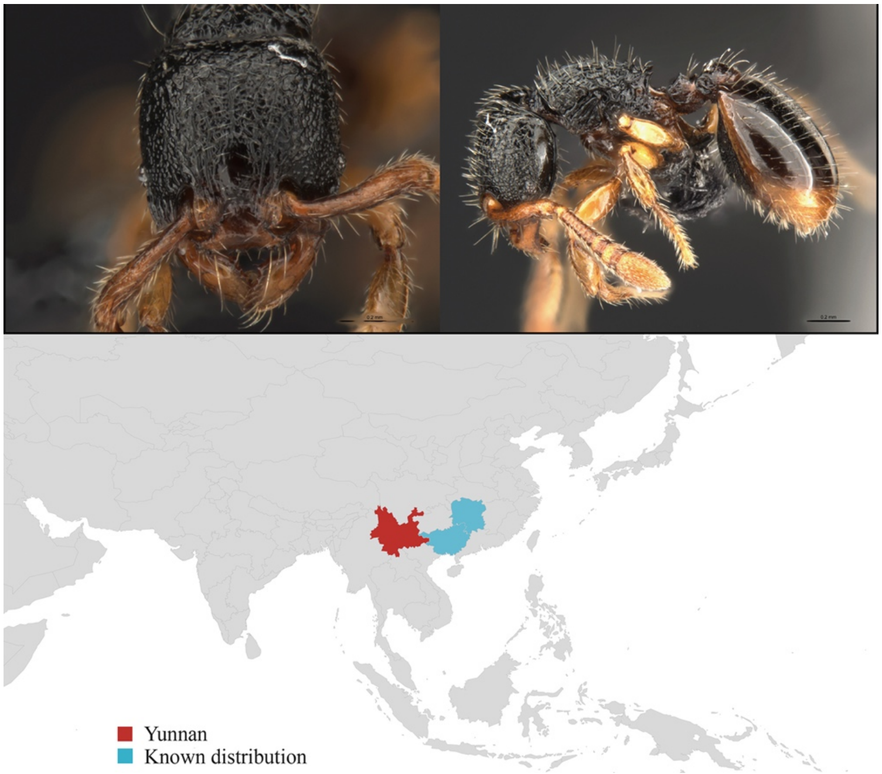

Figure 2.16 | ***Myrmecina guangxiensis.***
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.912° N, 101.285° E), Secondary forest, 05.vi.2013, 4 workers, 552m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.274° E), Limestone forest, 06.vi.2013, 1 worker, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.281° E), Limestone forest, 06.vi.2013, 2 workers, 650m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.960° N, 101.199° E), Rain forest, 10.vi.2013, 1 worker, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.963° N, 101.201° E), Rain forest, 13.vi.2013, 9 workers, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Yunnan (new record), Guangxi and Hunan (Figure 2.16C). This new record represents the western-most occurrence in the distribution of *Myrmecina guangxiensis*.

Taxonomic note. Identification is based on the key provided by Zhou et al. (2008).

Natural history. *Myrmecina guangxiensis* has been collected from leaf litter in rain forest, secondary forest and limestone forest.

***Odontoponera denticulata* (Smith, 1858)** (Figure 2.17)

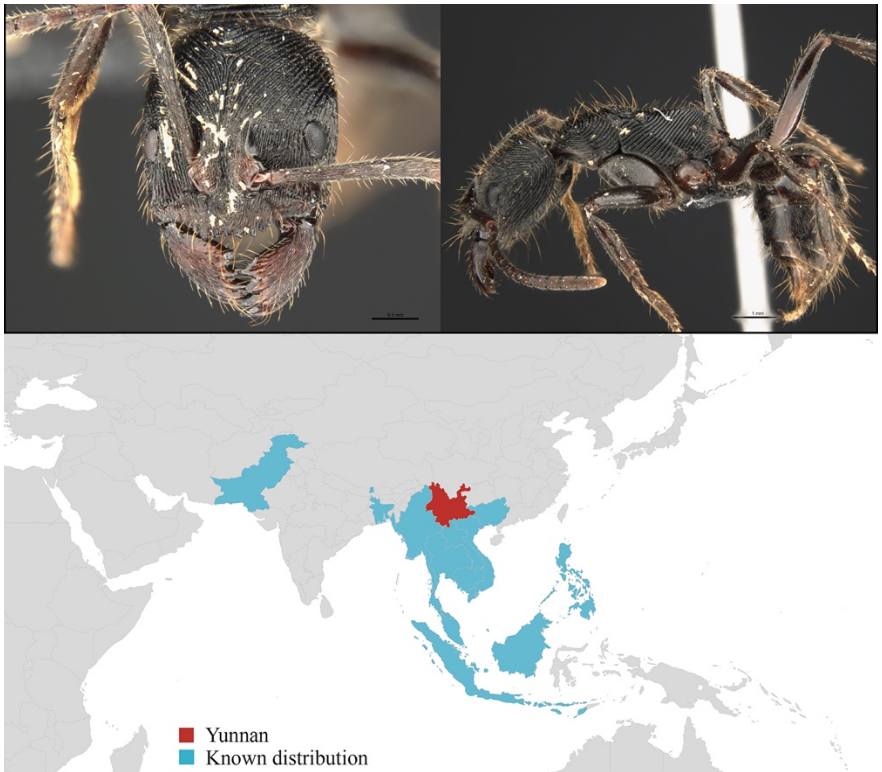

Figure 2.17 | ***Odontoponera denticulata.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: “Holy Hills” (21.920° N, 101.240° E), Secondary forest, 07.vi.2013, 1 worker, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; “Holy Hills” (21.920° N, 101.239° E), Secondary forest, 07.vi.2013, 2 workers, 665m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Secondary forest, 13.vi.2013, 1 worker, 825m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Secondary forest, 13.vi.2013, 1 worker, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 13.vi.2013, 3 workers, 805m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.963° N, 101.201° E), Rain forest, 13.vi.2013, 2 workers, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.964° N, 101.202° E), Rain forest, 13.vi.2013, 1 worker, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.907° N, 101.273° E), Rubber plantation, 12.vi.2013, 1 worker, 635m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.278° E), Rubber plantation, 12.vi.2013, 1 worker, 710m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 1 worker, 685m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.278° E), Secondary forest, 12.vi.2013, 1 worker, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.933° N, 101.269° E), Rubber plantation, 09.vi.2013, 1 worker, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.271° E), Rubber plantation, 09.vi.2013, 5 workers, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.270° E), Rubber plantation, 09.vi.2013, 2 workers, 645m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.269° E), Rubber plantation, 09.vi.2013, 1 worker, 645m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.924° N, 101.268° E), Rubber plantation, 06.vi.2013, 3 workers, 571m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 1 worker, 550m, Winkler sifting,

B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.284° E), Limestone forest, 06.vi.2013, 3 workers, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.912° N, 101.282° E), Limestone forest, 05.vi.2013, 1 worker, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.917° N, 101.274° E), Secondary forest, 08.vi.2013, 1 worker, 625m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.889° N, 101.267° E), Rubber Plantation, 14.vi.2013, 4 workers, 630m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.888° N, 101.266° E), Rubber Plantation, 14.vi.2013, 2 workers, 600m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.888° N, 101.266° E), Rubber Plantation, 14.vi.2013, 3 workers, 620m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.889° N, 101.267° E), Rubber Plantation, 14.vi.2013, 3 workers, 630m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.922° N, 101.268° E), Rubber Plantation, 14.vi.2013, 4 workers, 620m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.890° N, 101.267° E), Rubber Plantation, 14.vi.2013, 2 workers, 620m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Widely distributed in the Indo-Malayan subregion (Figure 2.17C).

Taxonomic note. The identification of our material is based on Yamane's (2009) redescription of *O. denticulata*.

Natural history. *Odontoponera denticulata* has been collected from the leaf litter in various habitats such as rain forest, secondary forest, limestone forest and rubber plantation.

Pheidole hongkongensis **Wheeler, 1928** (Figure 2.18)

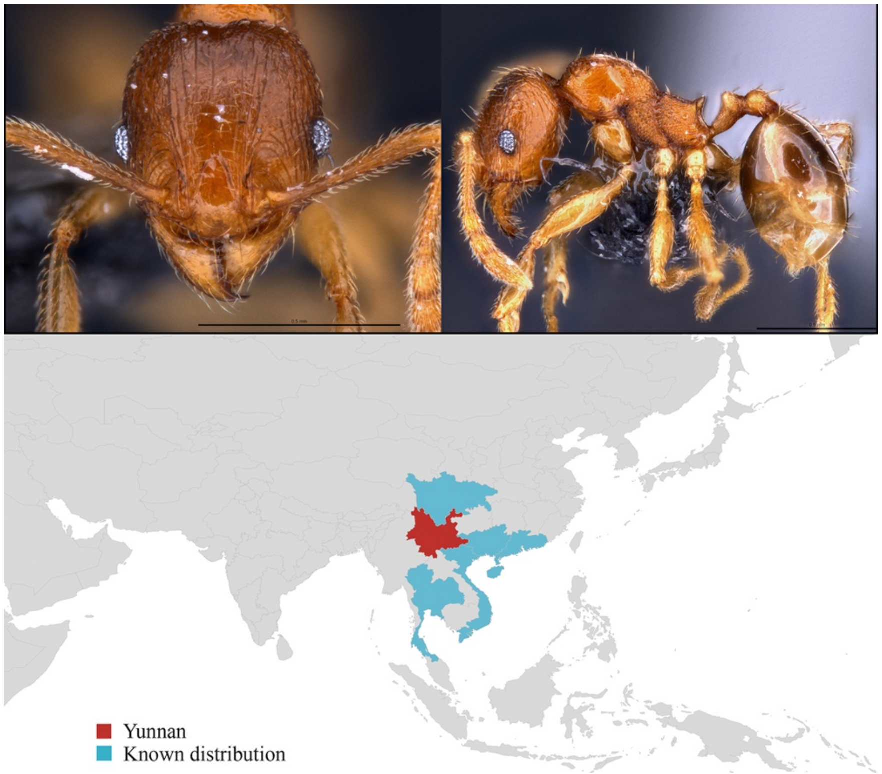

Figure 2.18 | ***Pheidole hongkongensis.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 1 worker, 550m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.274° E), Secondary forest, 05.vi.2013, 3 workers, 1 Soldier, 552m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.924° N, 101.268° E), Secondary forest, 05.vi.2013, 2 workers, 571m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.918° N, 101.271° E), Secondary forest, 05.vi.2013, 1 worker, 581m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.912° N, 101.285° E), Limestone forest, 06.vi.2013, 49 workers, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.912° N, 101.282° E), Limestone forest, 06.vi.2013, 6 workers, 1 Soldier, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.933° N, 101.269° E), Rubber plantation, 09.vi.2013, 3 workers, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 20 workers, 685m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.278° E), Secondary forest, 12.vi.2013, 1 worker, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.907° N, 101.273° E), Rubber plantation, 12.vi.2013, 3 workers, 635m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 13.vi.2013, 5 workers, 1 Soldier, 805m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.922° N, 101.268° E), Rubber Plantation, 14.vi.2013, 1 worker, 629m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. South China, Vietnam and Thailand (Figure 2.18C).

Taxonomic note. *Pheidole hongkongensis* can be identified with the identification key to northern Vietnamese *Pheidole* published by Eguchi (2008).

Natural history. *Pheidole hongkongensis* has been collected from leaf litter in secondary forest, limestone forest and rubber plantations. It has also been reported inhabiting the soil of woody gardens, forest edges and open areas (Eguchi 2008).

***Pheidole plagiaria* Smith, 1860** (Figure 2.19)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.912° N, 101.282° E), Limestone forest, 06.vi.2013, 2 workers, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.933° N, 101.269° E), Rubber Plantation, 09.vi.2013, 1 worker, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.960° N, 101.199° E), Rain forest, 10.vi.2013, 13 workers, 840m, Winkler sifting, B. Guénard, B.

Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 10.vi.2013, 2 workers, 830m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Widely distributed in the Australasian and Indo-Malayan subregions (Figure 2.19C).

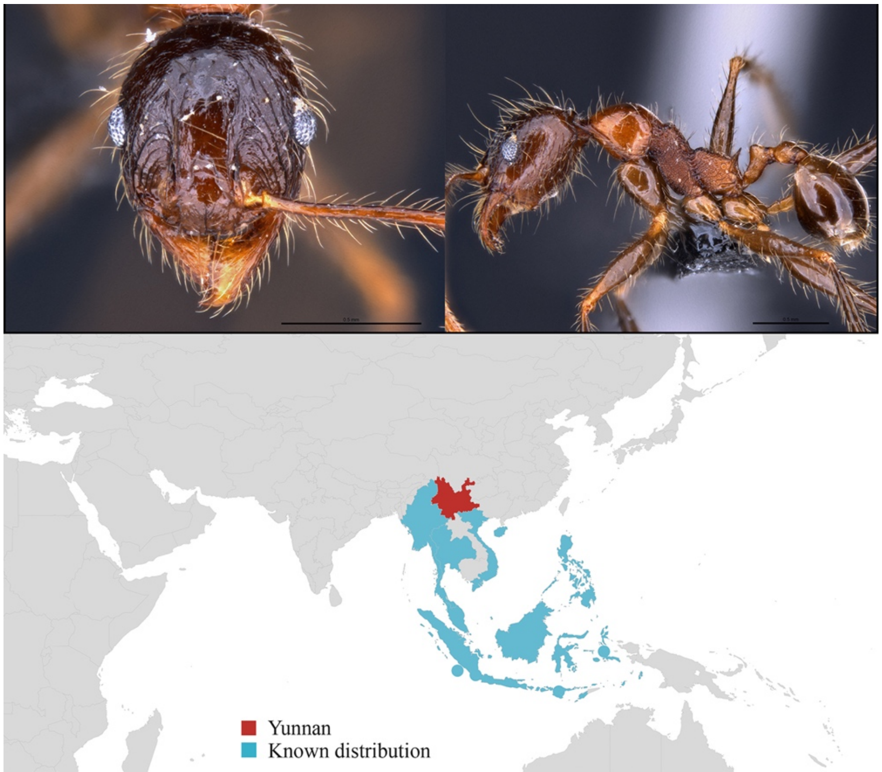

Figure 2.19 | ***Pheidole plagiaria.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Taxonomic note. *Pheidole plagiaria* can be identified with the identification key to Northern Vietnamese *Pheidole* provided by Eguchi (2008).

Natural history. *Pheidole plagiaria* has been collected from leaf litter from rain forest, limestone forest and rubber plantation. It has also been reported inhabiting in the soil of forest edge and open land (Eguchi 2008).

***Pheidole planifrons* Santschi, 1920** (Figure 2.20)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.274° E), Secondary forest, 05.vi.2013, 2 workers, 552m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.924° N, 101.268° E), Rubber plantation, 05.vi.2013, 3 workers, 571m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.283° E), Limestone forest, 06.vi.2013, 2 workers, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.912° N, 101.282° E), Limestone forest, 06.vi.2013, 4 workers, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.281° E), Limestone forest, 06.vi.2013, 2 workers, 650m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.916° N, 101.274° E), Limestone forest, 08.vi.2013, 2 workers, 615m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.271° E), Rubber plantation, 09.vi.2013, 1 worker, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.277° E), Rubber plantation, 12.vi.2013, 4 workers, 705m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.857° N, 101.277° E), Rubber plantation, 12.vi.2013, 1 worker, 710m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.907° N, 101.273° E), Rubber plantation, 12.vi.2013, 2 workers, 635m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.277° E), Secondary forest, 12.vi.2013, 2 workers, 685m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 9 workers, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.273° E), Secondary forest, 12.vi.2013, 1 worker, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Rain forest, 13.vi.2013, 3 workers, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site

(21.889° N, 101.267° E), Rubber Plantation, 14.vi.2013, 33 workers, 630m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.922° N, 101.268° E), Rubber Plantation, 14.vi.2013, 2 workers, 620m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Yunnan (new record), Vietnam, Thailand and Java (Figure 2.20C). This new record represents the northern-most occurrence in the known distribution of *Pheidole planifrons*.

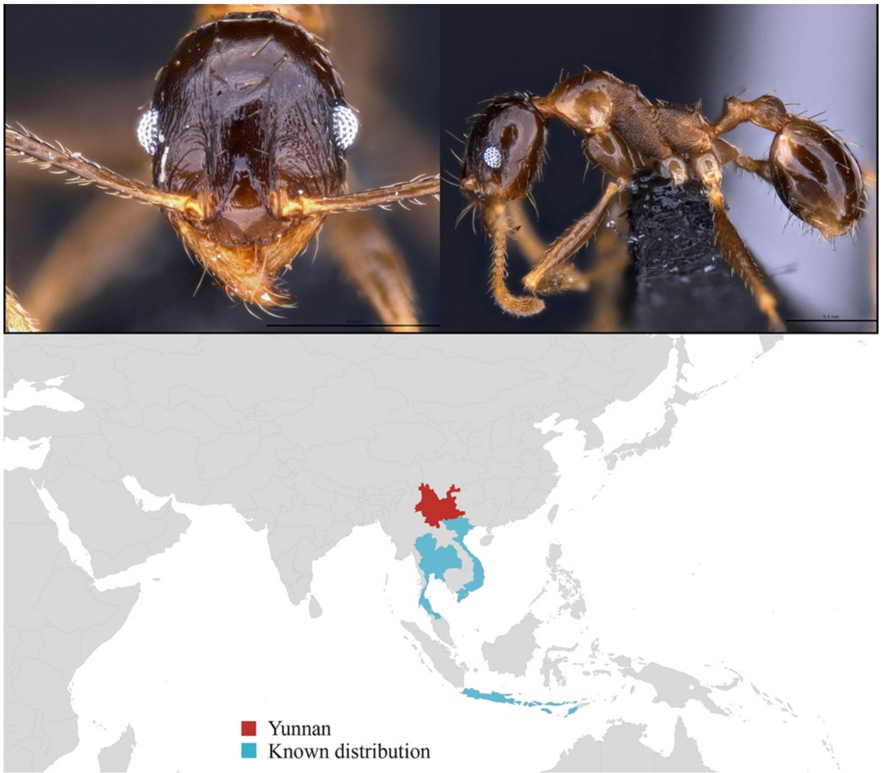

Figure 2.20 | ***Pheidole planifrons.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Taxonomic note. *Pheidole planifrons* can be identified with the identification key to Northern Vietnamese *Pheidole* provided by Eguchi (2008).

Natural history. *Pheidole planifrons* has been collected from leaf litter in rain forest, limestone forest and rubber plantations. It has also been reported inhabiting in the soil of forest edge and woody habitats (Eguchi 2008).

***Pheidole rugithorax* Eguchi, 2008** (Figure 2.21)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 3 workers, 1 Soldier, 550m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.283° E), Limestone forest, 06.vi.2013, 1 worker, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.281° E), Limestone forest, 06.vi.2013, 3 workers, 650m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

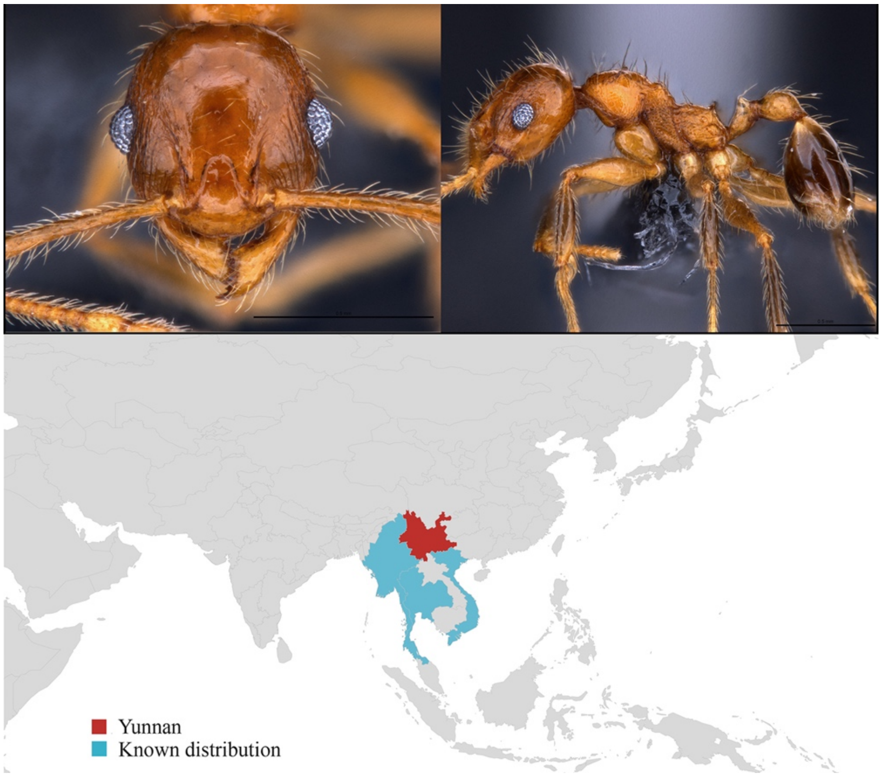

Figure 2.21 | *Pheidole rugithorax.*
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Distribution. Yunnan (new record), Vietnam, Myanmar and Thailand (Figure 2.21C).

Taxonomic note. *Pheidole rugithorax* can be identified with the identification key to Northern Vietnamese *Pheidole* provided by Eguchi (2008).

Natural history. *Pheidole rugithorax* has been collected from leaf litter in rain forest, secondary forest and limestone forest. Otherwise there is no available information on its biology.

***Pheidole smythiesii* Forel, 1902** (Figure 2.21)

Material examined. China, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 9 workers, 550m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.918° N, 101.271° E), Secondary forest, 05.vi.2013, 2 workers, 581m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.283° E), Limestone forest, 05.vi.2013, 1 worker, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 5 workers, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Widely distributed in South China, Vietnam, Thailand and India (Figure 2.22C).

Taxonomic note. *Pheidole smythiesii* can be identified with the identification key to Northern Vietnamese *Pheidole* provided by Eguchi (2008).

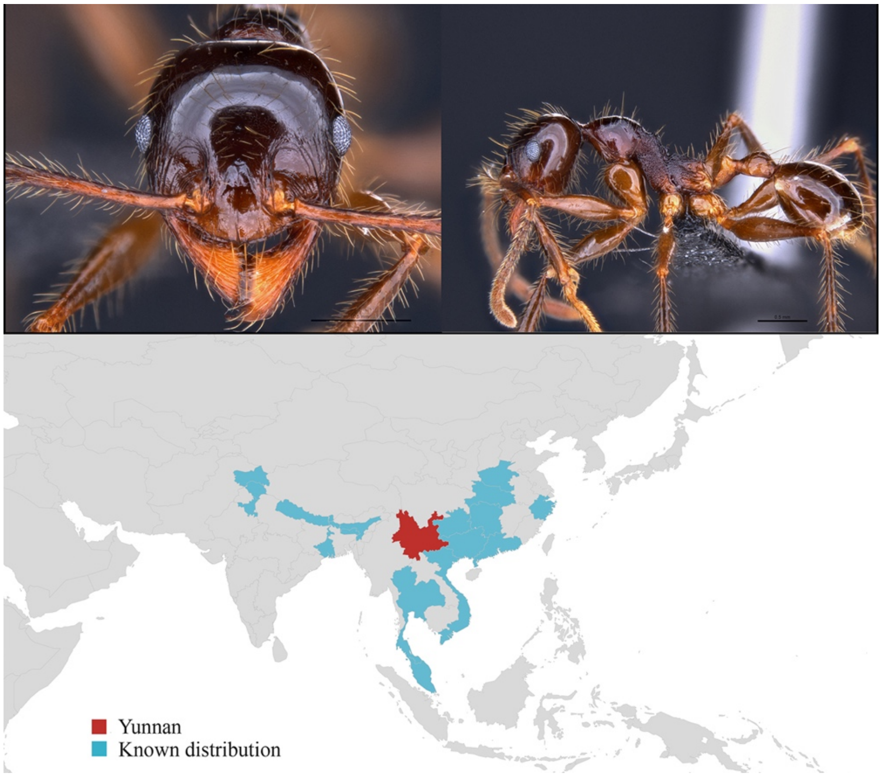

Figure 2.22 | ***Pheidole smythiesii.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Natural history. *Pheidole smythiesii* has been collected from leaf litter from secondary forest. Eguchi (2008) reported the species to usually inhabit woody habitats and sometimes open areas where it nests in the soil. *Pheidole smythiesii* is also known to tend aphid colonies (Alfred & Agarwal, 1990).

Pheidole tumida **Eguchi, 2008** (Figure 2.23).

Material examined. CHINA, Yunnan, Xishuangbanna: “Holy Hills” (21.920° N, 101.239° E), Rain forest, 07.vi.2013, 2 workers, 665m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Rain forest, 13.vi.2013, 2 workers, 825m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Rain forest, 13.vi.2013, 3 workers, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.277° E), Rubber plantation, 12.vi.2013, 4 workers, 705m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.907° N, 101.273° E), Rubber plantation, 12.vi.2013, 2 workers, 635m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.857° N, 101.277° E), Rubber plantation, 12.vi.2013, 3 workers, 710m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.277° E), Secondary forest, 12.vi.2013, 15 workers, 685m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 2 workers, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.278° E), Secondary forest, 12.vi.2013, 2 workers, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 4 workers, 2 Soldiers, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.934° N, 101.269° E), Rubber plantation, 09.vi.2013, 5 workers, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.933° N, 101.269° E), Rubber plantation, 09.vi.2013, 34 workers, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.270° E), Rubber plantation, 09.vi.2013, 2 workers, 645m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.271° E), Rubber plantation, 09.vi.2013, 3 workers, 645m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.931° N, 101.269° E), Rubber plantation, 09.vi.2013, 1 worker, 645m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.933° N, 101.269° E), Rubber plantation, 09.vi.2013, 2 workers, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.274° E), Secondary forest, 05.vi.2013, 1 worker, 552m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

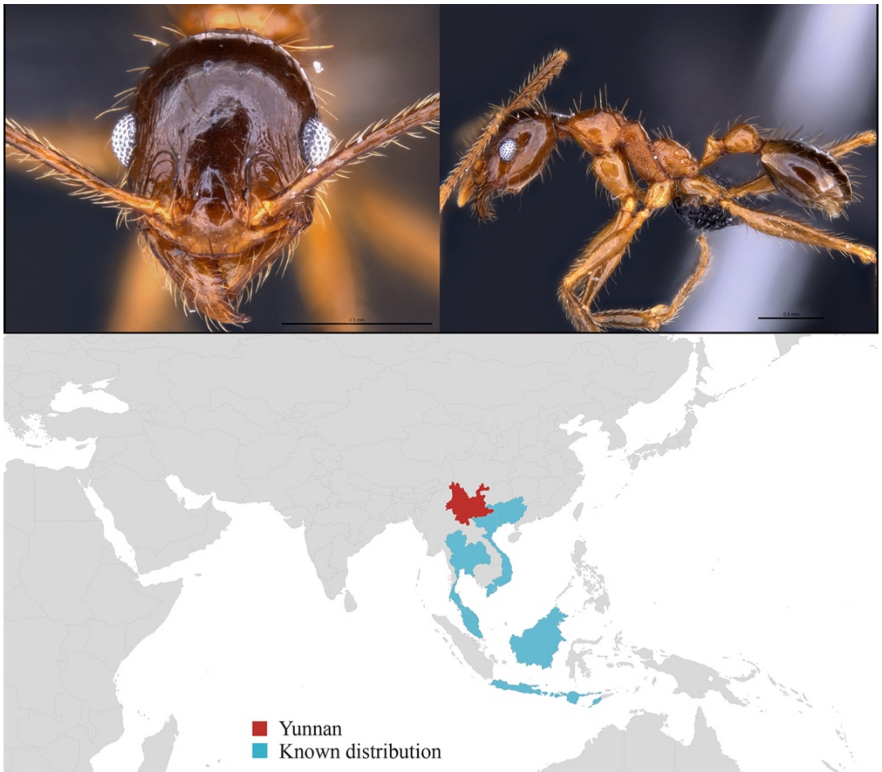

Figure 2.23 | *Pheidole tumida.*
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Distribution. Widely distributed in the Australasian and Indo-Malayan subregions (Figure 2.23C).

Taxonomic note. *Pheidole tumida* can be identified with the identification key to Northern Vietnamese *Pheidole* provided by Eguchi (2008).

Natural history. *Pheidole tumida* has been collected from leaf litter in rain forest, secondary forest and rubber plantation. It has also been reported nesting in the soil and rotting logs of forest edges (Eguchi 2008).

***Pheidole vieti* Eguchi, 2008** (Figure 2.24)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.912° N, 101.285° E), Limestone forest, 06.vi.2013, 3 workers, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.917° N, 101.274° E), Secondary forest, 06.vi.2013, 3 workers, 625m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.961° N, 101.200° E), Rain forest, 10.vi.2013, 3 workers, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

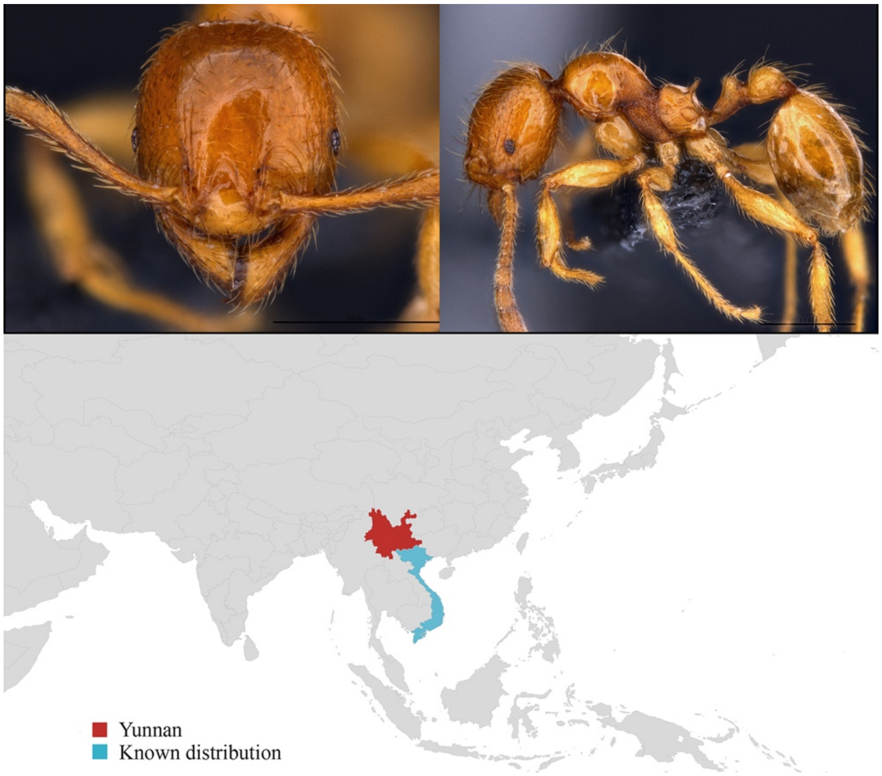

Figure 2.24 | *Pheidole vieti.*
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Distribution. Known from Yunnan (new record) and Vietnam (Figure 2.24C). This new record represents the northern-most occurrence in the distribution of *Pheidole vieti*.

Taxonomic note. *Pheidole vieti* can be identified with the key given provided by Eguchi (2008).

Natural history. *Pheidole vieti* has been collected from leaf litter from rain forest, secondary forest and limestone forest.

Pheidole zoceana **Santschi, 1925** (Figure 2.25)

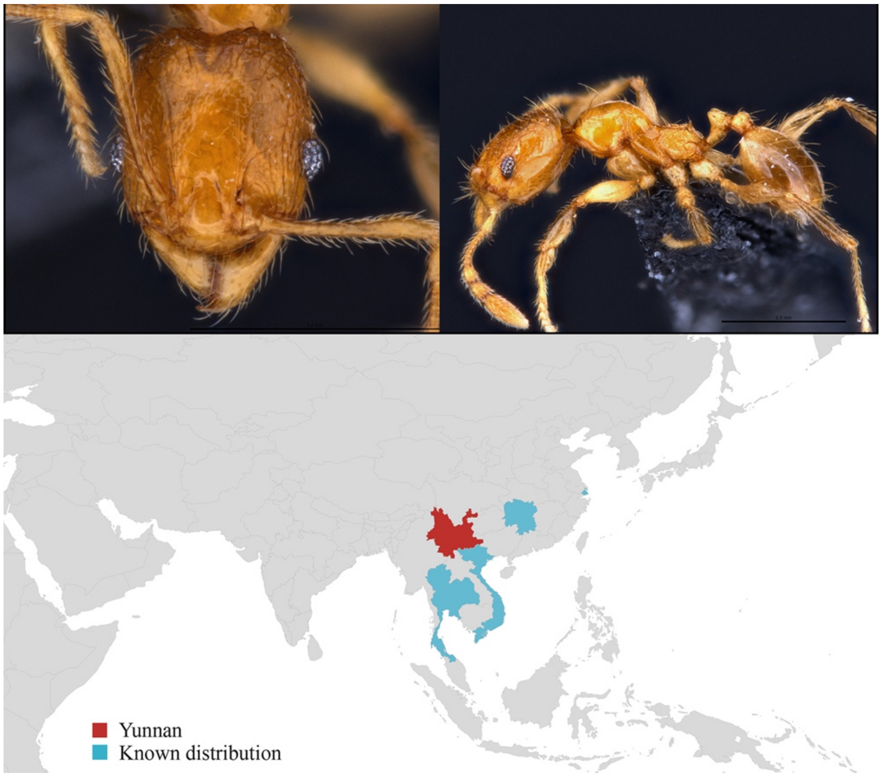

Figure 2.25 | ***Pheidole zoceana.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: "Holy Hills" (21.920° N, 101.240° E), Secondary forest, 07.vi.2013, 44 workers, 644m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; "Holy Hills" (21.920° N, 101.239° E), Secondary forest, 07.vi.2013, 5 workers, 665m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; "Holy Hills" (21.919° N, 101.239° E), Secondary forest, 07.vi.2013, 11 workers, 670m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Secondary forest, 13.vi.2013, 15 workers, 825m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Secondary forest, 13.vi.2013, 1 worker, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 13.vi.2013, 7 workers, 3 Soldiers, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.960° N, 101.199° E), Rain forest, 13.vi.2013, 25 workers, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 13.vi.2013, 5 workers, 805m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.963° N, 101.201° E), Rain forest, 13.vi.2013, 14 workers, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.964° N, 101.202° E), Rain forest, 13.vi.2013, 2 workers, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 2 workers, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 1 worker, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.271° E), Rubber Plantation, 09.vi.2013, 1 worker, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 77 workers, 550m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.912° N, 101.285° E), Limestone forest, 05.vi.2013, 22 workers, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.274° E), Secondary forest, 06.vi.2013, 2 workers, 552m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.924° N, 101.268° E), Rubber plantation, 05.vi.2013, 3 workers, 571m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.918° N, 101.271° E), Secondary forest, 05.vi.2013, 1 worker, 581m, Winkler sifting, B. Guénard, B. Blanchard and C.

Liu; XTBG (21.916° N, 101.274° E), Secondary forest, 05.vi.2013, 12 workers, 615m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Known from a few localities in China, Vietnam and Thailand (Figure 2.25C).

Taxonomic note. *Pheidole zoceana* can be identified with the identification key to Northern Vietnamese *Pheidole* provided by Eguchi (2008).

Natural history. *Pheidole zoceana* has been collected from leaf litter in rain forest, secondary forest and rubber plantations. It has also been reported nesting in the soil of forest edges and mountainous area (Eguchi 2008).

Prenolepis sphingthoraxa **Zhou & Zheng, 1998** (Figure 2.26)

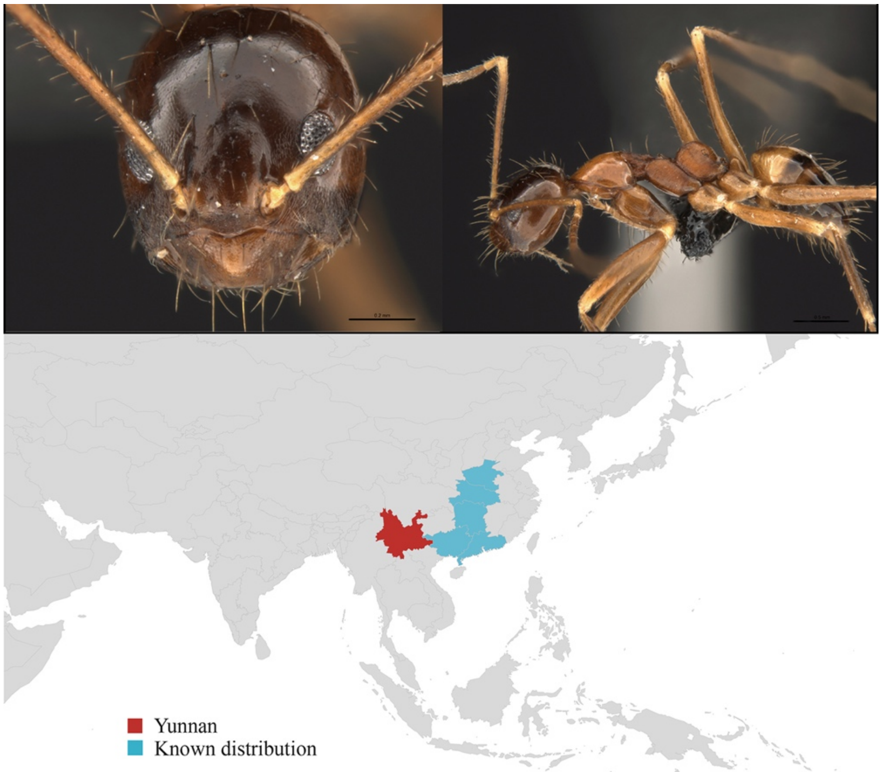

Figure 2.26 l *Prenolepis sphingthoraxa.*
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: Kilometer 55 station (21.960° N, 101.199° E), Rain forest, 10.vi.2013, 1 worker, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Known from Middle and South China (Figure 2.26C). This new record represents the western-most record in the distribution of *Prenolepis sphingthoraxa*.

Taxonomic note. The identification is based on the original description (Zhou and Zheng 1998).

Natural history. *Prenolepis sphingthoraxa* has been collected from leaf litter in rain forest and little is known about its bionomics.

Proceratium deelemani **Perrault, 1981** (Figure 2.27)

Material examined. CHINA, Yunnan, Xishuangbanna: Kilometer 55 station (21.964° N, 101.202° E), Rain forest, 13.vi.2013, 1 worker, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Known from Yunnan (new record), Singapore, Thailand and Borneo (Figure 2.27C). This new record represents the northern-most record in the distribution of *Proceratium deelemani*.

Taxonomic note. The identification of *Proceratium deelemani* is relatively straightforward with the key provided by Baroni Urbani and De Andrade (2003).

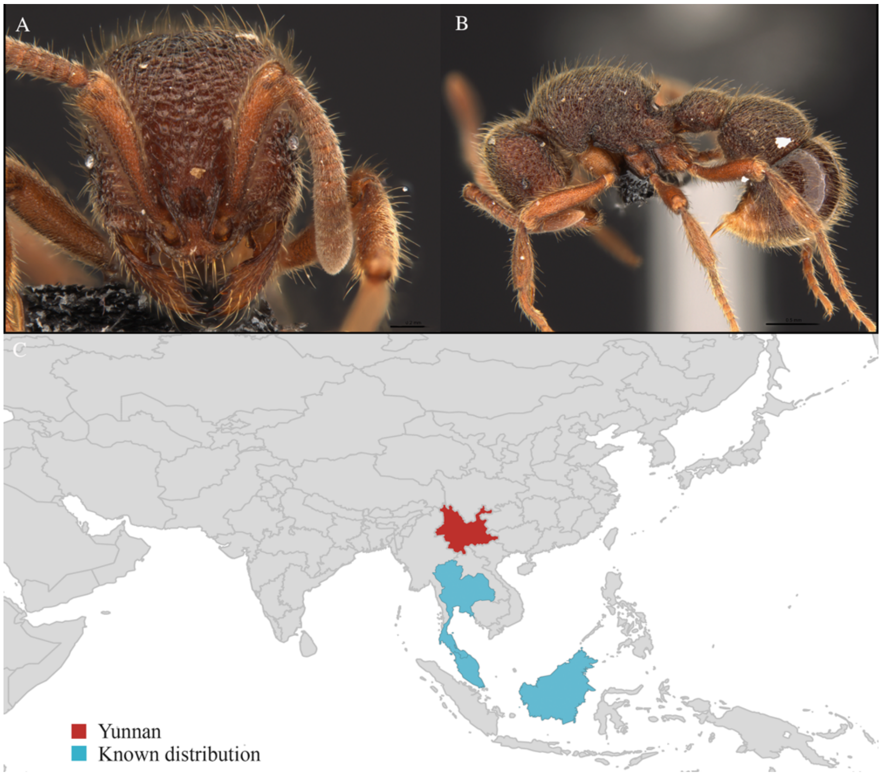

Figure 2.27 | ***Proceratium deelemani.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Natural history. *Proceratium deelemani* has been collected from leaf litter in rain forest, and little is known about its bionomics.

Recurvidris kemneri **(Wheeler & Wheeler, 1954)** (Figure 2.28)

Material examined. CHINA, Yunnan, Xishuangbanna: "Holy Hills" (21.919° N, 101.239° E), Secondary forest, 07.vi.2013, 1 worker, 670m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.857° N, 101.277° E), Rubber plantation, 12.vi.2013, 3 workers, 710m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 1 worker, 685m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.278° E), Secondary forest, 12.vi.2013, 1 worker, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.963° N, 101.201° E), Rain forest, 10.vi.2013, 7 workers, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Widely distributed in the Austral-Asian and Indo-Malayan subregions (Figure 2.28C). This new northern-most record represents an important extension in the distribution of *Recurvidris kemneri.*

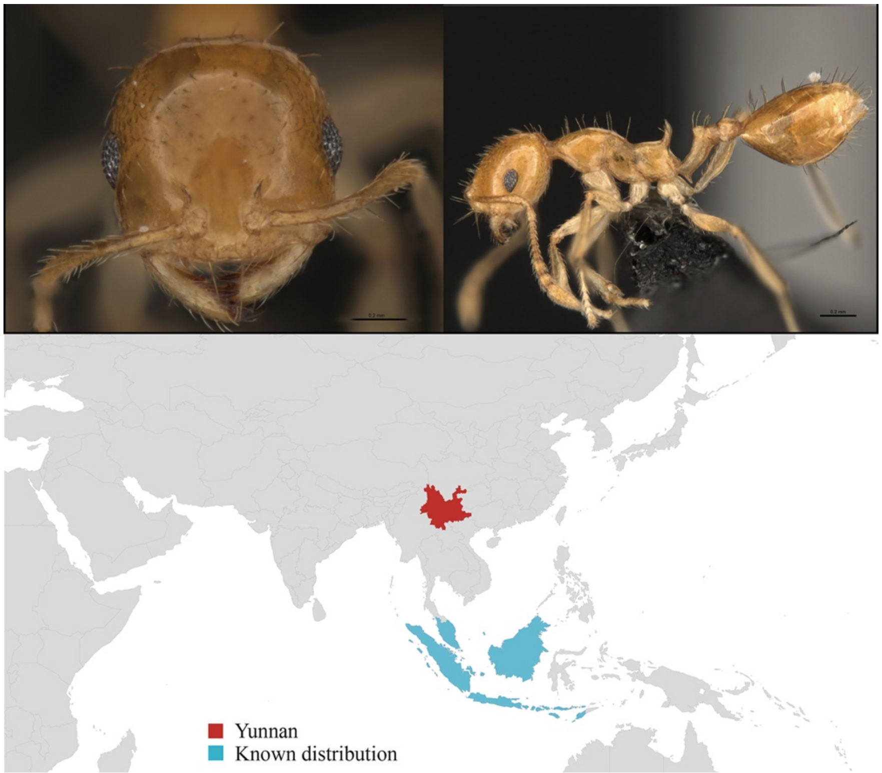

Figure 2.28 | *Recurvidris kemneri.*
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Taxonomic note. The identification is based on Bolton's (1992) key. Our material from Yunnan fits the re-description in the latter publication very well, even though the propodeal spines seem somewhat longer than in the material from Borneo. However, I consider this as a minor geographic variation.

Natural history. *Recurvidris kemneri* has been collected from leaf litter from rain forest, secondary forest and rubber plantation, and little is known about its bionomics.

***Strumigenys dyschima* (Bolton, 2000)** (Figure 2.29)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.911° N, 101.283° E), Limestone forest, 06.vi.2013, 2 workers, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

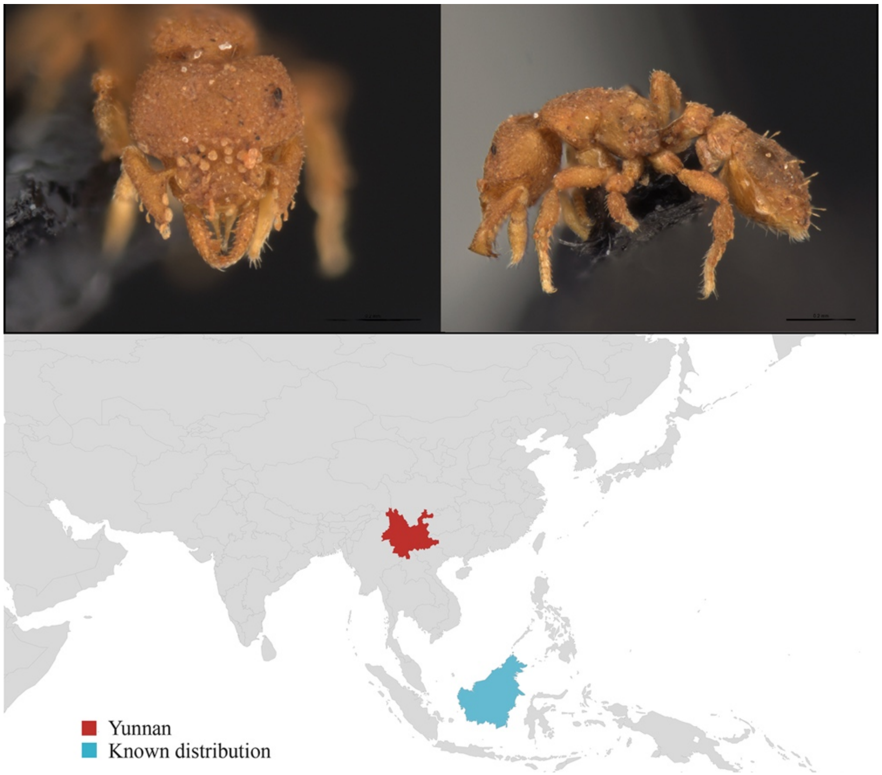

Figure 2.29 | *Strumigenys dyschima.*
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Distribution. Known from Yunnan (new record) and Borneo (Figure 2.29C). This new record represents an important extension in the northern range of the distribution of *Strumigenys dyschima.*

Taxonomic note. *Strumigenys dyschima* can be identified with the identification key given by Bolton (2000; treated as *Pyramica dyschima*).

Natural history. *Strumigenys dyschima* has been collected from leaf litter in limestone forest, and little is known about its bionomics.

Strumigenys kichijo **(Terayama, Lin & Wu, 1996)** (Figure 2.30)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.924° N, 101.268° E), Rubber Plantation, 05.vi.2013, 1 worker, 571m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.934° N, 101.269° E), Rubber Plantation, 09.vi.2013, 1 worker, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

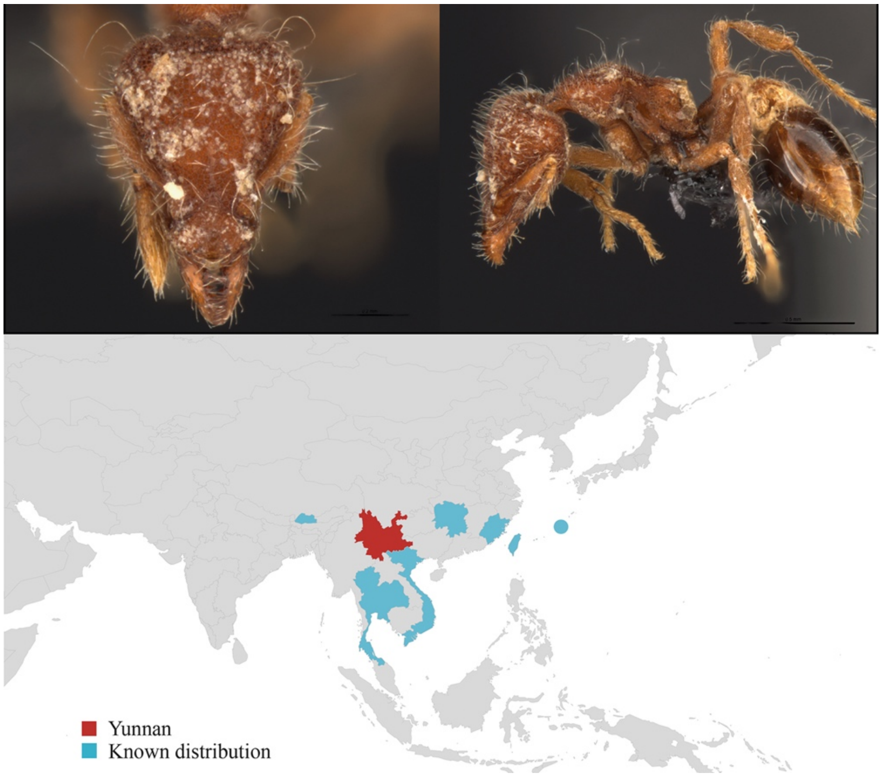

Figure 2.30 | ***Strumigenys kichijo.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Distribution. Widely distributed in Indo-Malayan subregions (Figure 2.30C).

Taxonomic note. *Strumigenys kichijo* can be identified with the identification key given by Bolton (2000; treated as *Pyramica kichijo*).

Natural history. *Strumigenys kichijo* has been collected from leaf litter in rubber plantations, and little is known about its bionomics.

***Strumigenys mitis* (Brown, 2000)** (Figure 2.31)

Material examined. CHINA, Yunnan, Xishuangbanna: “Holy Hills” (21.920° N, 101.239° E), Secondary forest, 07.vi.2013, 9 workers, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; “Holy Hills” (21.919° N, 101.239° E), Rain forest, 07.vi.2013, 7 workers, 670m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Secondary forest, 13.vi.2013, 40 workers, 825m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.966° N, 101.203° E), Secondary forest, 13.vi.2013, 1 worker, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 10.vi.2013, 19 workers, 830m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.961° N, 101.200° E), Rain forest, 10.vi.2013, 8 workers, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.960° N, 101.199° E), Rain forest, 13.vi.2013, 1 worker, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 13.vi.2013, 111 worker, 805m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.963° N, 101.201° E), Rain forest, 13.vi.2013, 122 workers, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.964° N, 101.202° E), Rain forest, 13.vi.2013, 50 workers, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.277° E), Secondary forest, 12.vi.2013, 1 worker, 685m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 12 workers, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.271° E), Rubber plantation, 09.vi.2013, 8 workers, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.932° N, 101.270° E), Rubber plantation, 09.vi.2013, 1 worker, 645m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.931° N, 101.269° E), Rubber plantation, 09.vi.2013, 1 worker, 645m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.924° N, 101.268° E), Rubber Plantation, 05.vi.2013, 1 worker, 571m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 82 workers, 550m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.274° E), Secondary forest, 05.vi.2013, 48 workers, 552m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.918° N, 101.271° E), Secondary forest, 05.vi.2013, 71 workers, 581m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.916° N, 101.274° E), Secondary forest, 08.vi.2013, 2 workers, 615m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.917° N, 101.274° E), Secondary forest, 08.vi.2013, 25 workers, 625m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Widely distributed in Austral-Asian and Indo-Malayan subregions (Figure 2.31C). This new record represents the northern-most known occurrence in the distribution of *Strumigenys mitis*.

Taxonomic note. *Strumigenys mitis* can be identified with the identification key given by Bolton (2000; treated as *Pyramica mitis*) and Bharti (2013, treated as *Pyramica mitis*).

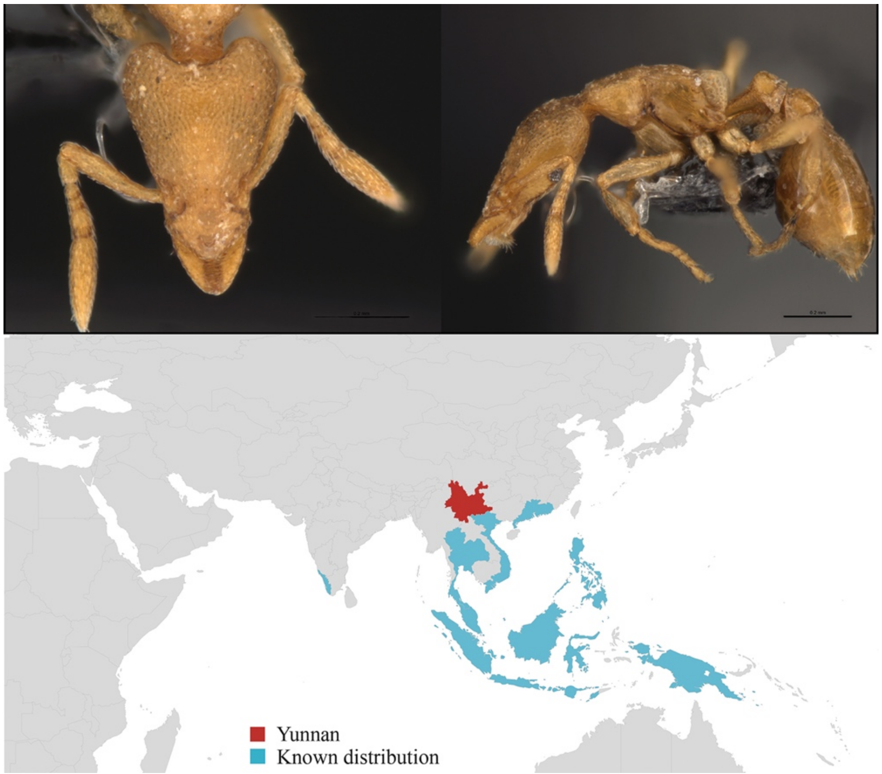

Figure 2.31 | ***Strumigenys mitis.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Natural history. *Strumigenys mitis* has been collected from leaf litter in rain forest, secondary forest and rubber plantations, and little is known about its bionomics.

Strumigenys nepalensis **Baroni Urbani & De Andrade, 1994** (Figure 2.32)

Material examined. CHINA, Yunnan, Xishuangbanna: "Holy Hills" (21.920° N, 101.240° E), Secondary forest, 07.vi.2013, 5 workers, 655m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; "Holy Hills" (21.920° N, 101.239° E), Secondary forest, 07.vi.2013, 12 workers, 665m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; "Holy Hills" (21.919° N, 101.239° E), Rain forest, 07.vi.2013, 1 worker, 670m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.963° N, 101.201° E), Rain forest, 13.vi.2013, 2 workers, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.277° E), Rubber Plantation, 12.vi.2013, 2 workers, 705m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.857° N, 101.277° E), Rubber Plantation, 12.vi.2013, 2 workers, 710m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.277° E), Secondary forest, 12.vi.2013, 2 workers, 685m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 3 workers, 690m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 4 workers, 685m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.278° E), Secondary forest, 12.vi.2013, 6 workers, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.858° N, 101.276° E), Secondary forest, 12.vi.2013, 1 worker, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 57 workers, 550m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.912° N, 101.285° E), Limestone forest, 06.vi.2013, 1 worker, 680m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.274° E), Secondary forest, 05.vi.2013, 13 workers, 552m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.283° E), Limestone forest, 06.vi.2013, 7 workers, 675m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.912° N, 101.282° E), Limestone forest, 06.vi.2013, 21 workers, 640m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.281° E), Limestone forest, 06.vi.2013, 21 workers, 650m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.888° N, 101.266° E), Rubber plantation, 14.vi.2013, 3 workers, 600m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Banna University construction site (21.888° N, 101.266° E), Rubber plantation, 14.vi.2013, 6 workers, 620m, Winkler sifting, B.

Guénard, B. Blanchard and C. Liu; Banna University construction site (21.922° N, 101.268° E), Rubber plantation, 14.vi.2013, 1 worker, 620m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

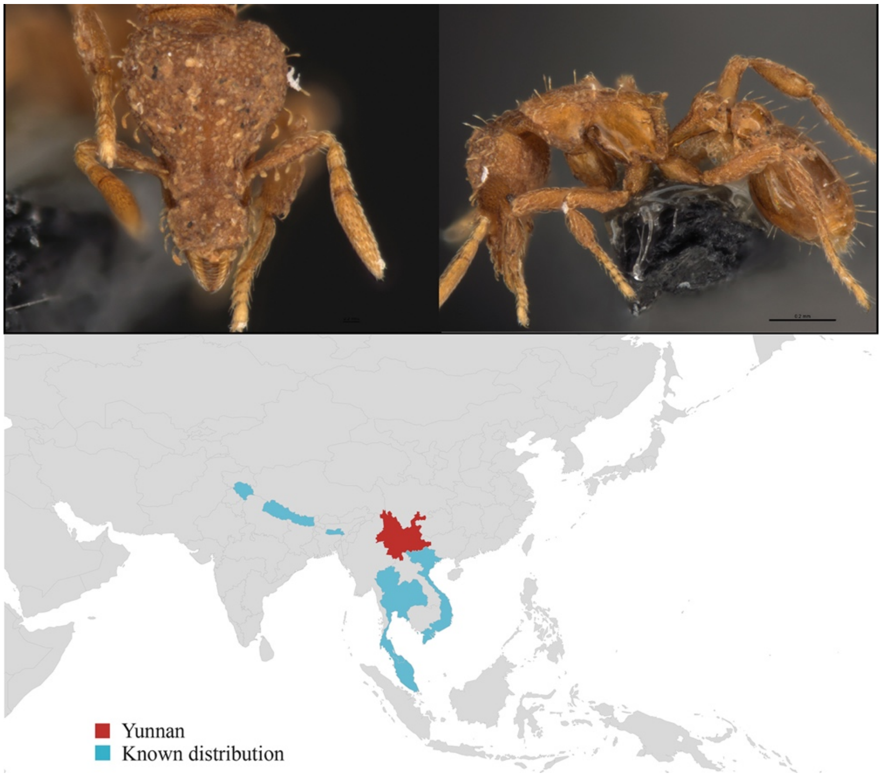

Figure 2.32 | *Strumigenys nepalensis.*
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Distribution. Known from Yunnan (new record), North Indian, Vietnam and Thailand (Figure 2.32C).

Taxonomic note. *Strumigenys nepalensis* can be identified with the identification key given by Bolton (2000; treated as *Pyramica nepalensis*).

Natural history. *Strumigenys nepalensis* has been collected from leaf litter in rain forest, secondary forest, limestone forest and rubber plantations, and little is known about its bionomics.

Strumigenys rallarhina **Bolton, 2000** (Figure 2.33)

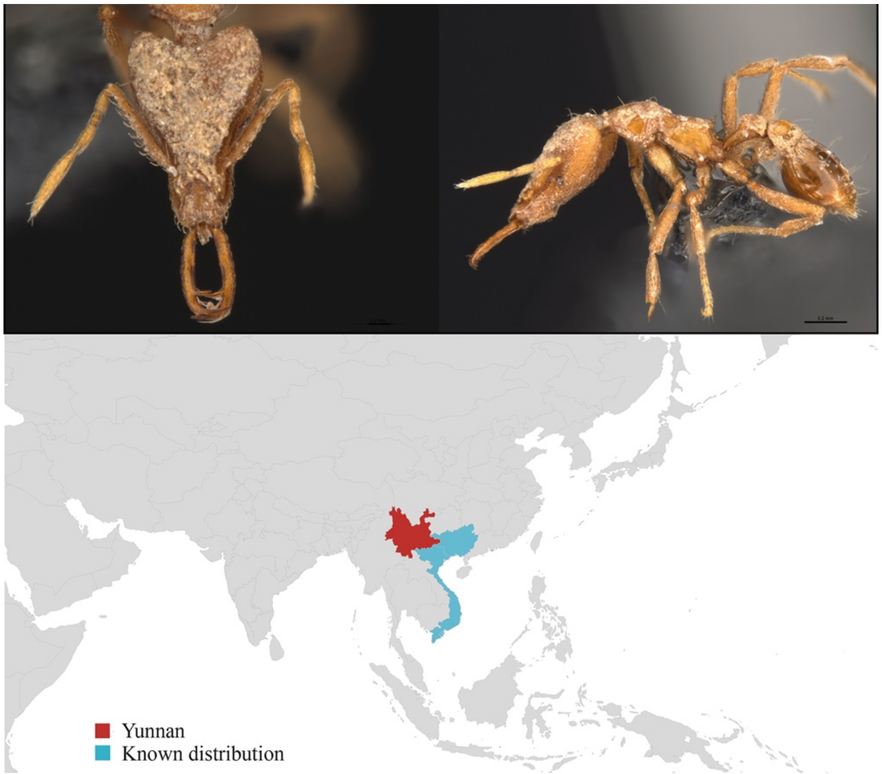

Figure 2.33 | ***Strumigenys rallarhina.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.272° E), Secondary forest, 05.vi.2013, 121 workers, 550m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.274° E), Secondary forest, 05.vi.2013, 34 workers, 552m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.918° N, 101.271° E), Secondary forest, 05.vi.2013, 35 workers, 581m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.916° N, 101.274° E), Secondary forest, 08.vi.2013, 7 workers, 615m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.917° N, 101.274° E), Secondary forest, 08.vi.2013, 44 workers, 625m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer

55 station (21.962° N, 101.200° E), Rain forest, 10.vi.2013, 22 workers, 830m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.961° N, 101.200° E), Rain forest, 10.vi.2013, 15 workers, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.960° N, 101.199° E), Rain forest, 10.vi.2013, 26 workers, 840m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 13.vi.2013, 9 workers, 805m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.964° N, 101.202° E), Rain forest, 13.vi.2013, 16 workers, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Known from Yunnan (new record), Guangxi and Vietnam (Figure 2.33C).

Taxonomic note. *Strumigenys rallarhina* can be identified with the identification key provided by Bolton (2000).

Natural history. *Strumigenys rallarhina* has been collected from leaf litter in rain forest and secondary forest, and little is known about its bionomics.

***Strumigenys sauteri* (Forel, 1912)** (Figure 2.34)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.918° N, 101.271° E), Secondary forest, 05.vi.2013, 10 workers, 581m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.917° N, 101.274° E), Secondary forest, 08.vi.2013, 3 workers, 625m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.962° N, 101.200° E), Rain forest, 13.vi.2013, 9 workers, 805m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.963° N, 101.201° E), Rain forest, 13.vi.2013, 3 workers, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

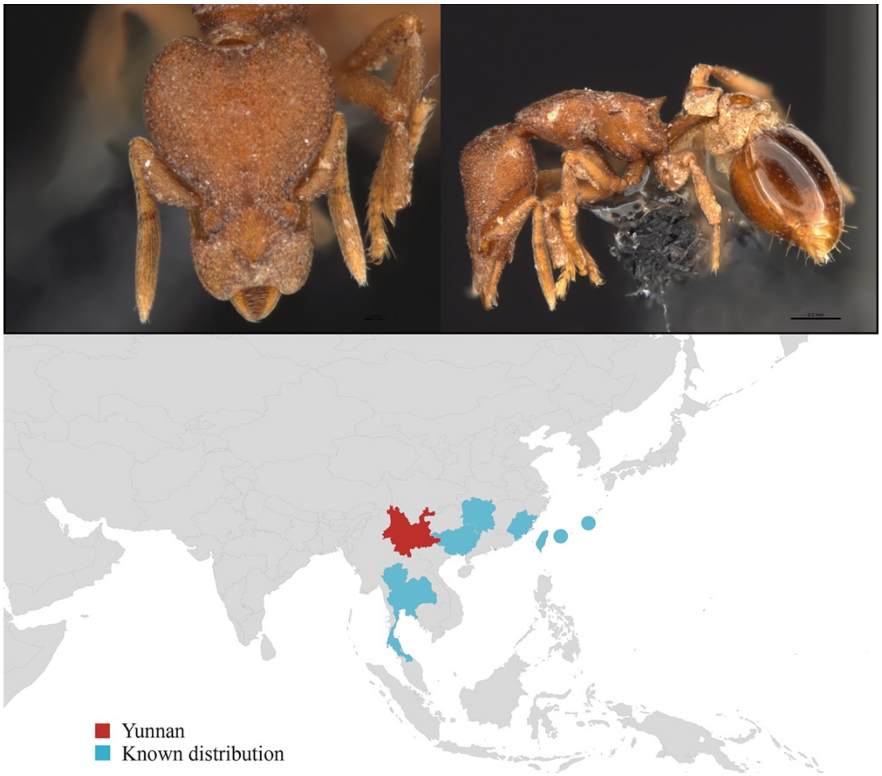

Figure 2.34 | ***Strumigenys sauteri.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Distribution. Widely distributed in Indo-Malayan subregions (Figure 2.34C).

Taxonomic note. *Strumigenys sauteri* can be identified with the identification key given by Bolton (2000; treated as *Pyramica sauteri*).

Natural history. *Strumigenys sauteri* has been collected from leaf litter in rain forest and secondary forest, and little is known about its bionomics.

Technomyrmex pratensis **(Smith, 1860)** (Figure 2.35)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.918° N, 101.271° E), Secondary forest, 05.vi.2013, 4 workers, 581 m, Winkler sifting, B. Guénard, B. Blanchard and

C. Liu; XTBG (21.919° N, 101.274° E), Secondary forest, 11.vi.2013, 4 workers, 590 m, Hand collection, B. Guénard, B. Blanchard and C. Liu.

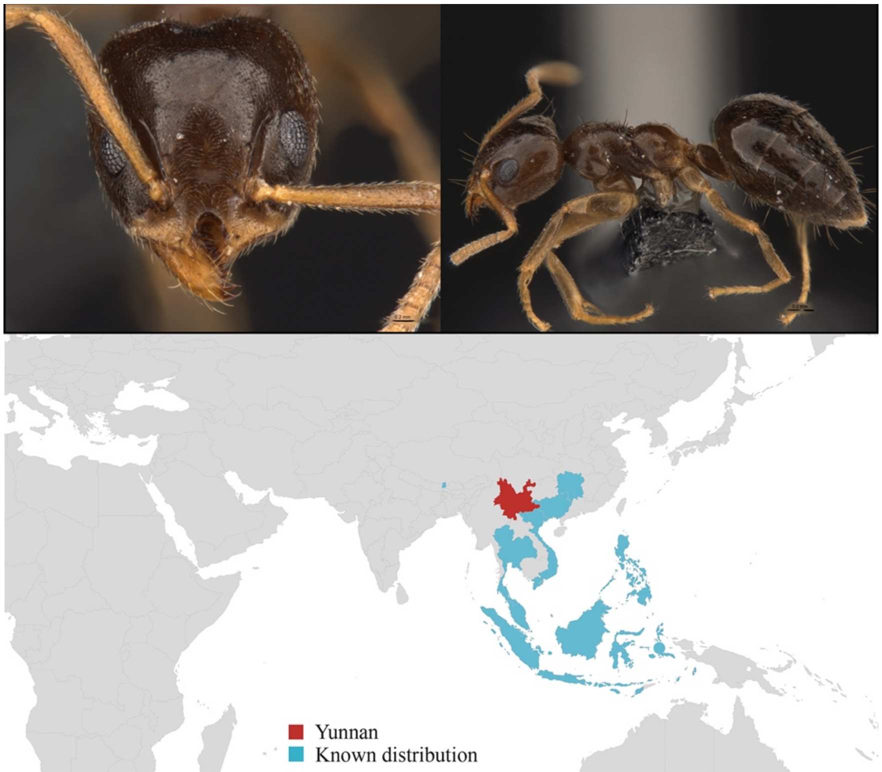

Figure 2.35 | *Technomyrmex pratensis.*
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Distribution. Widely distributed in the Austral-Asian and Indo-Malayan subregions (Figure 2.35C).

Taxonomic note. *Technomyrmex pratensis* is the only member of the *Technomyrmex pratensis* species group. It is a very conspicuous species within the genus, and its identification is very easy with the key provided by Bolton (2007).

Natural history. *Technomyrmex pratensis* has been collected from leaf litter in secondary forest, and little is known about its bionomics.

Tetramorium difficile **Bolton, 1977** (Figure 2.36)

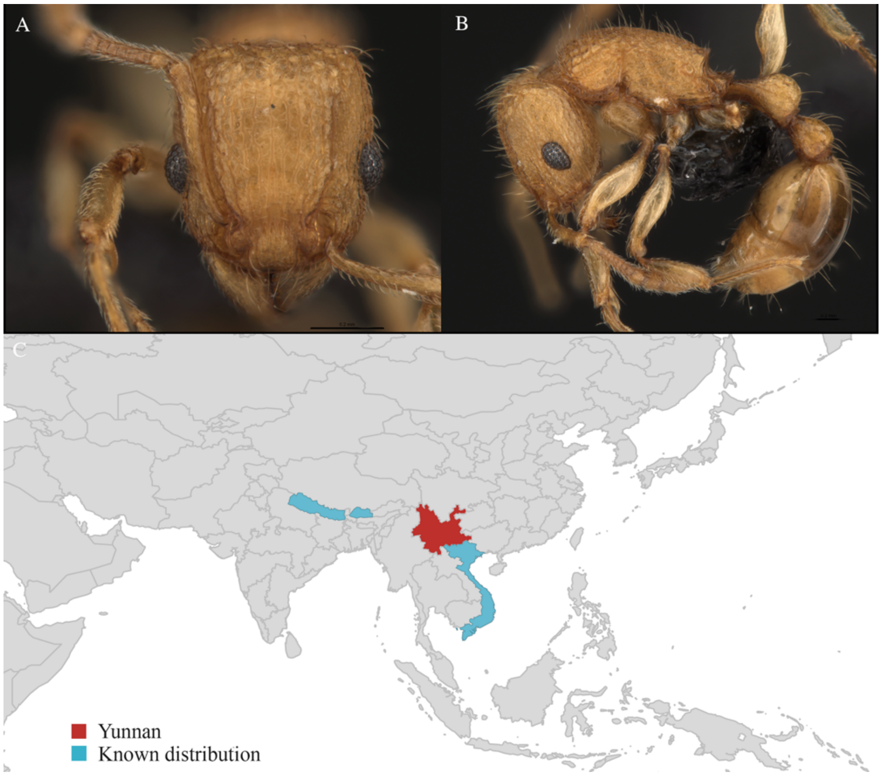

Figure 2.36 | ***Tetramorium difficile.***
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.918° N, 101.271° E), Secondary forest, 05.vi.2013, 2 workers, 552 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Known form Yunnan (new record), northern India, and Vietnam (Figure 2.36C).

Taxonomic note. *Tetramorium difficile* is a member of the *Tetramorium tonganum* group and can be identified with the key provided by Bolton (1977). However, *T. difficile* under its current definition is morphologically very close to *T. tonganum*. It is likely that both are conspecific and the material listed as *T. difficile* represents intraspecific forms of the very widespread *T. tonganum*.

Natural history. *Tetramorium difficile* has been collected from leaf litter in secondary forest, and little is known about its bionomics.

Tetramorium flavipes **Emery, 1893** (Figure 2.37)

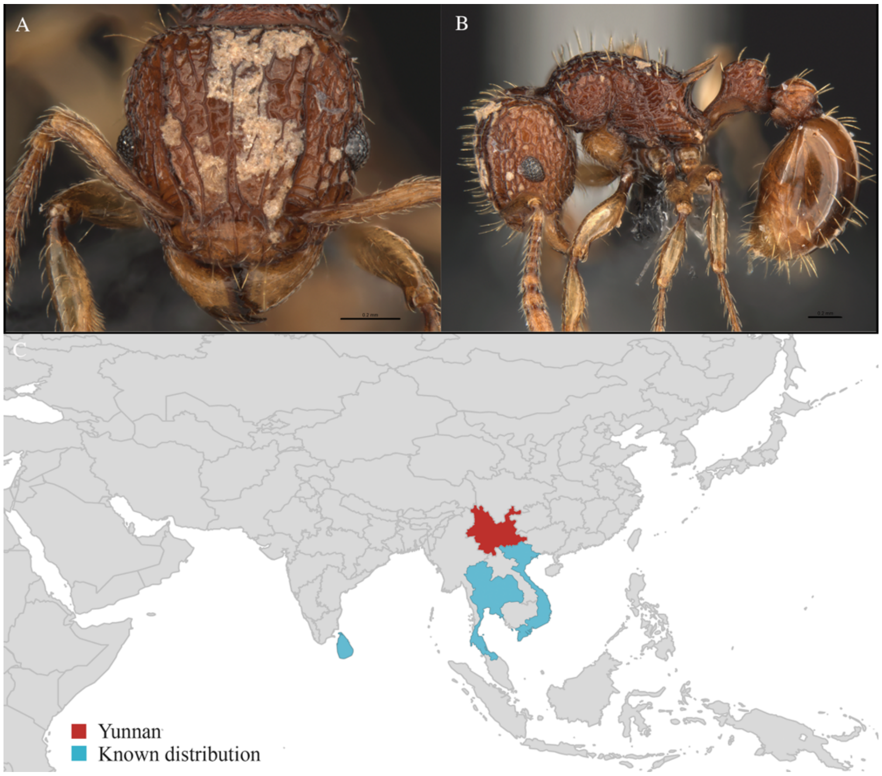

Figure 2.37 | *Tetramorium flavipes.*
(**A**) Head in front view. (**B**) Mesosoma in profile view. (**C**) Global distribution map.

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.918° N, 101.271° E), Secondary forest, 05.vi.2013, 35 workers, 552 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.917° N, 101.274° E), Secondary forest, 08.vi.2013, 33 workers, 625 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.961° N, 101.201° E), Rain forest, 10.vi.2013, 8 workers, 820m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Kilometer 55 station (21.963° N, 101.200° E), Rain forest, 13.vi.2013, 5 workers, 815m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Known from Yunnan (new record), Vietnam, Thailand and Sri Lanka (Figure 2.37C). This new record represents the northern-most record in the distribution of this species.

Taxonomic note. *Tetramorium flavipes* is a member of the *Tetramorium tortuosum* group. Its identification is relatively straightforward with the key given by Bolton (1977). However, *T. flavipes*, originally described from Thailand, is very close to *T. eleates* Forel, 1913 from Borneo and the Philippines, and as already pointed out by Bolton (1977), both could represent geographic variants of the same species.

Natural history. *Tetramorium flavipes* has been collected from leaf litter in secondary forest, and very little is known about its bionomics.

***Tetramorium parvispinum* (Emery, 1893)** (Figure 2.38)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.274° E), Secondary forest, 05.vi.2013, 155 workers, 550 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.924° N, 101.268° E), Rubber plantation, 05.vi.2013, 6 workers, 571 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.917° N, 101.270° E), Secondary forest, 05.vi.2013, 7 workers, 580 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.911° N, 101.281° E), Limestone rain forest, 06.vi.2013, 155 workers, 650 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.916° N, 101.274° E), Secondary forest, 08.vi.2013, 58 workers, 615 m, Winkler sifting, B. Guénard, B. Blanchard and

C. Liu; Menglun town (21.930° N, 101.269° E), Rubber plantation, 09.vi.2013, 2 workers, 640 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.890° N, 101.267° E), Rubber plantation, 14.vi.2013, 9 workers, 620 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Widely distributed in the Indo-Malayan subregion (Figure 2.38C).

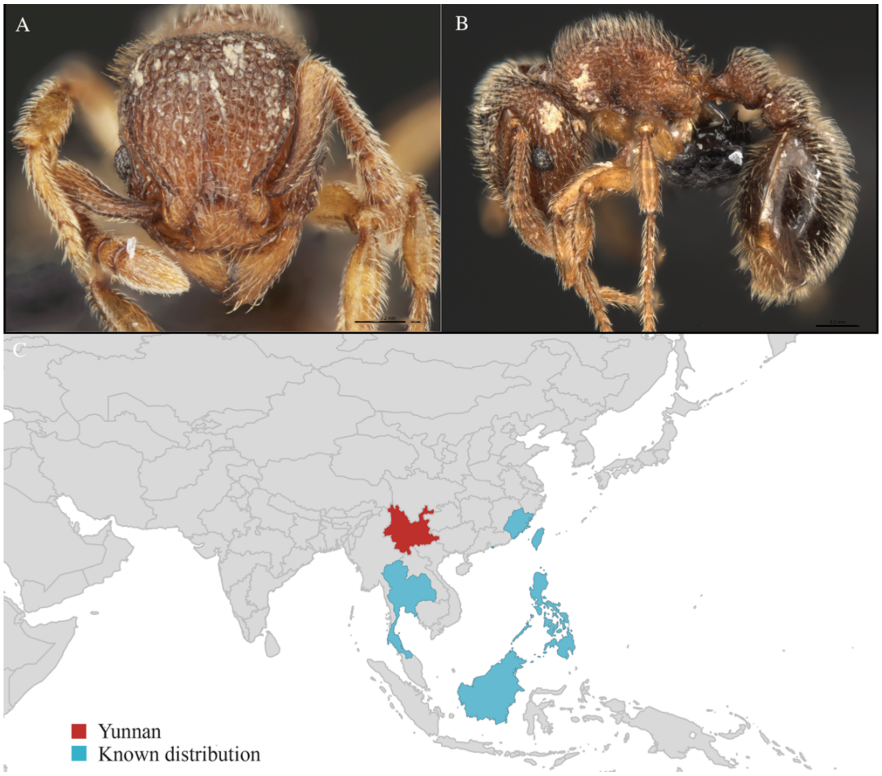

Figure 2.38 | *Tetramorium parvispinum.*
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Taxonomic note. *Tetramorium parvispinum* is a member of the *Tetramorium walshi* species group. It can be identified with the key presented by Bolton (1976; as *Triglyphothrix parvispina*)

Natural history. *Tetramorium parvispinum* has been collected from leaf litter in secondary forest, limestone forest and rubber plantations, and little is known about its bionomics.

***Tetramorium polymorphum* Yamane & Jaitrong, 2011** (Figure 2.39)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.917° N, 101.274° E), Rain forest, 05.vi.2013, 1 major worker, 552 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.918° N, 101.270° E), Rain forest, 05.vi.2013, 3 workers, 581 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.919° N, 101.272° E), Rain forest, 05.vi.2013, 10 workers, 550 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; "Holy Hills" (21.920° N, 101.239° E), Rain forest, 07.vi.2013, 10 worker, 665m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; XTBG (21.928° N, 101.256° E), Rain forest, 07.vi.2013, 10 workers, 565 m, Hand collection, B. Guénard, B. Blanchard and C. Liu; Man Sai village (21.860° N, 101.278° E), Rain forest, 12.vi.2013, 1 worker, 680 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. Known from Yunnan (new record), Laos and Thailand (Figure 2.39C). This new record represents the northern-most record in the distribution of *Tetramorium polymorphum*.

Taxonomic note. *Tetramorium polymorphum* is a member of the *T. walshi* species group. Its identification is not easy since the species was not known when Bolton (1976) published his revision of the genus *Triglyphothrix* (now Tetramorium), in which he provided keys to the Indo-Malayan and Austral-Asian *T. walshi* and *T. obesum* species groups. However, by combining Bolton's (1976) work with the recent species description of Yamane & Jaitrong (2011) the identification is relatively straightforward. It is very similar to the closely related and sympatric *T. kheperra* Bolton, 1976, and the identification key of Bolton (1976) will lead the user to that species. The recent addition to Bolton's key provided by Yamane and Jaitrong (2011) clearly separates both species.

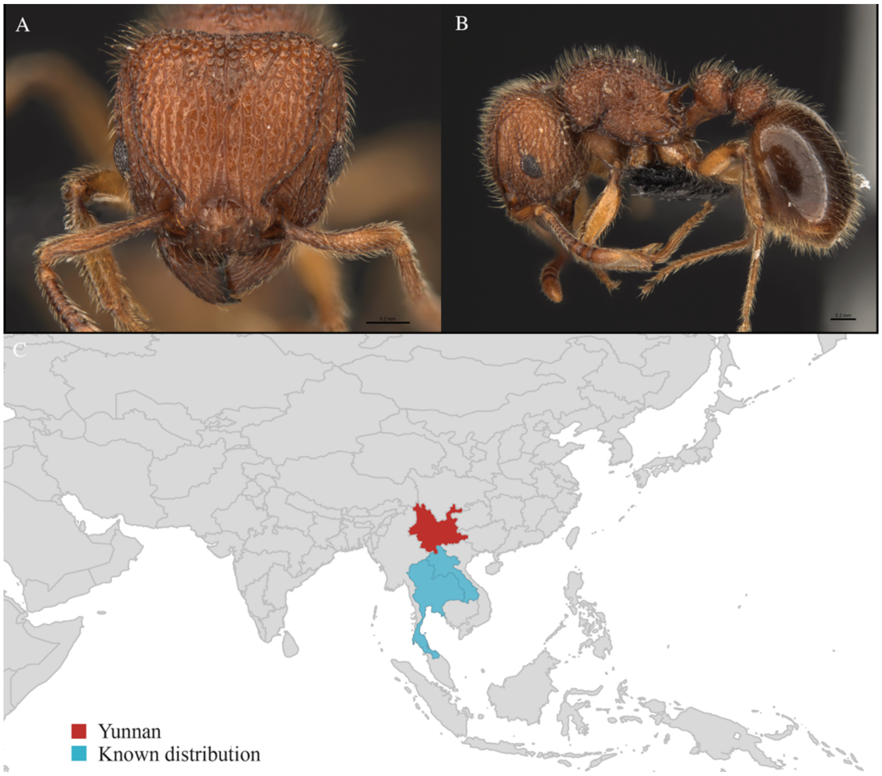

Figure 2.39 | ***Tetramorium polymorphum.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Natural history. *Tetramorium polymorphum* is a very special member of the genus *Tetramorium* since it is the only known species that possesses a polymorphic worker caste divisible into distinctive minor, media and major workers (Yamane & Jaitrong, 2011). Yamane and Jaitrong (2011) also report that this species is comparatively aggressive and hypothesize that the major worker could have a defensive function. In addition, they emphasize that *T. polymorphum* is only found in undisturbed rain forest habitats in Thailand and Laos. Our data from Yunnan supports this since it was predominantly sampled from rain forest.

Tetramorium tonganum **Mayr, 1870** (Figure 2.40)

Material examined. CHINA, Yunnan, Xishuangbanna: XTBG (21.919° N, 101.274° E), Secondary forest, 05.vi.2013, 9 workers, 552 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu; Menglun town (21.934° N, 101.269° E), Secondary forest, 09.vi.2013, 2 workers, 640 m, Winkler sifting, B. Guénard, B. Blanchard and C. Liu.

Distribution. *Tetramorium tonganum* is widely distributed in the Austral-Asian and Indo-Malayan subregions where it ranges from western Oceania to South East Asia (Figure 2.40C). Bolton (1977) has noted already that the species is widespread in its native range and has the characteristics of tramp species. It is very likely that future collections will reveal its presence in more Chinese provinces Southeast Asian countries.

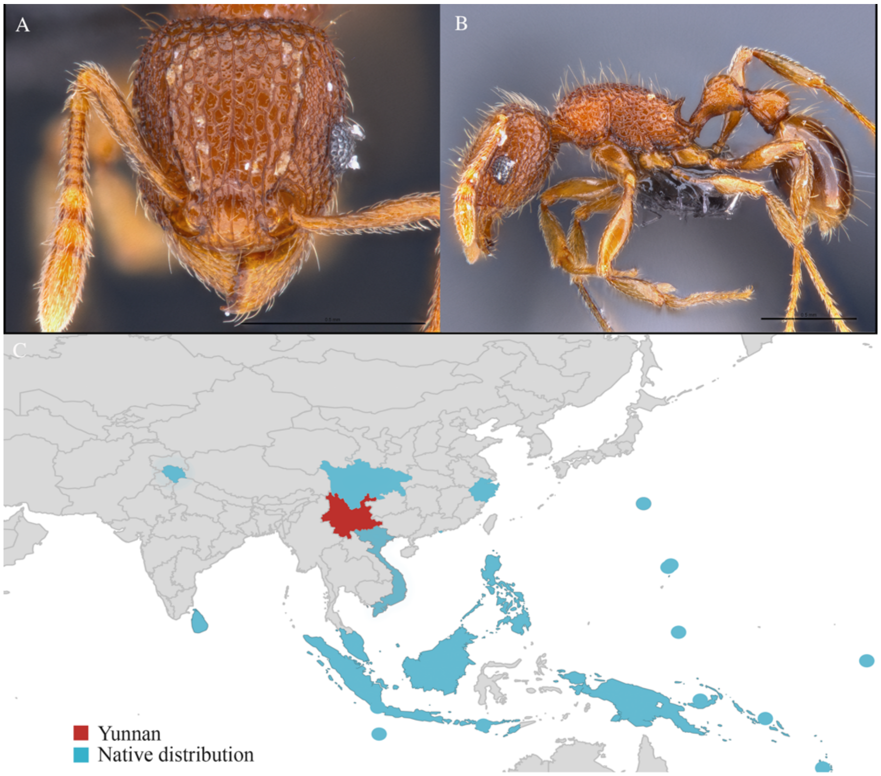

Figure 2.40 ǀ ***Tetramorium tonganum.***
(**A)** Head in front view. (**B)** Mesosoma in profile view. (**C)** Global distribution map.

Taxonomic note. *Tetramorium tonganum* belongs to the *Tetramorium tonganum* group and can be easily identified with the key provided by Bolton (1977).

Natural history. *Tetramorium tonganum* has been collected from leaf litter in secondary forest, and is known to be an exotic species in China (Guenard & Dunn, 2012). Despite its wide distribution and tramping ability, there is very little information about its biology. In addition to Bolton (1977), Sarnat and Economo (2012) also confirm that *T. tonganum* is able to establish populations outside its native range without damaging or significantly altering ecological or agricultural systems in its introduced habitats. They also report that *T. tonganum* is mostly found on vegetation in disturbed or edge habitats.

2.3.3 New Aenictus species description from Yunnan

2.3.3.1 The Aenictus ceylonicus species group

Diagnosis. The group was first diagnosed by Wilson (1964) and recently redefined by Jaitrong and Yamane (2011, 2013). The following definition is taken from the latter studies:

Antenna ten-segmented; with head in full-face view scape extending beyond half of head length, but not reaching the occipital corner of head; mandible linear, its basal and external margins almost parallel; masticatory margin with large apical tooth followed by medium-sized subapical tooth, 0-6 small denticles present between subapical tooth and basal tooth; with mandibles closed, a gap present between mandibles and anterior margin of clypeus; anterior clypeal margin weakly concave or almost straight, lacking denticles; frontal carina short and thin reaching to or slightly extending beyond the level of posterior margin of torulus; with head in full-face view curved anterior extension of frontal carina reaching to or extending beyond the level of anterior clypeal margin; parafrontal ridges absent; promesonotum usually convex dorsally and sloping gradually to propodeum (rarely with almost straight dorsal outline); subpetiolar process developed. Head and first gastral tergite smooth and shiny. Body yellowish, reddish or dark brown; typhlatta spot absent.

Notes. The *A. ceylonicus* group under the above definition contains 33 species (Jaitrong & Yamane 2013) and is clearly the most species-rich group in the genus. It is widespread in the southeastern Palaearctic, Oriental, Indo-Australian and Austral-Asian regions (Wilson, 1964; Shattuck, 2008; Jaitrong & Yamane, 2011, 2013). Its distinction from other groups is very straightforward on the basis of the linear mandible, the distinct gap between the mandibles and the anterior margin of the clypeus when the mandibles are closed, the almost straight or feebly concave anterior clypeal margin, and the lack of clypeal denticles. Some or most of the African *Aenictus* might be members of the group also (Wilson, 1964), but due to the lack of revisions or other modern taxonomic treatment their affinities remain unclear.

2.3.3.2 Update to the identification key of the *A. ceylonicus* group

The identification key to the South East Asian species provided by Jaitrong & Yamane (2013) contains 22 key couplets for 23 species. The new species described here needs to be included, thus in the following I slightly modify the first few key couplets without altering the remainder of the key.

1. Mandibles with 2–6 teeth/denticles between subapical and basal teeth (mandibles with more than 4 teeth/denticles in total) (Figure 2.44D)..2

- Mandibles with 0–1 tooth/denticle between subapical and basal teeth (mandibles with 3–4 teeth/denticles in total) (Figure 2.41A, B)..15

2a. Dorsal face of propodeum mostly smooth and shiny; lateral face of propodeum partly smooth and shiny (Figure 2.42A); postpetiole usually entirely smooth and shiny, rarely reticulate-punctate basally...2b

- Propodeum entirely sculptured (Figure 2.42B); postpetiole entirely sculptured or with smooth and shiny small area on dorsal face...6

2b. Metanotal groove noticeably present but weak; propodeal junction noticeably angulate with distinct tooth; subpetiolar process relatively elongate, subrectangular, and slightly projecting anteroventrally (Figure 2.43A)...*A. yangi*

- Character combination never as above; metanotal groove usually absent or strongly reduced, but always weaker than above; propodeal junction rounded to angulate without/with small tooth; subpetiolar process variable, ranging from strongly reduced and rounded to subrectangular, but never as elongate as above (Figure 2.43B, C, D, E)..3

From couplet 3 onwards there are no changes to the key presented by Jaitrong & Yamane (2013) and I refer to that publication.

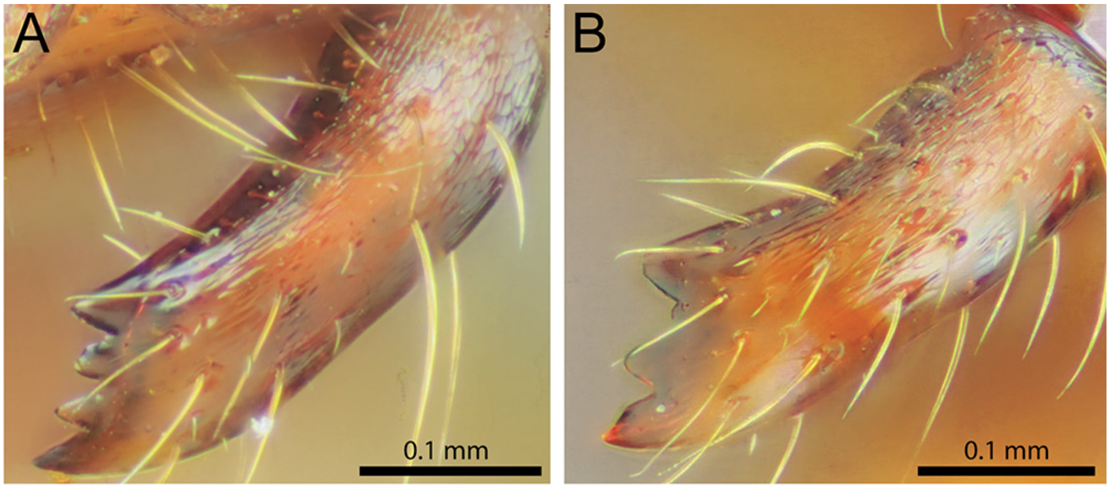

Figure 2.41 | Mandible showing masticatory margin showing different number of teeth.
(**A**) *A. maneerati* Jaitrong & Yamane **(B)** *A. watanasiti* Jaitrong & Yamane. Images are from Jaitrong & Yamane (2013)

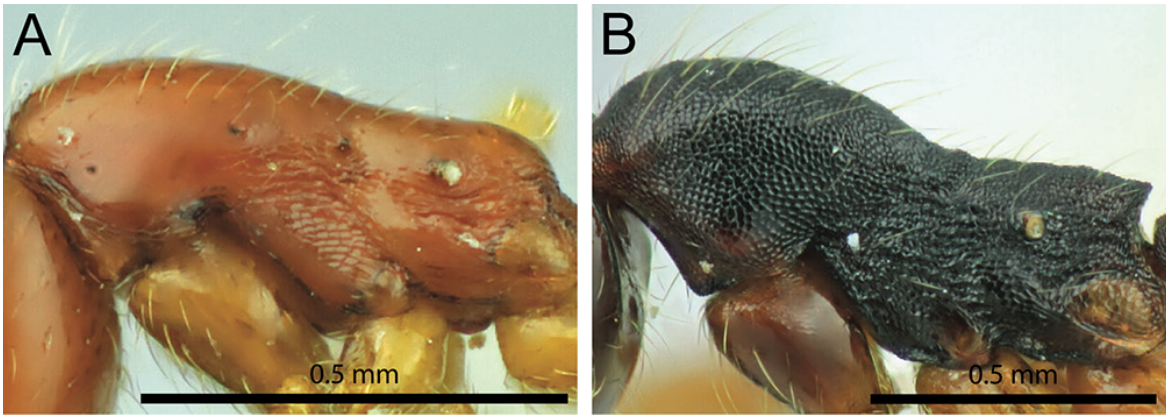

Figure 2.42 | Mesosoma in profile showing two types of propodeum.
(**A**) *A. longicephalus* Jaitrong & Yamane **(B)** *A. pinkaewi* Jaitrong & Yamane. Images are from Jaitrong & Yamane (2013)

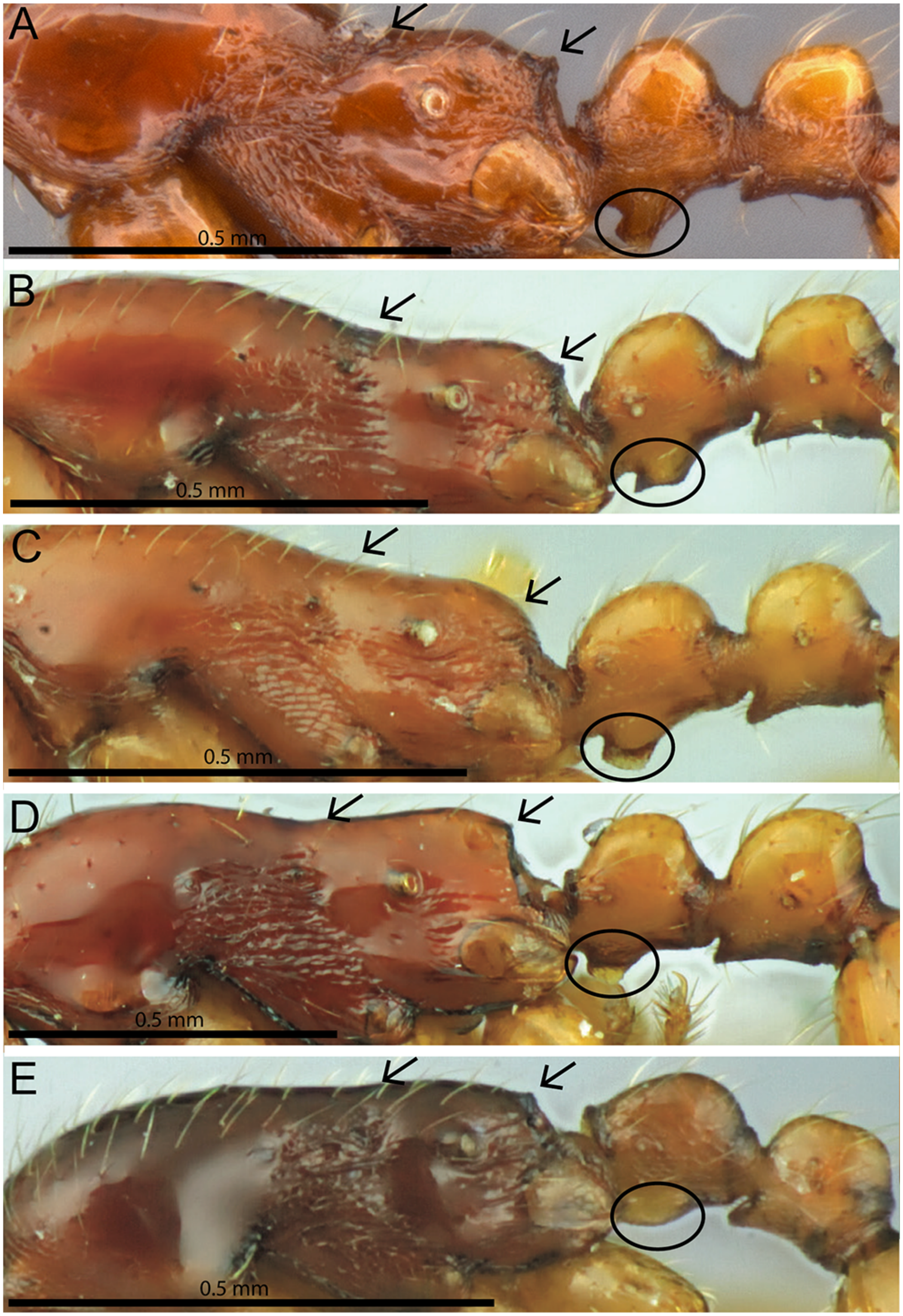

Figure 2.43 | Mesosoma and waist segments in profile of *Aenictus* species.
(A) *A. yangi* **sp. n. (B)** *A. baliensis* Jaitrong & Yamane **(C)** *A. longicephalus* Jaitrong & Yamane **(D)** *A. minipetiolus* Jaitrong & Yamane **E** *A. wiwatwitayai* Jaitrong & Yamane. Images except figure 3A are from Jaitrong & Yamane (2013). black arrows indicate metanotal groove and propodeal junction, black ellipse subpetiolar process**.**

2.3.3.3 *Aenictus yangi* sp. n. (Figure 2.43A, 2.44A, B, C, D)

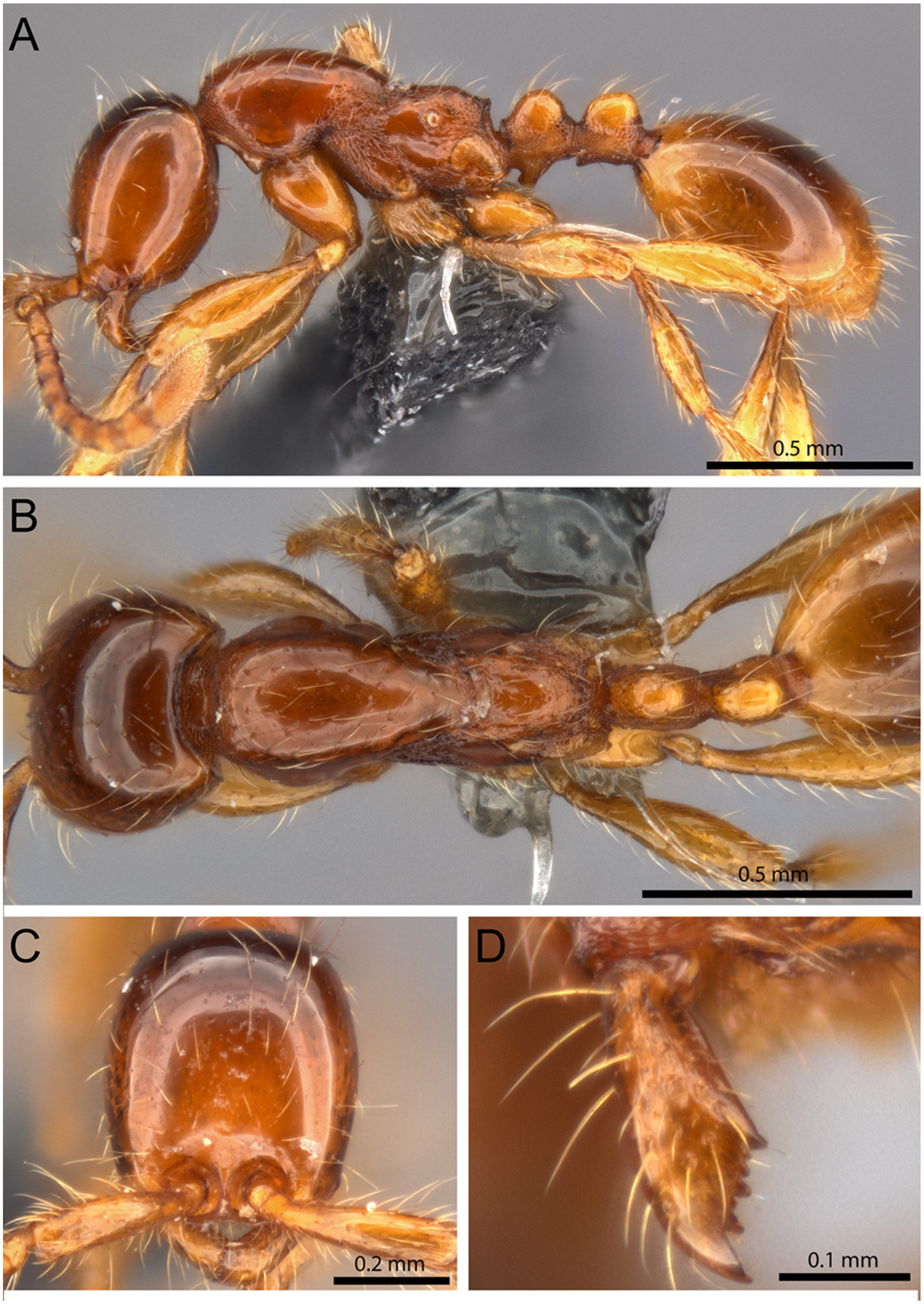

Figure 2.44 | *Aenictus yangi* sp. n. (CASENT0735503).
(A) Body in profile **(B)** Body in dorsal view **(C)** head in full-face view **(D)** right mandible in frontal view.

Type material. Holotype, pinned worker, China, Yunnan, Xishuangbanna, Man Sai village, 21°51'34.4" N, 101°16'39.6" E, 680m, young rain forest, leaf litter, 12.IIV.2013 (*B. Blanchard, B. Guénard & C. Liu*) (ISAS: CASENT0735503). Paratypes, 14 pinned workers, China, Yunnan, Xishuangbanna, Man Sai village, 21°51'34.4" N, 101°16'39.6" E, 680m, young rain forest, leaf litter, 12.IIV.2013 (*B. Blanchard, B. Guénard & C. Liu*) (BMNH: CASENT0717204; CAS: CASENT0735506; CASENT0735508; HLMD: CASENT0735507; ISAS: CASENT0717203; CASENT0735495; CASENT0735496; CASENT0735498; MCZ: CASENT0735505; MHNG: CASENT0735504; NHMB: CASENT0735501; PUPAC: CASENT0735500; SKYC: CASENT0735499; THNHM: CASENT0735497).

Non-type material. China, Yunnan, Xishuangbanna, Man Sai village, 21°51'34.4" N, 101°16'39.6" E, 680m, young rain forest, leaf litter, 12.IIV.2013 (*B. Blanchard, B. Guénard & C. Liu*).

Diagnosis. *Aenictus yangi* differs from other South East Asian members of the *A. ceylonicus* group by the following combination of characters: head in full-face view distinctly longer than broad (CI 82–90); masticatory margin of mandible with seven teeth/denticles; antennal scapes relatively long (SI 76–86); metanotal groove noticeably present but weak; propodeal junction noticeably angulate with distinct tooth; subpetiolar process relatively elongate, subrectangular, and slightly projecting anteroventrally; propodeum laterally mostly smooth and shiny, weakly irregularly rugulose at base, and weakly reticulate-punctate near propodeal junction; petiole and postpetiole mostly smooth and shiny with lower portions reticulate-punctate.

Worker measurements (N=17). TL 2.21–2.60; HL 0.51–0.57; HW 0.43–0.50; SL 0.33–0.42; ML 0.69–0.87; PL 0.17–0.20; CI 82–90; SI 76–86.

Worker description. Head in full-face view distinctly longer than broad (CI 82–90), sides convex, posterior head margin straight to very weakly convex; occipital margin bearing a distinct carina. Antennal scapes relatively long (SI 76–86), extending beyond 2/3 of head length but not reaching posterior head margin. Frontal carinae relatively short and indistinct, reaching the level of posterior margin of torulus. Parafrontal ridges absent. Anterior clypeal margin weakly to moderately concave, not concealed by curved anterior extension of frontal carina. Masticatory margin of mandible with large acute apical tooth followed by one medium-sized subapical tooth, one small denticle, one medium-sized tooth, two smaller denticles, and medium-sized basal tooth, reaching total of seven teeth/denticles; basal margin straight. Maximum width of gap between anterior clypeal margin and mandibles about 1.0 to 1.4 times broader than maximum width of mandible. Promesonotum convex dorsally and sloping gradually to metanotal groove; metanotal groove noticeably present but weak; mesopleuron relatively long, clearly demarcated from metapleuron by weak groove; metapleural gland bulla relatively large, its maximum diameter about 1.7 to 2.1 times longer than distance between propodeal spiracle and metapleural gland bulla. Propodeum in profile with feebly convex dorsal outline; propodeal junction noticeably angulate with distinct tooth; declivity of propodeum moderately concave and encircled by strongly developed rim. Petiole in profile higher than long, its dorsal outline strongly convex; subpetiolar process relatively elongate, subrectangular, and slightly projecting anteroventrally. Postpetiole slightly smaller than petiole, its dorsal outline strongly convex. Head including antennal scape entirely smooth and shiny. Mandibles predominantly unsculptured, smooth and shiny with weak, superficial striation basally. Promesonotum entirely smooth and shiny; mesopleuron and metanotal groove irregularly rugulose; propodeum laterally mostly smooth and shiny, weakly irregularly rugulose at base, and weakly reticulate-punctate near propodeal junction. Petiolar node and postpetiole mostly smooth and shiny with lower portions reticulate-punctate. Head and mesosoma dorsally with abundant erect to subdecumbent hairs. Head, mesosoma, and gaster usually reddish brown, always distinctly darker than yellow to light yellowish brown mandibles, antennae, petiole, postpetiole, and legs.

Etymology. The new species is dedicated to Da-Rong Yang from the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. I want to thank him for his great support of the first author's studies in the area.

Distribution and ecology. At present, the new species is only known from Xishuangbanna in southern Yunnan (Figure 2.45). The type locality is a tropical lowland rainforest situated at an elevation of around 550 m. The new species was only collected twice, both times through leaf litter extraction. Nevertheless, as for most *Aenictus*, I strongly suspect that *A. yangi* has a more hypogaeic lifestyle and might be more abundant in the soil stratum. The use of specific collection techniques that target subterranean army ants, such as subterranean oil baiting (Weissflog et al., 2001), will likely yield additional material of this species. Unfortunately, due to the limited available material there is no additional information about its ecology.

Taxonomic notes. The identification of *A. yangi* within the *A. ceylonicus* species group can be easily performed with the updated identification key provided above. The new species is morphologically most similar to *A. baliensis* Jaitrong & Yamane, 2013 (Bali), *A. longicephalus* Jaitrong & Yamane, 2013 (Lombok), *A. minipetiolus* Jaitrong & Yamane, 2013 (Lombok), and *A. wiwatwitayai* Jaitrong & Yamane, 2013 (Thailand). However, *A. yangi* can be immediately separated from these by the development of the metanotal groove, the shape of the propodeum and the subpetiolar process, and the sculpture on the mesosoma and waist segments (see Figure

2.43 for details). *Aenictus yangi* can be easily separated from *A. brevipodus* Jaitrong & Yamane, 2013 (Thailand), and *A. formosensis* Forel, 1913 (Taiwan) by the number of mandibular teeth, shape of the head, the shape and punctate of petiole and postpetiole, and the shape of subpetiolar process.

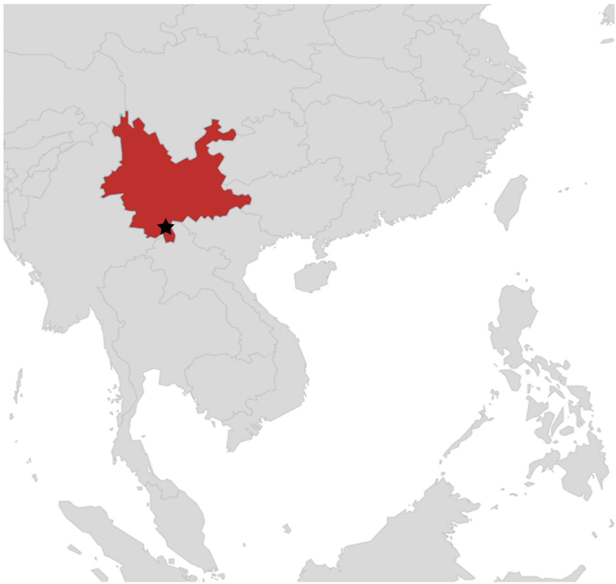

Figure 2.45 | Type locality of *A. yangi* sp. n.
Black star indicades the sampling locility. Red indicates Yunnan Province, China.

2.4 Discussion

The total number of named ant species in China is 939, but the true species richness is expected to be significantly higher, perhaps as high as 1200 to 1600 species (Guenard and Dunn 2012). The collection of these 40 new ant records for Yunnan and 17 for China through Winkler extraction, combined with the discovery of the extremely rare ant species *Stigmatoma scrobiceps* (Guenard et al. 2013), should encourage myrmecologists to consider leaf litter extraction as one of the primary methods to collect leaf litter ants, especially for places where this method has not previously been used. Nevertheless, further sampling methods that specifically target different strata will very likely yield additional species, which is especially true for hypogaeic and arboreal ant communities.

Based on our collections, many newly recorded species, such as *Discothyrea clavicornis, Myrmecina curvispina,* and *Odontoponera denticulata* are relatively common. The reason why those species were never reported from Yunnan before may be due to different collection techniques and/or misidentifications. For example, *Odontoponera denticulata* has long been misidentified as *Odontoponera transversa* (Yamane 2009). Another reason may be that some of the newly recorded species have been described only recently outside of Yunnan and/or China, such as *Myrmecina curvispina* and *Pheidole tumida* (Zhou et al. 2008, Eguchi 2008).

Many new species records in our collection such as *Aenictus artipus, A. maneerati, A. paradentatus, Discothyrea clavicornis*, *Dolichoderus laotius*, *Gesomyrmex kalshoveni*, *Gnamptogenys treta*, *Pheidole plagiaria, P. planifrons*, *P. rugithorax, P. tumida, P. vieti, Recurvidris kemneri, Strumigenys dyschima, S. mitis*, *Tetramorium difficile*, *T. flavipes*, *T. parvispinum*, and *T. tonganum*, are at the northern limit of their known distribution in Yunnan. Interestingly, the occurrence of several species in Yunnan, such as *Discothyrea clavicornis, Gesomyrmex kalshoveni, Gnamptogenys treta, Recurvidris kemneri*, and *Strumigenys dyschima* constitutes a disjunction from the rest of their known distribution in the Malay Peninsula. At present, it is unclear if these represent sampling artifacts and the ranges are actually continuous in the region, if these species ranges represent true biogeographic disjunctions, or if they are actually different species. Only future diversity inventories and taxonomic treatments, of which this paper represents one modest contribution, can answer these questions and further resolve the biodiversity map for ants and other organisms.

Despite the comparatively short collecting time I invested in the inventory of the myrmecofauna, I was able to identify 145 species, of which over 30% represent new records. This increases the list of known species for Yunnan by 10%, and there are still more than 60 species that I tentatively consider undescribed. This shows how little was previously known about the ant fauna of the region, and I am convinced that more intensive sampling in different habitats and microhabitats will likely reveal the presence of even more species or help improve the current taxonomic resolution. In this context, I think that Yunnan should be considered an area of high biodiversity value and deserving of attention of both biologists and conservationists. Regrettably, this interesting biota is being degraded at an alarming speed, particularly due to the rapid expansion of rubber plantations in the area (Li et al. 2007).

3. Reorganization of taxonomic, functional, and phylogenetic ant biodiversity after conversion to rubber plantation

3.1 Introduction

The current era of human-domination of Earth's ecosystems has led to anthropocentric conversion of a significant proportion of Earth's surface to agroecosystem. The expansion of human agriculture activities is driving an increasing loss of tropical forest (Hansen et al. 2013) and is likely to have serious impacts on biodiversity worldwide (Laurance et al. 2014). In Southeast Asia, agroecosystems such as oil palm plantations cover a large area and continue to expand, resulting in dramatic impacts on biodiversity (e.g. Fayle et al. 2010). In recent years the "Rubber Juggernaut" has been expanding rapidly, largely by replacing natural forest in Southeast Asia (Ziegler et al. 2009, Warren-Thomas et al. 2015). The implications of the emergence of this new habitat for both ecological processes and biodiversity conservation are not yet well understood. Here, I investigate the organization of ant biodiversity, an ecologically dominant component of these ecosystems, in a mixed landscape of forest and rubber habitat in Southeast Asia.

For many taxa, a decline of species richness is a common outcome of conversion of forests to agroecosystem (Philpott et al. 2008b), including rubber plantation (Meng et al. 2012). However, the responses of other dimensions of biodiversity, such as functional and phylogenetic diversity, and changes in the organization of biodiversity in space (e.g. beta diversity), are not well documented or understood. The nature of these responses has important implications for our understanding of the community ecology of both natural and agricultural ecosystems (Cavender-Bares et al. 2009, Swenson et al. 2012, Weinstein et al. 2014).

If species richness declines with conversion from forests to rubber plantation, a natural question is whether the new species assemblages are random with respect to species identity, functional traits, and phylogeny. This question sheds light on a broader debate in ecology, the extent to which ecological communities are structured by stochastic factors such as ecological drift (Hubbell 2001), or more deterministic assembly forces (Chase and Leibold 2003). In the former view, species differences (including functional and phylogenetic differences) are not important in determining which species occupy which communities. Although rubber habitats may have reduced functional and phylogenetic diversity due to reduced richness, these reductions should be consistent with random expectations. In this scenario, beta diversity should also mainly follow random expectations, where overlap between spatially separated rubber habitats is consistent with null models.

Under a deterministic scenario, various non-random processes such as competition and species sorting could structure communities (Chase and Leibold 2003). For example, if rubber habitat is acting as an ecological filter, then only a subset of forest species may colonize and survive there. This leads to a decline of beta diversity (within habitat type) along with the decline in alpha diversity, because the same subset of forest species should be found in rubber habitat in even spatially disparate locations. This diversity decline may be associated with a clustered functional structure with reduced functional alpha and beta-diversity if the habitat is filtering a subset of functional traits (Kraft et al. 2007). Phylogenetic diversity may also be reduced if the species able to persist in rubber plantation are clustered on the phylogeny. This could occur if either functional traits have some phylogenetic signal, or because the ecological filter effect is acting on other non-functional traits with phylogenetic signal (Srivastava et al. 2012).

Another deterministic hypothesis involves a strong role of competition in structuring communities (Kunstler et al. 2012). If competition limits the coexistence of similar species, then the remaining communities should be overdispersed in functional and/or phylogenetic space (Lovette and Hochachka 2006). Thus, while species richness may be reduced in rubber plantation, those species are more functionally or phylogenetically disparate than random expectations. It is worth noting that mutualisms, host–pathogen interactions, plant–insect interactions, or other density-dependent processes have also been hypothesized to lead to patterns of clustering and/or overdispersion deviating from null expectations (Cavender-Bares et al. 2009).

Whatever the mechanisms driving community assembly, changes in ant community functional structure in agroecosystems have potentially important consequences. Functional diversity has been defined as "the value and range of those species and organismal traits that influence ecosystem functioning" (Tilman 2001). It links species diversity and ecosystem functioning, and thus could be a tool to predict the functional consequences of agricultural activities (Petchey and Gaston 2006). For example, researchers have found that high agricultural intensification could reduce functional diversity of mammals and birds at a higher rate than the loss of species richness, indicating a disproportionate effect on ecosystem functioning (Flynn et al. 2009). The low level of ant functional redundancy in tropical forest indicates that the species loss in secondary forest may cause more severe declines of ecosystem functioning (Bihn et al. 2010).

More generally, ants have been used as environmental indicator in previous studies where they are a powerful monitoring tool for studying the effects of human-induced habitat change thanks to their abundance, ease of sampling, and sensitivity to environmental disturbance

(Andersen and Majer 2004). Moreover, ants play an important role in ecosystem functioning (Bihn et al. 2010, Ewers et al. 2015), such as biological control (Philpott et al. 2008a), seed dispersal (Levey and Byrne 1993), ecosystem engineering (Hölldobler and Wilson 1990), and nutrient cycling (Del Toro et al. 2012).

The study area near Xishuangbanna, Yunnan, China, is located within the Indo-Burma biodiversity hotspot (Myers et al. 2000), and harbors a large fraction of Chinese biodiversity in its tropical landscape (Yang et al. 2004, Liu et al. 2015). Like many parts of SE Asia, the expansion of rubber plantation is dramatically changing the landscape in this area (Liu and Slik 2014), making it a pressing need to understand implications for biodiversity. Ant community composition in rubber plantation has not been well characterized in the region, with (to our knowledge) only one thorough ant survey has been performed to date (Hosoishi et al. 2013). That study, from an agriculture-dominated landscape in Cambodia, found a much simplified ant community in rubber habitat with a prominent role of exotic species. The Xingshuabanna area provides an interesting contrast as it is composed of a mosaic landscape with natural forest interspersed with dominant rubber plantations and other minor crops (e.g. banana plantations).

I analyzed the effects of conversion of forest to rubber plantation on the alpha, beta, and gamma diversities of ground ant communities, with three overall aims. First, I sought to characterize changes across the taxonomic, functional, and phylogenetic dimensions of biodiversity. Second, I tested the hypothesis that conversion to rubber plantation facilitated the establishment and dominance of exotic species, as has been observed in a previous study (Hosoishi et al. 2013). Third, I tested three hypotheses describing community processes underlying changes in biodiversity in the agroecosystem: 1) *Stochastic assembly*: if ant community structured by stochastic process in rubber plantation, I expected that the loss of functional and phylogenetic diversities are consistent with null expectations at both local (alpha diversity) and landscape scale (gamma diversity). The taxonomic, functional, and phylogenetic beta diversities will also be consistent with null expectation. 2) *Environmental filtering*: If environmental filtering plays an important role of structuring ant community in rubber plantation, I expect that ant communities would be functional and phylogenetically clustered, as would be expected if traits are phylogenetically conserved at both local (alpha diversity) and landscape (gamma diversity) scales. Moreover, ant assemblies in the similar environment such as rubber plantation will lead to low taxonomic, functional, phylogenetic beta diversity. 3) *Biotic structuring*: If biotic processes such as competition mainly primarily shaped ant community structure, communities in rubber plantations would be functionally and phylogenetically overdispersed in local (alpha) and landscape (gamma) scales.

3.2 Methods

3.2.1 Study site

This study was carried out in Xishuangbanna prefecture (21°55′N, 101°15′E) located in Yunnan Province, a tropical region in southern China. In this area, rubber plantation has expanded dramatically during the past 20 years due to the massive expansion of smallholder rubber farms (Figure 3.1), and has become the main driver of local habitat loss and fragmentation (Liu and Slik 2014).

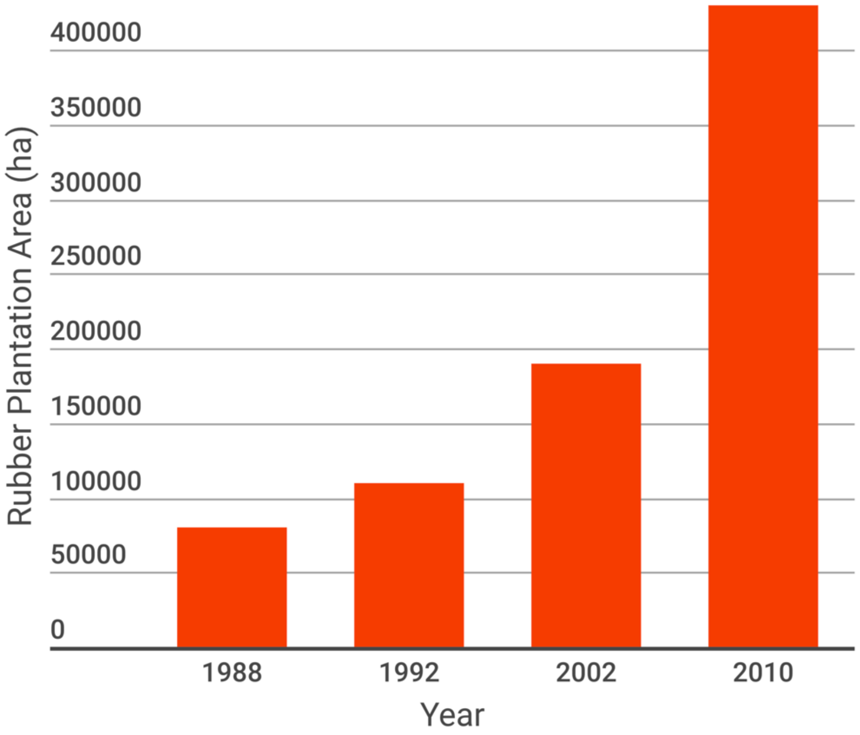

Figure 3.1 | Expansion of rubber plantation from 1988 to 2010 in Xishuangbanna.
Data from Chen et al. 2016.

3.2.2 Sampling of ants

In July 2013, I sampled leaf litter ants from 11 sites in 2 rubber plantation and 24 forest sites from 3 natural reserve (Figure 3.2). The distance between sites varies between 200m-10km. At each sampling site, I established a 20-m-side quadrat (400 m^2) and collected leaf litter samples (from 1 m^2 quadrat) at four corners of the 400 m^2 quadrat. Furthermore, leaf litter within the 400 m^2 quadrat was also collected at 12 sub-sites to cover the variety of available microhabitats available (e.g. base of a large tree, near decaying wood, under on accumulation of leaf litter, near more open leaf litter habitats, etc.) and obtain more accurate data on species composition and richness of each site. Ants were collected and extracted by mini Winkler extractors for 72 hours using the shuffling method as described in Guénard and Lucky (2011) to limit sampling artifacts.

Ant samples were sorted to morphospecies, point-mounted, and identified to species or, if undescribed, assigned a standardized morphospecies code. All mounted and alcohol-preserved ant specimens are currently located in Biodiversity and Biocomplexity Unit at the Okinawa Institute of Science and Technology Graduate University.

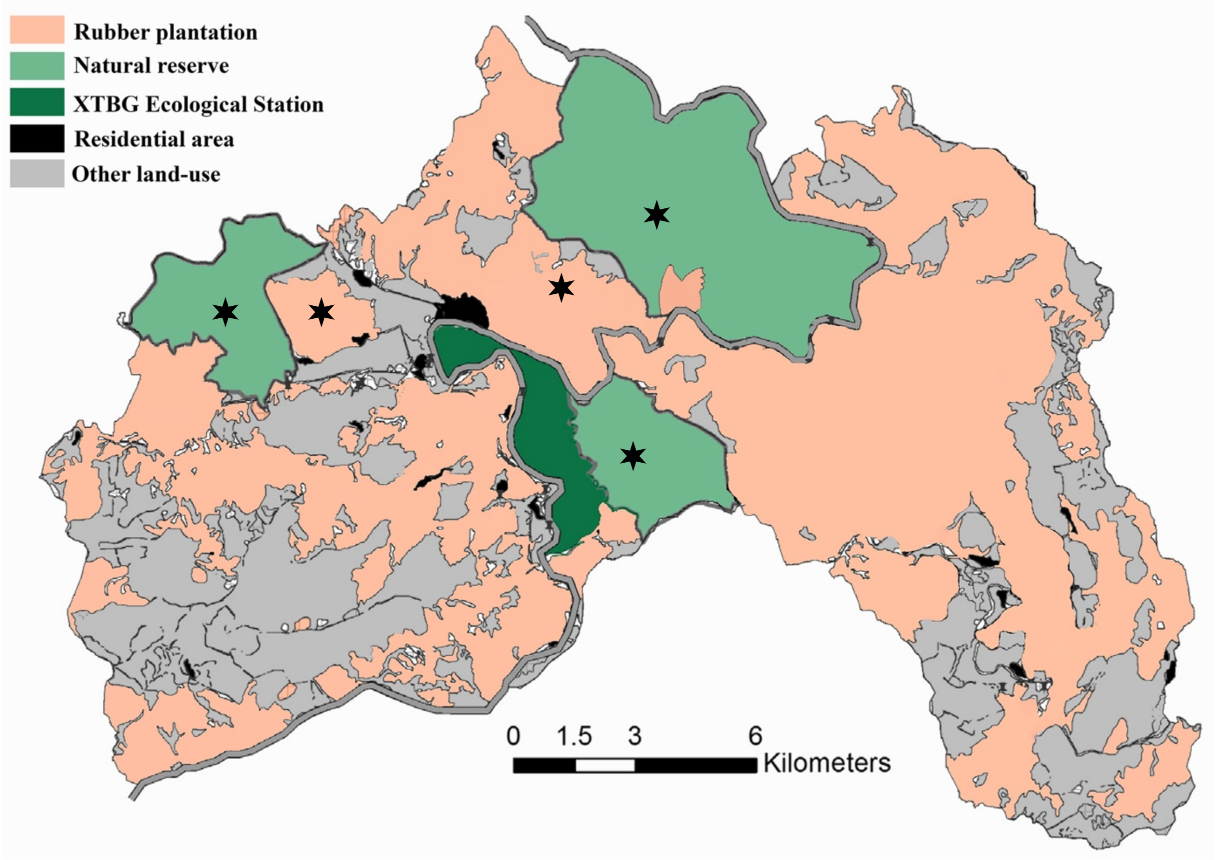

Figure 3.2 | Map of Menglun Town, Xishuangbanna, China.
Leaf litter ants were collected in 11 rubber plantation sites from 2 rubber plantations, and 24 forest sites from 3 natural reserve (✶). Map was modified from Yi et al. (2014).

3.2.3 Functional traits

My aim was to quantify ant functional diversity through morphological traits relevant to resource use and microhabitat preference. Although using traits to characterize the functional roles of species undoubtedly misses some aspects of species' ecologies, direct links have been demonstrated between functional traits and diet, foraging pattern, as well as habitat preference (Gibb et al. 2015). The functional traits measured for each species were as follows.

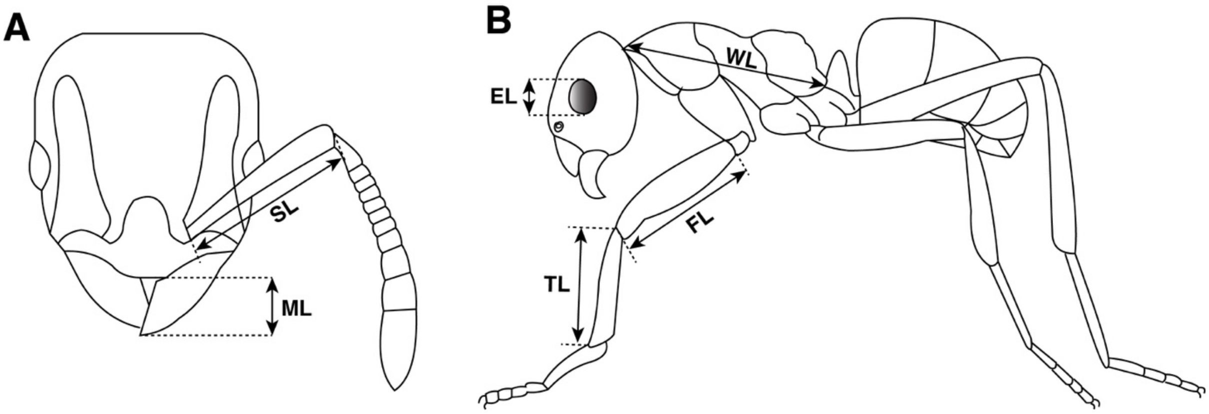

Figure 3.3 | Schematic line drawings illustrating the functional traits measurements. **(A)** Head in full-face view, SL: scape length, ML: mandible length. **(B)** Body in profile view, EL: eye length, WL: Weber's length, FL: femur length, TL: tibial length, leg length = FL+TL.

Weber's length

Measured as the maximum length from the anterior edge of the pronotum to the posterior edge of the propodeum. I measured Weber's length as the indicator of total body size, which related to many ecological life history traits such as resource use (Weiser and Kaspari 2006).

Relative eye length

Eye size is related to ant food searching and navigation (Weiser and Kaspari 2006). Eye size could also be an indication of habitat occupation since ants living underground likely do not need vision as much as ants living above the ground do (Keller 2011). Relative eye length was measured as the ratio of eye length to mesosoma length.

Relative scape length

Scape length might have important effects on receiving chemosensory information (Weiser and Kaspari 2006). Ants with long scape length may be more sensitive to pheromone trails (Weiser and Kaspari 2006). I measured relative scape length as the ratio of scape length to mesosoma length.

Relative mandible length

Ant mandible length might indicate specialization in a predatory role, and thus can have important effects on the type of resources consumed (Weiser and Kaspari 2006). Relative mandible length was measured as the ratio of mandible length (the maximum length from the basal margin to the apical tooth of the mandible) to mesosoma length.

Relative leg length

Longer legs allow faster and more efficient locomotion and foraging (Weiser and Kaspari 2006). Relative leg length was measured as the ratio of leg length (hind femur + hind tibia) to mesosoma length.

For all ant traits measurements, up to 5 randomly selected individuals of each species were measured. Only minor workers were measured if the ant species has distinct major and minor workers. In total, 754 workers representing 186 leaf litter ant species were measured.

3.2.4 Community phylogeny

To construct a community phylogeny, I used posterior sets of ant-wide phylogenies generated during in a separate project (Economo et al. *In Revision*). These trees share many of the features of other ant wide phylogenies (Moreau et al. 2006, Moreau and Bell 2013) but incorporate the latest molecular data generated during subfamily-level phylogenetic work (Brady et al. 2014, Ward et al. 2015) to maximize coverage of genera. The tree sets capture relationships between subfamilies and genera, but structure within trees follow a random branching process to resolve polytomies, similar to other efforts using mammals (Kuhn et al. 2011), producing a set of trees that collectively integrate over phylogenetic uncertainty. The trees were initially constructed to match richness of species in each genus, but then pruned to only include the number of species in each genus I detected in our study. I used 100 of these trees taken from the posterior sets, and over all these trees the phylogenetic distance between two congeneric species reflects the average divergence between species of that genus although the position of species varies within genera among individual trees. While the phylogenetic structure at the genus level and above captures the majority of phylogenetic structure of these communities, our results are limited to signal at these deeper phylogenetic scales due to the lack of resolution of recent phylogenetic structure. For the analyses in this paper, both described and undescribed species were placed randomly into genera, and before analysis the tree was pruned to only include taxa collected in the field surveys. All phylogenetic analyses such as phylogenetic signal, phylogenetic alpha, beta, and gamma diversity calculations were performed on all 100 trees.

3.2.5 Phylogenetic signal

Blomberg's K (Blomberg et al. 2003) and Pagel's λ (Pagel 1999) were used to investigate if there is phylogenetic signal for habitat preference (forest versus rubber plantation), as well as the five morphological traits. Both indices test whether an observed distribution of traits differs from expected with the traits evolving under Brownian model (Pagel 1999, Blomberg et al. 2003, Münkemüller et al. 2012). For both Blomberg's K and Pagel's λ, a value of 1 indicates phylogenetic signal with traits evolved under Brownian model, whereas a value close to 0 indicates no phylogenetic signal. The range of Pagel's λ is from 0 to 1, however, the value of Blomberg's K can be greater than 1, indicating strong phylogenetic signal and traits conservatism.

I calculated K and λ values for each traits and habitats for the 100-tree set. To evaluate the statistical significance of the presence phylogenetic signal, I first compared the observed K values to the K values of null distribution generated by simulating random traits on the phylogeny; second, I estimated the probability of the observed λ differs the null hypothesis of λ equal to 0 (no phylogenetic signal) using likelihood ratio test. Phylogenetic signals (Blomberg' K and Pagel's λ), and their statistical significance were calculated using *phylosig* function in R package *phytools* (Revell 2012).

3.2.6 Estimation of taxonomic diversity

3.2.6.1 Taxonomic alpha and gamma diversity

I used species richness (the number of ant species in each site) as an indicator of taxonomic diversity. Taxonomic gamma diversities in forest and rubber plantation were simply represented by the total number of ant species collected in each habitat. As ants are super organisms and often encountered/sampled in whole colonies, diversity metrics based on individual abundances can be problematic (Gotelli et al. 2011).

3.2.6.2 Taxonomic beta diversity

The Raup-Crick dissimilarity metric (β_{rc}) was used to calculate taxonomic beta diversity of ant communities within forest and rubber plantations. β_{rc} is a null model based metric that is alpha-diversity independent (Chase et al. 2011). β_{rc} ranges from -1 to 1, indicating that the observed dissimilarity of two communities is lower than (reaching -1), higher than (reaching 1), or as similar (reaching 0) as expected by chance. Thus, the mean value of β_{rc} among all sites in one habitat that is close to 0 indicates a stochastic assembly, while a mean value higher or lower than 0 suggests deterministic community assembly (see also Püttker et al. 2015 for further details).

I compared the mean β_{rc} based on ant presence-absence data among sites within forest and rubber plantation habitats to investigate the main driver of species coexistence in rubber plantations. Since the delineation of the species pool is very important for calculating the Raup-Crick metric (Chase et al. 2011), I identified the species pool as all ant species I collected in this study since they are potentially able to colonize the sampling sites. I calculated β_{rc} using the R script provided by Chase (2011). To visualize taxonomic beta diversity, I performed a two-dimensional nonparametric multidimensional scaling (NMDS) based on the value of β_{rc} between sites using R package *Vegan* (Oksanen et al. 2015).

In order to test whether the average β_{rc} is significantly different from random expectation, I compared the observed β_{rc} in forest, rubber and rubber versus forest (rubber X forest) to the β_{rc} of 1000 randomized ant communities of the same species richness for each sites using Wilcoxon Mann Whitney test in R 3.0.2 (R Development Core Team 2008). Randomized communities were generated by randomizing the community data matrix using “Independent Swap” approach following the R code described in Swenson (2014).

3.2.7 Estimation of functional and phylogenetic diversity

The following analyses of functional and phylogenetic alpha, beta, and gamma diversity (FD, PD, MPD, MNTD, D_{pw} and D_{nn}) were calculated following Swenson (2014) by using R package *Picante* (Kembel et al. 2010).

3.2.7.1 Functional and phylogenetic alpha diversity

Functional alpha diversity of ant communities in each sampling site was calculated using Petchey & Gaston's FD (Petchey and Gaston 2006). In order to calculate FD, the z-standardized trait values were converted into a Euclidean distance matrix, and then were clustered to produce a trait dendrogram representing the functional relationship among ant species using UPGMA method (see Mouchet et al. 2008 for further details on the distance and clustering algorithms). I chose the combination of Euclidean distance and UPGMA clustering because they gave the highest cophenetic correlation coefficient between the original distances and the distances estimated form the resulting dendrogram (0.87). The Euclidean distance matrix generation and UPGMA clustering were conducted by R functions *dist* and *hclust*, respectively. For each site, I summed the branch lengths of the dendrogram corresponding to species present to calculate FD.

Phylogenetic alpha diversity was calculated using Faith's phylogenetic diversity (PD) (Faith 1992), mean pairwise distance and mean nearest taxon distance (MPD and MNTD; Webb et al. 2002).

Standardized effect sizes (SES) of functional alpha diversity (SES_{FD}) and phylogenetic alpha diversity (SES_{PD}, SES_{MPD}, and SES_{MNTD}) were calculated using the SES formula as below in order to detect the differences between observed values versus communities generated by null models. The standardized effect sizes of MPD (SES_{MPD}) and MNTD (SES_{MNTD}) are equivalent to net relatedness index (NRI), and the nearest taxon index (NTI). I multiplied NRI and NTI by -1, and therefore, negative value indicates phylogenetic clustering, and positive value represents phylogenetic overdispersion.

$$SES = (Mean_{obs} - Mean_{null}) / s.d._{null} \tag{1}$$

Null model communities for analyzing functional and phylogenetic alpha diversities were generated by randomizing the community data matrix using "Independent Swap" approach for 1000 times following the R code in Swenson (2014).

3.2.7.2 Functional and phylogenetic beta diversity

Both functional and phylogenetic beta diversity was calculated using two distance-based measurement metrics, the present-absent weight pairwise distance metric (D_{pw}), and the present-absent weight nearest neighbor distance metric (D_{nn}) (Swenson 2011a). D_{pw} generally reflect the overall dissimilarity between communities, while D_{nn} is likely better for qualifying the patterns among close related species between different communities (Swenson 2011a). Standardized effect sizes of functional and phylogenetic beta diversities (Functional SES_{Dpw} and SES_{Dnn}; Phylogenetic SES_{Dpw} and SES_{Dnn}) were also calculated using SES formula mentioned before. Null model communities for analyzing functional and phylogenetic beta diversities were generated by randomly shuffling the names of taxa cross the traits matrix or the tips of phylogenetic tree for 1000 times following the R code in Swenson (2014). Two-dimensional nonparametric multidimensional scaling (NMDS) was also used to visualize the standardized effect sizes of functional and phylogenetic beta diversities.

3.2.7.3 Functional and phylogenetic gamma diversity

Functional gamma diversity was calculated as the Petchey & Gaston's FD of all the species inhabited in each habitat. For phylogenetic gamma diversity, I calculated the Faith's PD of all the species collected in each habitat for 100 trees. I then compared the observed functional and phylogenetic gamma diversities in both habitats to the functional and phylogenetic gamma diversities of 1000 randomized ant communities of same species richness (forest: *n=163*; rubber plantation *n=83*).

3.2.7.4 Statistical significance tests

Wilcoxon Mann Whitney test was used to investigate the statistical significance of the average functional and phylogenetic alpha diversity compare to null model. I used Welch two sample t-test to investigate whether the observed functional and phylogenetic beta diversity, as well as phylogenetic gamma diversity in each habitat is significantly different from the null expectation. All calculations and analyses were conducted in R 3.0.2.

3.3 Results

I collected 186 ant species from 52 genera with our field sampling. Among them, 163 species from 48 genera were found in forest and 83 species from 38 genera were found in rubber plantation. According to the classification provided in Guénard and Dunn (2012), six potentially exotic species were found in our collection. Among them, *Anoplolepis gracilipes* Smith and *Strumigenys membranifera* (Emery), and *Tetramorium tonganum* Mayr were only found in one site of rubber plantation. *Tapinoma melanocephalum* Fabricius, *Technomyrmex albipes* Smith, and *Monomorium pharaonis* Linnaeus were found in both natural forest and rubber plantation, however, their occurrences were very low compared to other native ant species. All the results presented below are based on using all captured 186 species as a regional species pool.

3.3.1 Taxonomic diversity

Leaf litter ant species richness declined dramatically in rubber plantation with an average of 32 species (31.7±0.98) found in forest habitat sites and only 23 (23.1±0.87) species found in rubber plantation habitat (Figure 3.4).

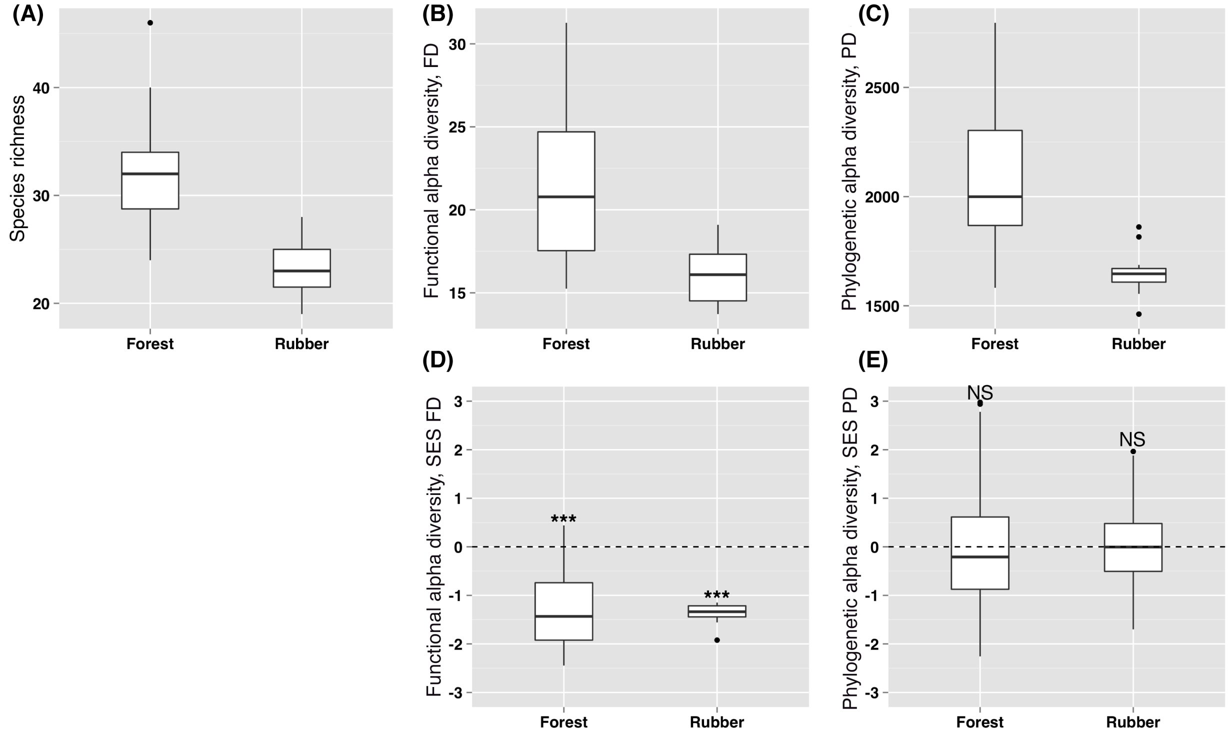

Figure 3.4 I Ant alpha diversities in forest and rubber plantation.
(A). Ant species richness, **(B).** observed functional diversity (Petchey & Gaston's FD), and **(C).** observed phylogenetic diversity (Faith's PD) declined in rubber plantation. After correcting for species richness, functional diversity declined more than a null expectation based on randomly assembled communities in both habitats (**D**, scaled by SES FD), while phylogenetic diversity in both habitats was consistent with null expectation (**E**, scaled by SES PD). Asterisks indicate statistical significance (**: p<0.001, NS: not significant; Mann-Whitney test between observed distribution and null distribution of FD and PD). The box encloses the 25-75th percentiles of the values, the whisker extends to 1.5 times the interquartile range.

Mean beta diversity (β_{rc}) between sites in rubber plantations was lower than in forest habitats (-0.78 vs. -0.31), and β_{RC} across the two habitats was higher than within each habitat (Figure 3.5A). Despite the variation observed between pairs of sites, mean β_{rc} between sites in rubber plantation was more similar than expected by chance ($p<0.001$, Mann-Whitney test; Figure 3.5A). However, the mean β_{rc} in forest and the mean β_{rc} across the two habitats were not significantly different from null expectation ($p=0.94$, and $p=0.16$ respectively, Mann-Whitney test; Figure 3.5A). There is a clear separation between forest and rubber plantation in the NMDS plot (Figure 3.5D). These results indicate that ant communities in rubber plantations were composed of a non-random subset of forest species, and as a result rubber ant communities were more similar to each other than expected by chance.

3.3.2 Functional diversity

With the decline in species richness, there was a sharp decline of functional diversity as well (Figure 3.4B). Moreover, FD declined more than a null expectation based on randomly assembled communities with the same reduced species richness ($p<0.001$ in both habitats, Mann-Whitney test; Figure 3.4D). In the aggregate, the species in rubber plantation showed significantly lower functional gamma diversity compared to randomly generated communities, however, ant species in forest exhibited a functional gamma diversity comparable to null model (Figure 3.6B, C). Those results indicate that the ant functional traits are clustered at a local and landscape scales in rubber plantations, with functional unique species being lost relative to forest habitats.

Functional beta diversity (the pairwise metric, Functional D_{pw}) was lower than the null expectation in both rubber and forest habitat (with both $p<0.001$, Welch two sample t-test; Figure

3.4B), while beta diversity across the two habitats was higher than within each habitat and more consistent with null expectations (*p*=0.732, Welch two sample t-test). A clear separation between ant community in forest and rubber plantation in the NMDS plot was also found (Figure 3.5E). I found similar pattern of functional beta diversity by using the nearest-neighbor metric (Functional D_{nn}, Figure 3.7).

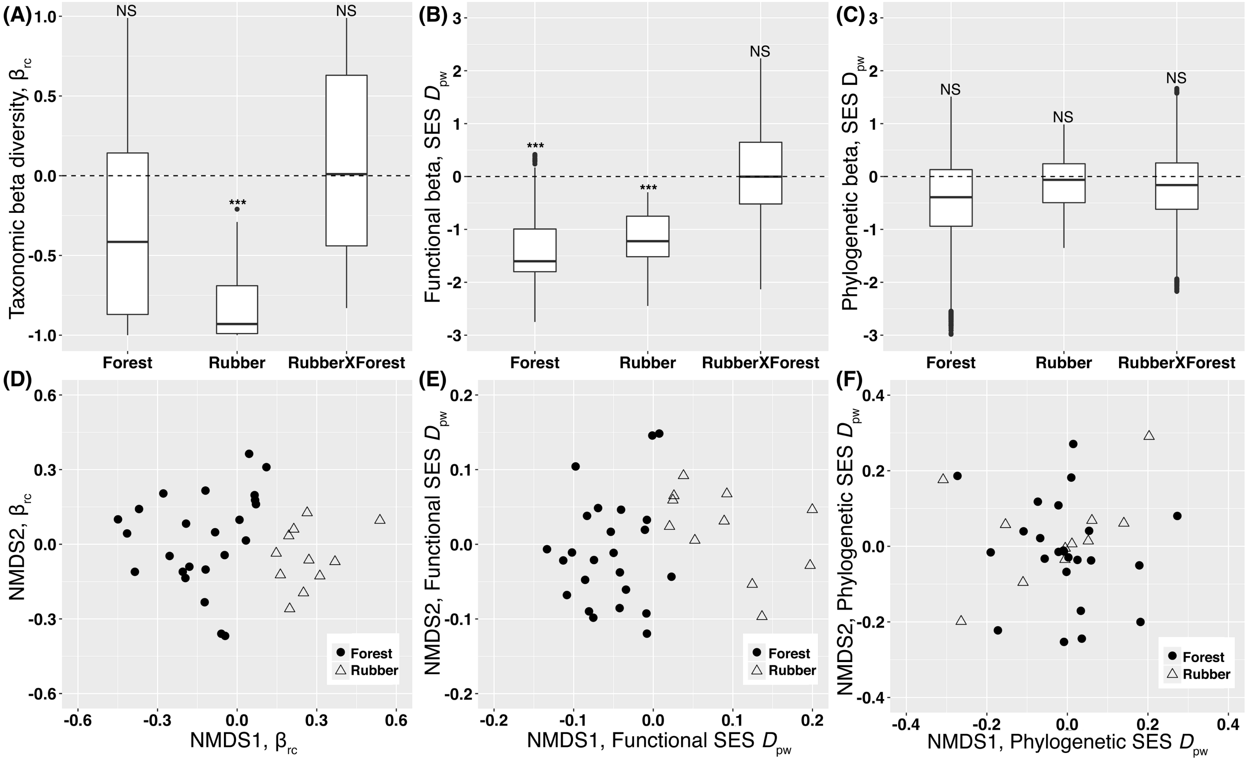

Figure 3.5 I Ant beta diversities between pairs of local communities in forest and rubber plantation.

(A) Taxonomic beta-diversity (β_{rc}); **(B)** functional beta diversity (represented by SES D_{pw}); **(C)** phylogenetic beta diversity (represented by SES D_{pw}).

(D, E, F) Non-metric multidimensional scaling (NMDS) ordination of sites within forest and rubber plantation based on different beta diversity indices (β_{rc}, Functional SES D_{pw}, and Phylogenetic SES D_{pw}, respectively). For β_{RC}, we compared the β_{rc} of each habitat to the β_{rc} of 1000 randomized communities with the same species richness (**: $p<0.001$, Mann-Whitney test). For functional and phylogenetic beta diversity, we compared respective observed D_{pw} to the D_{pw} of null expectations (**: $p<0.001$, NS: not significant; Welch two sample t-test). The boxes enclose the 25-75th percentiles of the values, the whiskers extends to 1.5 times the interquartile range.

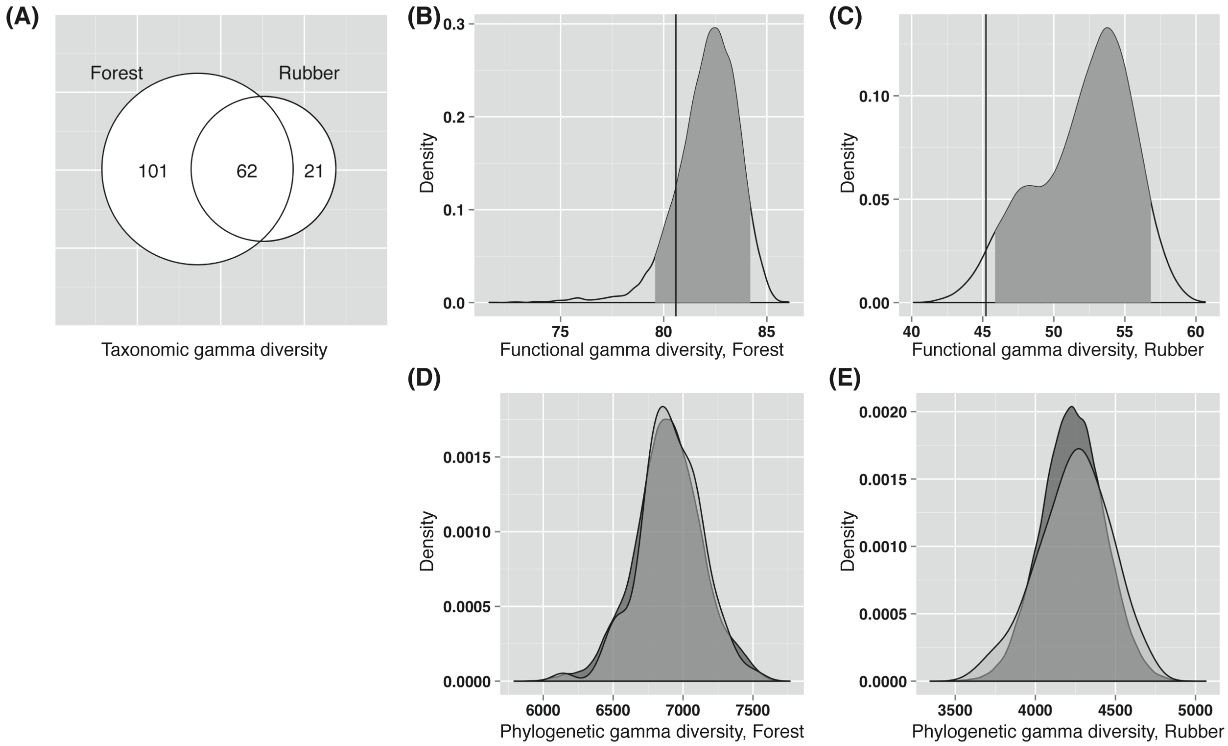

Figure 3.6 | Ant gamma diversities in different habitats.
(A) Taxonomic gamma diversity in forest and rubber plantation. Venn diagram shows that the number of species collected from each habitat, as well as the number of species shared in both habitats. For functional gamma diversity **(B and C)**, vertical back lines are observed functional diversity, and distributions are the density of functional diversity derived from null model (n=10000) of the same species richness as observed communities. Shaded regions indicate 95% of the null distributions. For Phylogenetic gamma diversity **(D and E)**, distributions with light grey shade are the density of observed phylogenetic gamma diversity of 100 trees. The distributions with dark grey shade are the density of phylogenetic diversity derived from null model (n=1000 for each of 100 tree) of the same species richness as observed communities. No significantly differences were found between observed and null expected phylogenetic gamma diversity (*p*=0.48, *p*=0.67 for forest and rubber plantation, respectively, Welch two sample t-test).

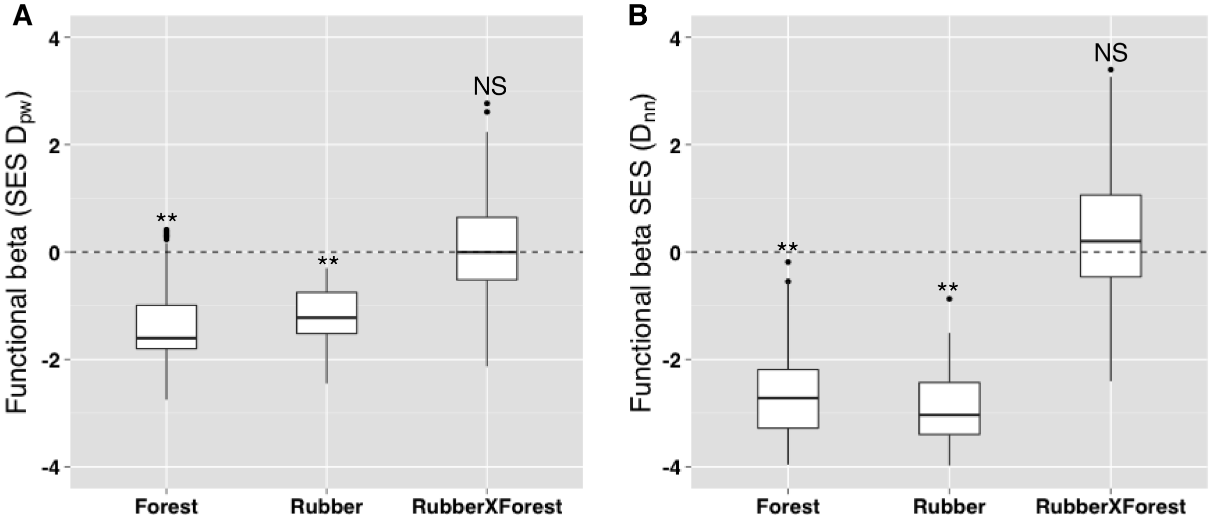

Figure 3.7 | Functional beta diversity using two metrics shows similar patterns.
(**A)** D_{pw} and **(B)** D_{nn} (represented by SES D_{pw}, and SES D_{nn}) in forest and rubber plantation. Functional beta diversity in both forest and rubber plantation are significantly lower than null expectation. The functional beta diversity between ant communities across forest and rubber plantation was consistent with null expectation. (**: $p<0.001$; NS: not significant, Weltch two sample t-test between observed functional beta distribution and null functional beta distribution). The box encloses the 25-75th percentiles of the values, the whisker extends to 1.5 times the interquartile range.

3.3.3 Phylogenetic diversity

To the extent that functional traits reflect evolutionary history, phylogenetic patterns may reflect patterns of functional diversity. I made a "co-phylogeny" plot between phylogeny and the functional dendrogram of 184 ant species in this study to show the relationship between phylogenetic and functional patterns (Figure 3.8).

I measured the phylogenetic signal for habitat preference and the five functional traits I used by using of Blomberg' K and Pagel's λ. In general, results of both indices were consistent with each other, except only one case (forest; Figure 3.9). All the functional traits exhibited phylogenetic signal using either Blomberg' K or Pagel's λ (Figure 3.9), indicating that the functional traits used in this study were conserved phylogenetically. For the habitat preference, ant community in forest exhibited significant nonrandom phylogenetic pattern, when calculated with Pagel's λ, but not with Blomberg' K (Figure 3.9); ant community in rubber plantation showed no phylogenetic signal with both indices (Figure 3.9).

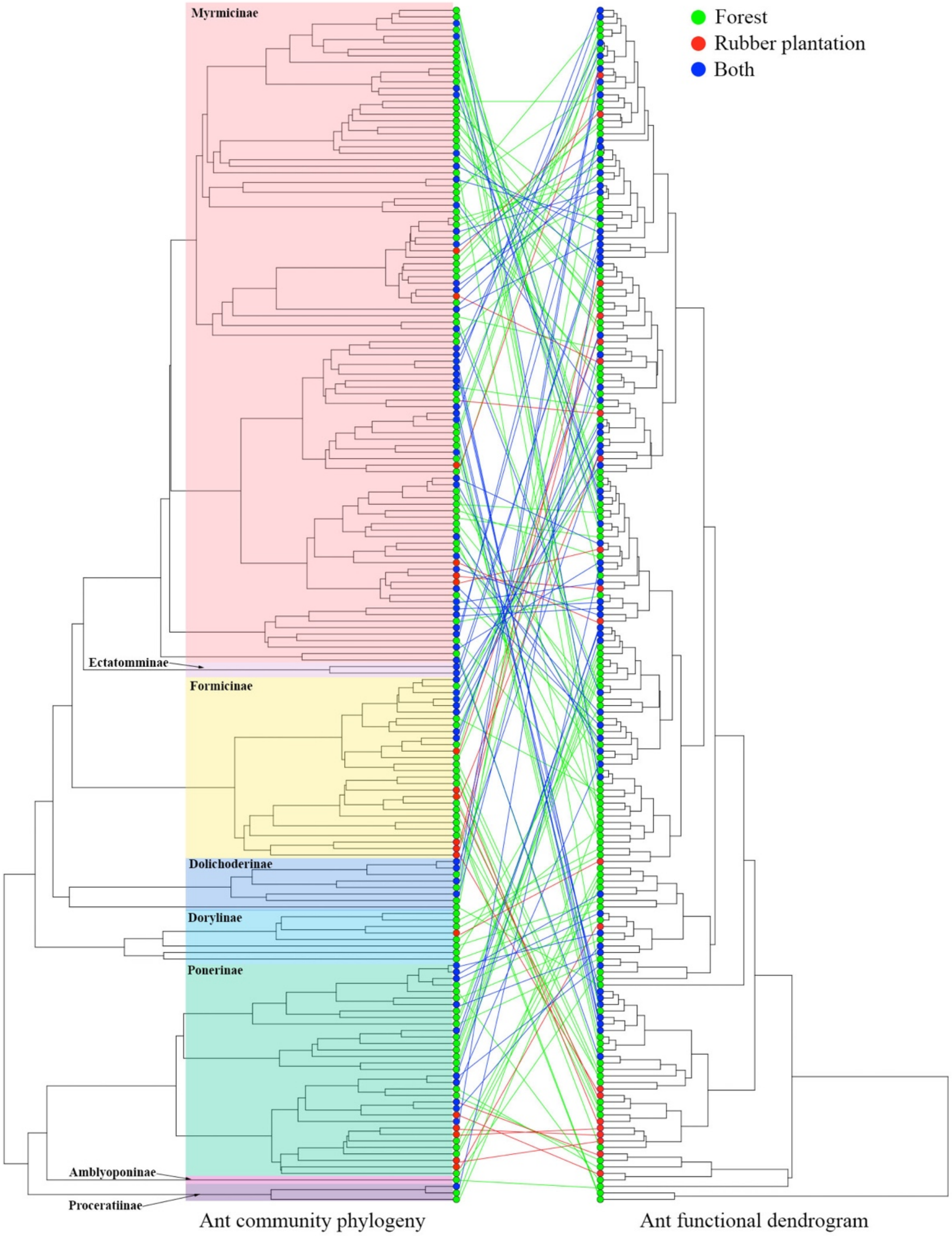

Figure 3.8 | The phylogeny (left) and functional dendrogram (right) of 184 ant species in this study.
Color of circle indicates the habitat inhabited by that species. The lines link the same species between phylogeny and functional dendrogram.

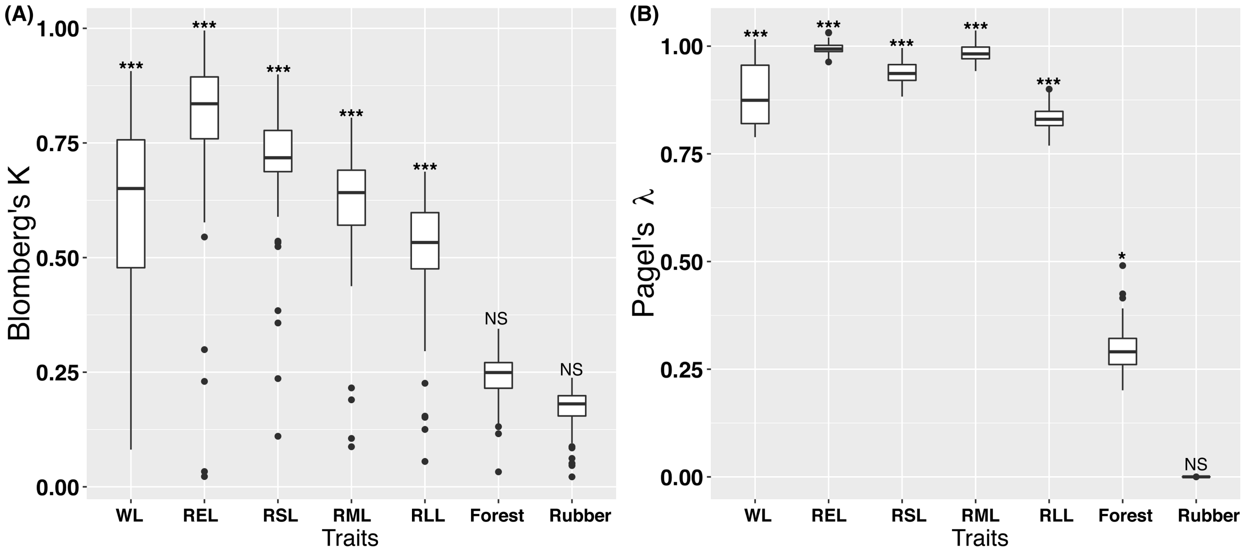

Figure 3.9 | Phylogenetic signal for functional traits and habitats.
Phylogenetic signal was calculated using **(A)** Blomberg's K statistics (Blomberg et al. 2003), and **(B)** Pagel's λ (Pagel 1999). A value of K/ λ close to 1 indicates phylogenetic signal under Brownian motion, while a value of K/ λ close to 0 indicates no phylogenetic signal. The box encloses the 25-75th percentiles of the values, the whisker extends to 1.5 times the interquartile range. **WL**: Weber's length; **REL**: relative eye length; **RSL**: relative scape length; **RML**: relative mandible length; **RLL**: relative leg length. Stars indicate statistical significance (**: p<0.001, *: $p<0.05$).

There was also a sharp decline in phylogenetic diversity as a result of the decline in species richness (Figure 3.4C), however this decline was consistent with the null expectation for random assembled communities (p=0.30, p=0.32 for forest and rubber plantation, Mann-Whitney test; Figure 3.4E). The phylogenetic diversity of local forest and rubber habitats was also not significantly different from random expectations, which suggests that ants coexisting in the same habitat are phylogenetically random.

Pairwise phylogenetic beta matrix (phylogenetic D_{pw}) showed no differences between observed phylogenetic turnover and the phylogenetic turnover of random ant assemblies generated by the null model (p= 0.13, and p=0.35 for forest and rubber plantation, Welch two sample t-test; Figure 3.5C), and there was no clear separation in NMDS plot (Figure 3.5F). Similar phylogenetic beta diversity pattern was also found when using nearest neighbor phylogenetic beta matrix (phylogenetic D_{nn}, Figure 3.10). There also were no differences between observed and null expected phylogenetic gamma diversity in both habitats (p=0.48, p=0.67 for forest and rubber plantation, respectively, Welch two sample t-test; Figure 3.6D, E).

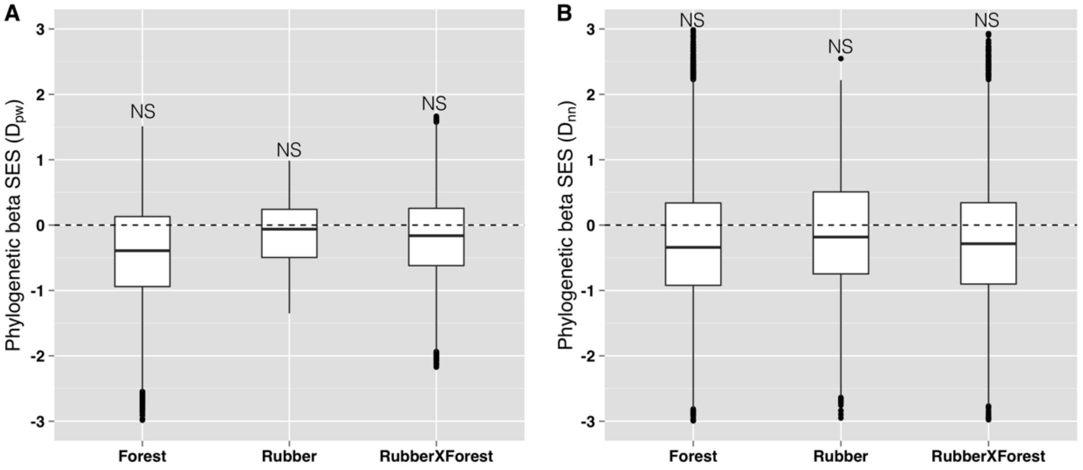

Figure 3.10 | Phylogenetic beta diversity between sites within forest and rubber plantation. D_{pw} (A) and D_{nn} (B) showed the similar pattern. No differences were found between phylogenetic beta diversity and the null expectation in both habitats. The box encloses the 25-75th percentiles of the values, the whisker extends to 1.5 times the interquartile range.

3.4 Discussion

Our results highlight changes to biodiversity within and across ecological communities associated with conversion from diverse tropical forest habitat to rubber monoculture, a rapidly emerging agroecosystem in Southeast Asia. I found a striking decline of ant species richness in rubber plantations as compared with nearby forest habitats. This pattern echoes previous findings showing habitat conversion from primary or secondary forests to monoculture plantations in many groups of organisms (Philpott et al. 2008b), including ants (Fayle et al. 2010).

This decline of alpha diversity was not random with respect to species identity; taxonomic beta diversity in rubber plantations was overall lower than would be expected if local communities were assembled by chance from the source pool. Moreover, taxonomic beta diversity was highest across forest x rubber community pairs than within either habitat, indicating a divergence in community structure. This was also confirmed by the NMDS analysis, which showed separation between ant communities sampled in forest and rubber habitats based on differences in species composition. These results support the hypothesis of environmental filtering, where the decrease of alpha diversity is due to the selective establishment of certain species that are tolerant of rubber habitat. Our results support the idea that anthropogenic disturbance such as agriculture activities, and forest clearing increases the importance of deterministic, niche-based processes, leading to biotic homogenization (Vellend et al. 2007, Banks-Leite et al. 2012, Karp et al. 2012, Püttker et al. 2015).

In absolute terms, functional diversity was much reduced in rubber plantations compared with forest communities. This overall reduction pattern would be expected simply due to the decline of species richness (Flynn et al. 2009), but we found rubber habitats to be less functionally diverse than would be expected by chance indicating functional clustering in local communities. This pattern was also found on the landscape level; functional gamma diversity of ants in rubber plantation habitat, but not forest habitat, was lower than null expectations based on the entire pool of species. The lower-than expected functional beta diversity in rubber habitat showed that not only were local communities functionally simplified, but a similar functional structure was repeated in local communities across the landscape. Finally, there was an overall divergence in functional structure of ant communities among forest and rubber habitats that was not only explained by species richness differences. This indicated the emergence of a functionally distinct community in rubber plantation. In total, these results support a more deterministic, niche-based species assembly process (environmental filtering) in rubber plantation with respect to functional traits.

Interestingly, our results showed that functional traits of ant communities are also clustered in forest with lower than expected functional alpha and beta diversities. While taxonomic beta diversity in forest is significantly higher than in rubber plantation, no differences were detected in functional beta diversity within the different forest and rubber plantation habitat types (after accounting for differences in species richness). These results indicate that analysis of taxonomic beta diversity alone may miss important aspects of community patterns. Indeed, it is possible to have two communities with very high species turnover but very low functional turnover (Swenson 2011a, b).

All the functional traits measured in Xishuangbanna ant communities exhibited phylogenetic signal, indicating that more close related species share similar functional traits. These results are consistent with other studies, which found significant phylogenetic signal on ant body size (Machac et al. 2011, Donoso 2014). However, a recent study focused on Malagasy ants showed a lack of phylogenetic signal on most morphological traits (Blaimer et al. 2015). Overall, there is less phylogenetic signal in habitat preferences, however, Pagel's λ detected slightly significant phylogenetic signal in forest habitats. This inconsistency between Blomberg' K and Pagel's λ may due to the fact that Pagel's λ is a more sensitive measure of phylogenetic signal compared to Blomberg' K (Münkemüller et al. 2012).

The results from measures of phylogenetic diversity were generally consistent with random community assembly with respect to phylogenetic structure. Ant communities in both forest and rubber plantation exhibited phylogenetic diversity consistent with null expectations.

In addition I did not find any differences between observed and expected phylogenetic beta diversity of ant communities from either natural forest or rubber habitats, indicating a random pattern of phylogenetic turnover that mirrors the null expectation.

Although a correlation was found between functional traits and phylogeny (e.g. significant phylogenetic signal), I did not find significant patterns of phylogenetic diversity in this study as we did in functional diversity. One possible explanation may be that the functional traits are not strongly conserved in our study (the K values for all traits were below 1). Swenson (2011a) reported that the strong correlation between functional and phylogenetic beta diversity was only found when K is greater than two. Kraft et al. (2007) also showed that phylogenetic local dispersion could mirror functional local dispersion when traits are very strong conserved in the regional pool.

In summary, I found evidence for environmental filtering in taxonomic and functional dimensions of ant biodiversity, but random assembly in the phylogenetic dimension. The different patterns in functional and phylogenetic diversity in this study, even in the presence of phylogenetic signal, may indicate that using phylogenetic dispersion as a proxy for trait dispersion and the underlying assembly processes could be misleading (Gerhold et al. 2015). Indeed, the aspects of phenotypes captured by functional and phylogenetic analyses are not equally relevant to community assembly. For example, the forest or rubber habitats may be amenable to certain combinations of functional traits as measured by our morphological variables, leading to functional clustering. At the same time, other phylogenetically-correlated aspects of individual and colony-level phenotypes may lead to more intense competition between closely related species, leading to different patterns of phylogenetic diversity.

Interestingly, in contrast to previous findings from a rubber plantation in Cambodia (Hosoishi et al. 2013), I found a very limited presence of exotic and invasive ant species in rubber habitat at our site in China. Only a few exotic species were collected and with low occurrences, and most were also present in the forest habitat. One potential explanation for the discrepancy between our results and those of Hosoichi and collaborators (2013) lies in the differences in the scale of the rubber plantation studied in these studies; with the rubber plantation in Cambodia being large, contiguous industrial operation with limited nearby forest habitat, whereas at our study sites rubber plantations are interspersed with tracts and fragments of natural forest in a mixed landscape. Indeed, while richness is reduced in rubber habitats relative to native forest at our sites, it is possible that the presence of nearby native forest maintains a higher diversity of species in the rubber plantation than would otherwise not be able to persist in larger rubber monoculture. The presence of a more diverse native community could also explain the reduced impact of exotic species. Of course, the above reasons for differences across the two studies remain speculative as replicated studies on the effects of landscape structure on agroecosystem communities are necessary to rigorously address this question, but would represent an interesting direction for future work.

From a conservation perspective, our results echo previous findings demonstrating that conversion from natural forest to rubber plantation is a pressing concern for biodiversity conservation in Southeast Asia (Ziegler et al. 2009, Warren-Thomas et al. 2015). This is especially true due to the increasing demand of natural rubber worldwide driving the conversion from natural forest to rubber plantation (Warren-Thomas et al. 2015). It is likely that both a loss of species richness, and the functional simplification of ant communities could have downstream effects on ecosystem processes and the populations of other insect groups. Studies have already suggested some solutions that could potentially minimize biodiversity and ecosystem function loss in rubber plantation, such as mixed-species agroecosystems including native and crop species in order to increase the microhabitat heterogeneity (Phommexay et al. 2011). Such approaches have proven to be beneficial in other agroecosystems such as coffee plantations (Perfecto et al. 2005).

4. Mountain metacommunities: climate and spatial connectivity shape ant diversity in a complex landscape

4.1 Introduction

Untangling the ecological and evolutionary processes that regulate spatial biodiversity patterns is a central goal of basic and applied biology (Ricklefs 1987, Rosenzweig 1995, Holyoak et al. 2005). Both theory and empirical studies have shown that environmental gradients and spatial processes are important factors underpinning species distributions and community composition (Hubbell 2001; Chase and Ryberg 2004, Leibold et al. 2010, Vellend 2010; Chase and Myers 2011; HilleRisLambers et al. 2012). It is well-established that environmental tolerances can limit which species from a regional source pool are able to co-occur in a given locality (Leibold 1998, Van der Gucht et al. 2007, Allen et al. 2011, Kraft et al. 2015). Likewise, spatial patterns of habitat connectivity can either promote or inhibit the movement of species among environmentally similar habitat patches, with potential effects on alpha and beta diversity (Forbes and Chase 2002; Chase and Ryberg 2004). The relative contribution of environmental factors and spatial factors in shaping species richness as well as community structure patterns have been evaluated in different systems (Cottenie 2005, Beisner et al. 2006, Mykrä et al. 2007). However, the ways in which environmental factors interact with spatial factors to shape biodiversity patterns remains a controversial issue in ecology, and the results might shed light on the balance of underlying deterministic versus stochastic processes. This balance, in turn, may determine the relative importance of different metacommunity processes, such as species sorting, mass effects, and neutral dynamics (Leibold et al. 2004).

In many landscapes, environmental factors and spatial factors are intertwined as complex environmental gradients can result in complex spatial structure, both of which likely influence local diversity and patterns of metacommunity composition. For example, strong environmental gradients not only filter species locally, but might also act on spatial structure facilitating or limiting the dispersal of species among local communities, and therefore leading to a more complex metacommunity structure. Mountainous landscapes are a perfect example of this: species are usually limited to certain elevational ranges (Rahbek 1995), due to their ecophysiological tolerances, rather than existing at all elevations, and therefore their movement is limited to complicated networks of environmentally similar and variably connected habitat. This imposes a complex spatial structure to the metacommunity at each elevation, and that spatial structure (e.g. area, connectivity) itself may vary with elevation and impact diversity patterns.

The majority of studies examining biodiversity patterns along elevational gradients have focused on the effects of environmental covariates with elevation (e.g. temperature, precipitation, or environmentally driven biotic variables such as productivity), which have consistently been shown to have an effect on both physiological tolerances (Bishop et al. 2016) and community composition (Rahbek 1995, Graham et al. 2009, Sanders and Rahbek 2012). The effects of spatial structure such as elevation-area correlations and geometric constraints have received some attention, mainly through the decline of area with increasing elevation and the species-area relationship as well as the mid-domain effect caused by overlapping ranges in a bounded domain (e.g. Sanders 2002). However, less attention has been paid toward elevational gradients in connectivity.

Recently, theory has been developed that synthesizes how aspects of landscape geomorphology, namely elevational gradients in the area and connectivity of environmentally similar habitat, may drive biodiversity patterns (Bertuzzo et al. 2016, henceforth "BEA"). The premise of this work is that mountains are not "cones", but exist in a complicated "fluvial" landscapes shaped by geohydrology, the statistical properties of which are well understood. This theory made two predictions: first, habitat area actually peaks at mid-elevations in fluvial landscapes rather than the lowest elevations. Second, sites from mid-elevations are considered to be more interconnected than low and high elevation sites (e.g. valleys and mountain tops) because of the higher connectivity among the mid-elevational sites within the fluvial landscape. As a consequence of these two predictions, species richness (alpha diversity) should be highest at mid-elevations, showing a hump-shaped pattern (Bertuzzo et al. 2016), because alpha diversity should be promoted both by increased area and connectivity (e.g. Economo and Keitt 2010). In addition, although it was not explicitly considered by BEA, one can also infer that beta-diversity within elevational bands should show a mid-elevation minimum, because beta-diversity is sensitive to spatial connectivity and dispersal limitation among environmentally similar habitats. This occurs because dispersal has a homogenizing effect on communities, and in the absence of dispersal the dynamics of local communities can lead to divergence in community structure. This is true in models where dynamics are governed by stochastic processes such as ecological drift (e.g. Hubbell 2001, Economo and Keitt 2008) and those governed by deterministic dynamics such as predator-prey, host-parasite, competition, or consumer-resource dynamics (e.g. Mouquet and Loreau 2003, Cadotte and Fukami 2005, Cadotte et al. 2006). However, other potentially relevant factors were not included by the BEA model, for example evolutionary history could limit the lineages available to colonize different elevational ranges, meaning that species arrival rate could be different across elevations. These intriguing theoretical advances have not yet been addressed empirically.

In this study I examine the drivers of species diversity patterns in complex mountainous landscapes, and particularly in context of the new theoretical developments, using a case study of ant communities in the Hengduan mountains, China. Ant biodiversity along elevational gradients have been explored by numerous studies, with two major patterns reported: hump-shaped patterns with a mid-elevation species richness peak (Sanders 2002, Sanders et al. 2003, Bishop et al. 2014, Colwell et al. 2016), or monotonically decreasing species richness with elevation (Robertson 2002, Sanders et al. 2007, Machac et al. 2011, Kwon et al. 2014). Different factors have been suggested as important drivers of ant diversity patterns across elevation by various studies, such as temperature (Sanders et al. 2007, Machac et al. 2011, Kwon et al. 2014), area (Sanders 2002), and geometric constraints (Sanders 2002, Colwell et al. 2016). However, the underlying causes of ant elevational diversity gradients is complicated in that multiple factors could interact with other processes such as landscape geomorphology, and therefore more comprehensive studies on the interactions of those factors are needed (Szewczyk and McCain 2016)

The Hengduan Mountains region, which forms the southeastern section of the Qinghai-Tibet Plateu, is located within the South-Central China biodiversity hotspot (Myers et al. 2000). The region is characterized by its steep topographic gradients resulting from a series of mountain ranges and deep gorges oriented from north to south. A number of factors including landscape geomorphology, microhabitat differentiation, and geographic isolation are thought to make this region one of the most diverse temperate regions in the northern hemisphere (Wu and Wang

1983). Due to high levels of diversity and endemism, this region has drawn significant research interest over the years (Fu et al. 2006, Wu et al. 2013a, Wu et al. 2013b, Wen et al. 2016).

I evaluated the effects of environmental gradients and spatial factors on ant community patterns in this complex mountainous landscape. Toward this end, I investigated ant taxonomic and phylogenetic diversity patterns by surveying ants along a transect spanning a 5000m elevational gradient, and performed a multifaceted analysis of drivers of alpha and beta diversity using a combination of variance partitioning, beta diversity partitioning, and null modeling. First, I examined whether species richness declines monotonically or exhibits a hump-shaped relationship with elevation. Second, I tested whether beta diversity (and its nestedness and turnover components) is driven more by environmental gradients or spatial factors overall, and secondarily whether spatial connectivity metrics predict beta diversity better than geographic distance alone within similar elevations. Third, I compared the patterns I observed to the predictions of the BEA model (i.e. mid-elevation maximum in alpha diversity and minimum in beta diversity) and investigated whether the assumptions of the model (i.e. mid-elevation peak in area and connectivity) derived from idealized fluvial landscapes apply to this real-world system.

4.2 Methods

4.2.1 Study area and ant community data

This study was carried out within Hengduan Mountains region (range from 24°40′N to 34°00′N and 96°20′E to 104°30′E, Figure 4.1). Our ant community data are based on comprehensive surveys in the Hengduan Mountains region carried out from 2009 to 2011, including three expeditions to Sejila Mountain, Demula Mountain, and Galongla Mountain. During each survey, ants were sampled along an interval of roughly every 250m elevation. In total, 17 sites from

Sejila mountains (2000 to 4500m), 24 sites from Demula mountain (1500 to 4750m), and 20 sites from Galongla Mountains (740 to 4300m) were sampled (Figure 4.1). Details on each sampling site information are provided in Table 4.1.

At each sampling site, our goal was community characterization, rather than a complete or "strict" inventory *sensu* Longino & Colwell (1997). In other words, I sought to survey a large number of communities in a standardized and repeatable way so that they can be compared across gradients, but I do not attempt to comprehensively survey every species at each site. I thus established a 10-m-side-quadrat (100 m^2), and randomly selected five 1-m^2 quadrats within the 100 m^2 quadrat. Within each 1-m^2 quadrats, I first collect leaf litter ants using Davis Sifter. I then collect soil ants by digging and sifting 20 cm deep soil. Furthermore, I collected ants from 10 sub-sites within the 100 m^2 quadrat by using Davis Sifter, hand collection, and beating sheet for 5-person-hours to cover different microhabitats to get more accurate data on species richness

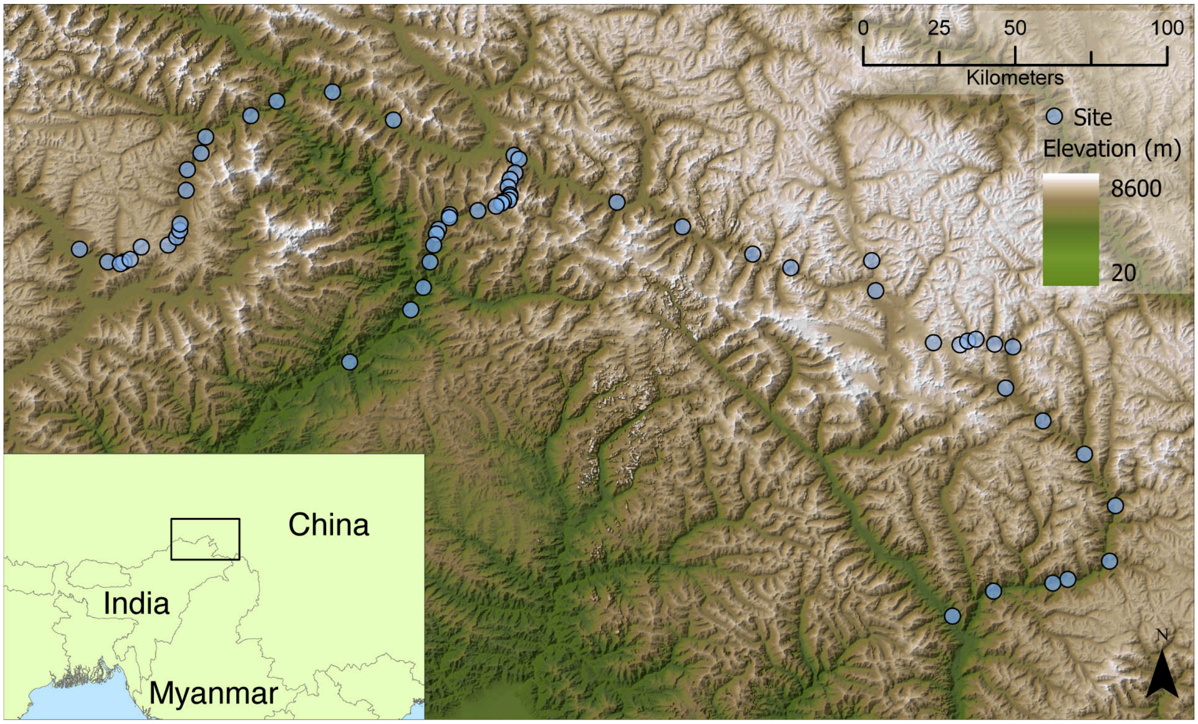

Figure 4.1 | Sampling map of this study, blue dots indicate sampling sites.

and composition of each site. All the ants were pooled together as a single sample for each site. I used species richness estimators for four sites from different elevations, to ensure that the richness variation I measure is correlated with variation in the estimated total richness (Figure 4.2). All the ant samples were then point-mounted and identified to species or (if undescribed) morphospecies level. All the specimens are located in Xu's collection at Southwest Forestry University in China.

Table 4.1 I Sampling site information (SR: Ant species richness).

Site	Mountain	Latitude	Longitude	Elevation (m)	SR
D01	Mt. Demula	30.076	95.314	2225	8
D02	Mt. Demula	29.997	95.451	2510	11
D03	Mt. Demula	30.083	95.912	2750	6
D04	Mt. Demula	29.856	96.028	3000	5
D05	Mt. Demula	29.688	96.385	3250	4
D06	Mt. Demula	29.646	96.456	3550	4
D07	Mt. Demula	29.753	96.767	3750	4
D08	Mt. Demula	29.666	97.036	3940	5
D09	Mt. Demula	29.581	96.839	4250	5
D10	Mt. Demula	29.452	97.013	4563	7
D11	Mt. Demula	29.346	97.280	4776	0
D12	Mt. Demula	29.529	97.136	4500	4
D13	Mt. Demula	29.359	97.279	4276	9
D14	Mt. Demula	29.379	97.157	4000	4
D15	Mt. Demula	29.300	97.178	3776	13
D16	Mt. Demula	29.505	97.277	3608	5
D17	Mt. Demula	29.248	97.452	3250	9
D18	Mt. Demula	29.172	97.411	3000	7
D19	Mt. Demula	28.977	97.633	2750	6
D20	Mt. Demula	28.851	97.606	2450	11
D21	Mt. Demula	28.739	97.373	2250	14
D22	Mt. Demula	28.814	97.414	2050	21
D23	Mt. Demula	28.678	97.366	1750	14
D24	Mt. Demula	28.751	97.169	1590	17
S1	Mt. Sejila	29.623	94.590	3000	10
S2	Mt. Sejila	29.786	94.677	3250	6
S3	Mt. Sejila	29.782	94.693	3500	3
S4	Mt. Sejila	29.691	94.774	3750	2
S5	Mt. Sejila	29.644	94.737	4000	1
S6	Mt. Sejila	29.732	94.761	4250	1
S7	Mt. Sejila	29.791	94.730	4548	0
S8	Mt. Sejila	29.831	94.781	4250	2
S9	Mt. Sejila	29.703	94.945	4000	2
S10	Mt. Sejila	29.776	94.829	3750	2
S11	Mt. Sejila	29.827	94.847	3500	2

… continued on the next page

Table 4.1 (*Continued*)

Site	Mountain	Latitude	Longitude	Elevation (m)	SR
S12	Mt. Sejila	29.921	94.886	3250	4
S13	Mt. Sejila	29.898	94.948	3000	1
S14	Mt. Sejila	29.927	94.838	2750	3
S15	Mt. Sejila	29.943	94.805	2500	5
S16	Mt. Sejila	30.208	94.941	2250	10
S17	Mt. Sejila	30.144	95.177	2023	11
G1	Mt. Galongla	29.888	95.892	2960	3
G2	Mt. Galongla	29.998	95.959	3220	1
G3	Mt. Galongla	29.935	95.718	3460	1
G4	Mt. Galongla	29.817	95.885	3720	2
G5	Mt. Galongla	29.958	95.709	3987	0
G6	Mt. Galongla	29.860	95.716	4268	0
G7	Mt. Galongla	29.955	95.916	3972	0
G8	Mt. Galongla	29.888	95.911	3700	0
G9	Mt. Galongla	29.810	95.817	3460	1
G10	Mt. Galongla	29.924	95.811	3280	1
G11	Mt. Galongla	29.961	95.694	2960	1
G12	Mt. Galongla	29.762	95.613	2750	7
G13	Mt. Galongla	29.879	95.594	2540	8
G14	Mt. Galongla	29.821	95.583	2250	7
G15	Mt. Galongla	29.855	95.741	1960	7
G16	Mt. Galongla	29.830	95.605	1740	16
G17	Mt. Galongla	29.780	95.684	1450	31
G18	Mt. Galongla	29.566	95.616	1200	42
G19	Mt. Galongla	29.510	95.519	1030	38
G20	Mt. Galongla	29.281	95.379	740	41

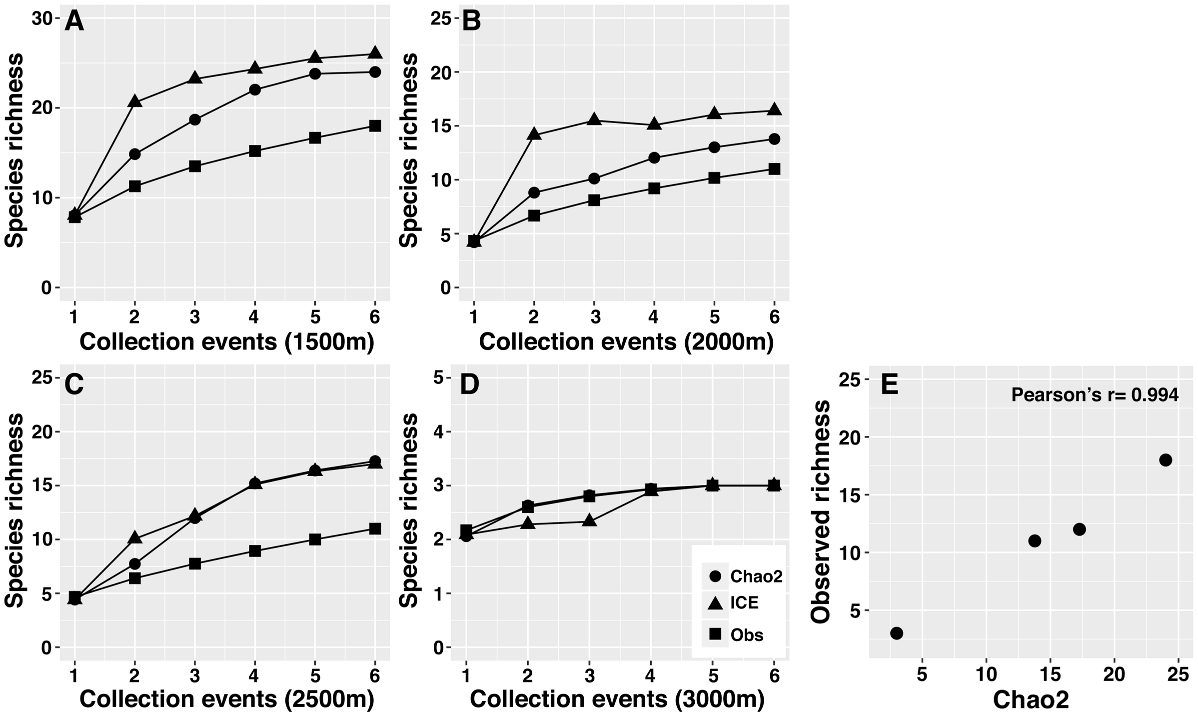

Figure 4.2 | Estimates of ant species richness sampling effectiveness using nonparametric richness estimators.
(A — D). Species accumulation curves of 4 sampling sites based on 6 total collection events of each site. (E). Relationship between total observed species richness and Estimated total species richness (Chao2) for 4 sites. Chao2: Chao2 estimator, ICE: Incidence-based coverage estimator, and Obs: observed species richness. Our sampling method was targeted at characterizing richness variation across environmental gradients using standardized sampling, rather than attempting a complete inventory at all 55 sites. However, I used richness estimators at four sites across elevation to compare estimated richness with our observed richness, and confirm that they are correlated. Ant species richness estimators (ICE and Chao2) were calculated based on the ant samples collected from 5 1-m2 quadrats (5 collection events) and hand & beating sheet (considered 1 collection event for this purpose) of each of four test sampling sites (1500m, 2000m, 2500m, and 3000m) using the software EstimateS (Colwell 2013). These subsamples together match the sampling procedure applied at each site. While our sampling did not generally capture all species to be in the community, the estimators had saturated and the correlation between observed species richness and estimated total species richness (Chao2) was high (Pearson's r= 0.994) indicating that our sampling characterized differences in species richness.

4.2.2 Geomorphology and elevational connectivity

Elevation information was acquired from the USGS (2006) Shuttle Radar Topography Mission (SRTM) 1 Arc-Second data with 30m spatial resolution and projected to Universal Transverse Mercator Zone 47N. The UTM projection minimizes distortions among area, distance, and geometry for a given zone of interest. Area for each elevational band was calculated by summing pixels falling within the bands, and with an alternate method by summing the total surface area of each elevational band in a triangulated irregular network (TIN) model, which I confirmed gave near-identical results (Figure 4.3). Before evaluating habitat connectivity, I first define a 400 m elevation range buffer that species can move without any cost (hypothetic species niche width along elevation). I evaluate habitat connectivity by calculating cost distance among all localities that are within the 400 m buffer (the analyses were also performed at 300 m and 500 m buffers to test for sensitivity in buffer size). This is achieved by calculating path lengths between pairs of sites, weighting as more costly steps and paths that leave the 400 m elevational range. Input rasters were calculated for each survey location by subtracting the origin elevation from the DEM and taking the absolute value. In this way, all points start from a local zero and resist moving either higher or lower in elevation uniformly in the cost distance calculation. The resulting raster was binned by 400 m to create bands of elevation values with no impact on the cost distance relationship. Bins were reclassified to integers, by ones, up to the maximum elevation value, such that the first bin of 0-400 is 1, and 400-800 is 2 and so on. The costs were then assigned based on the bins, for example, 0-400 m away will have the cost of 1 and 400-800 m away will have the cost of 2 and so forth. Raster processing and cost distance analysis was done using ArcGIS Desktop Version 10.3, which calculates cost distance from each survey site to all other sites as distance traveled multiplied by weight, in this case, the reclassified raster, to find the optimum least cost path. In order to account for the potential sampling bias when evaluating habitat connectivity, I also calculate the cost distance based on 3000 randomly generated sites across the entire landscape.

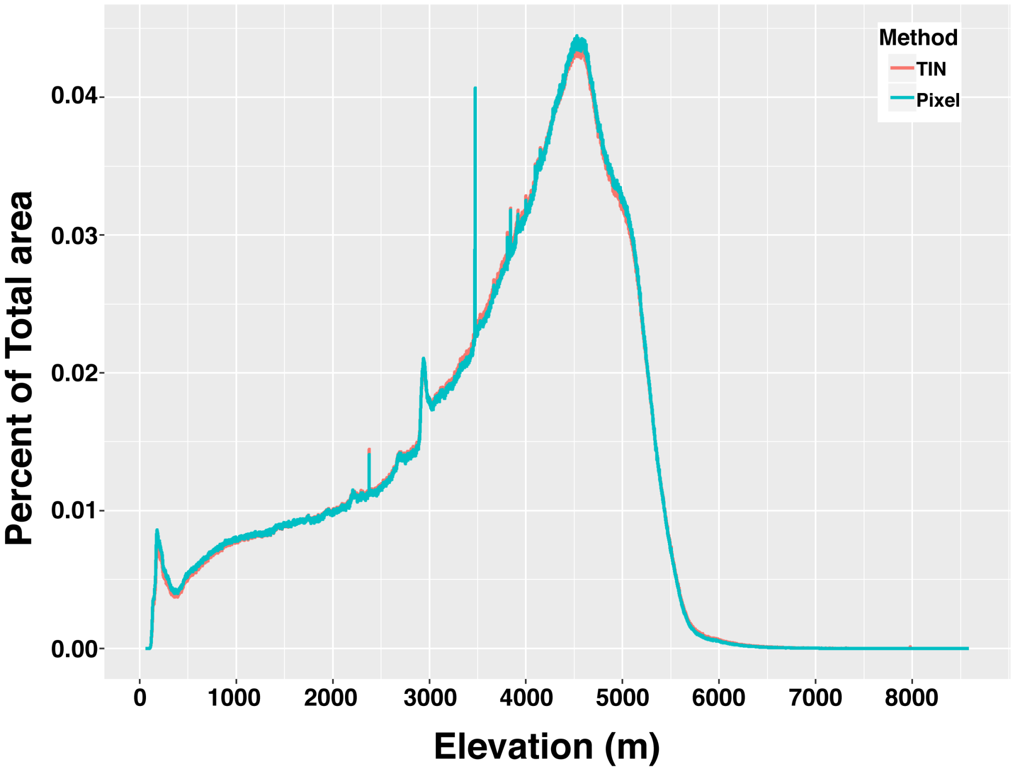

Figure 4.3 I The percent of total area at each elevation as calculated by different methods, summing the pixels (blue line) and summing the area from the TIN (red line).
I compared the proportion of surface area for every one meter elevation calculated using two methods, to ensure they are equivalent. The first method uses the pixel count from the DEM at each elevation as a proxy of surface area. The other method was developed by Jenness J. S. (2004) as a means to replicate the increased accuracy of surface area estimations as can be derived from a Triangulated Irregular Network (TIN). I employed the toolset “DEM Surface Tools for ArcGIS” created by Jenness, J. S. (2013)” to calculate surface area that considers the differences caused by slope. Area calculated with each method is nearly identical.

4.2.3 Climatic and spatial variables

I tested whether local climate would affect taxonomic and phylogenetic biodiversity patterns of ants in Hengduan Mountains. I used the 19 bioclimatic variables from WorldClim (Hijmans et al. 2005) coincident with the GPS coordinates of our study sites. I first divided those variables into precipitation- and temperature-related subsets. Second, for each subset, I remove all climatic variables with weak explanatory power (Spearman’s correlations between variables and responses |ρ|<0.1). Third, for each climatic subset, I addressed collinearity by investigating the bivariate correlations between all possible pairs of variables. If |ρ|>0.7, the variable with lower explanatory power was removed (see Dormann et al. 2013 for detail). I finally selected Annual Mean Temperature (Bio1), Mean Diurnal Range (Bio2), Isothermality (Bio3), Annual Precipitation (Bio12), and Precipitation Seasonality (Bio15) as unique sets of temperature- and precipitation-related variables for our study area. In a fourth step, for the climate characterization of each site, separate principal component analyses for the precipitation- and temperature-related variables were conducted to further reduce the dimensionality. Since PC1 explained >99% of the variance for both variables, the others components were discarded. For estimation of climatic distance among sites, Euclidean climate distance matrix was generated based on the five climatic variables.

4.2.4 Phylogeny

The community phylogenies were derived from separate project to reconstruct large-scale ant phylogenies with all described ant taxa (and associated phylogenetic uncertainty) represented (Economo et al. In Revision). By integrating the molecular data generated by other ant-wide phylogenies (Moreau et al. 2006, Moreau and Bell 2013, Brady et al. 2014, Ward et al. 2015), those trees provide reliable relationships between subfamilies and genera, but represent uncertainty within genera and among species. For the analyses in our study, I generated subset of phylogenies by using the 100 trees from the posterior sets of the large-scale ant phylogenies. I first pruned those trees to only include the number of species in each genus collected in our fieldwork. Then I randomly placed all the species (both described and undescribed) in each genera (see also the Methods in Liu et al. 2016 for details).

4.2.5 Phylogenetic alpha diversity

Phylogenetic alpha diversity of each ant assemblage was estimated by calculating the mean phylogenetic distance (MPD) (Webb et al. 2002). In order to test for non-random patterns of ant phylogenetic structure, I calculated standardized effect size of MPD (net relatedness index, NRI) by the equation below, where Mean_{obs} is the observed MPD within each site, $\text{Mean}_{\text{null}}$ and $\text{s.d.}_{\text{null}}$ are the mean and standard deviation of MPD distribution of the null communities. Null model communities were generated by randomizing the community data matrix using "Independent Swap" method with 1000 iterations. I conducted this calculation across all 100 phylogenies and then extracted the arithmetic mean of the NRI distribution. MPD and NRI were calculated by using *ses.mpd* function in R Package *Picante* (Kembel et al. 2010). I multiplied NRI by -1 and therefore, a positive value indicates phylogenetic overdispersion, and a negative value indicates phylogenetic clustering.

$$SES = (Mean_{obs} - Mean_{null}) / s.d._{null}$$

4.2.6 Taxonomic and phylogenetic beta diversities

Taxonomic beta diversity (TBD) between ant assemblages was calculated using pairwise Sørensen dissimilarity (TBD_{sor}) and was further partitioned into turnover (TBD_{sim}) and nested-resultant (TBD_{sne}) components following the framework of Baselga (2010). TBD_{sim} is the dissimilarity only due to species turnover, while TBD_{sne} is nested-resultant dissimilarity which only captures the richness differences among nested communities (Baselga 2010). It is worth noticing that TBD_{sne} measures the fraction of total dissimilarity that is not due to species replacement, instead of nestedness *per se* (Baselga 2012).

Phylogenetic beta diversity (PBD) was calculated using PhyloSor distance matrix (PBD_{sor}) and was also decomposed into turnover (PBD_{sim}) and nestedness (PBD_{sne}) components, where PBD_{sne} measure the differences due to the differences in Faith's PD, and PBD_{sim} is measure of 'true' lineage turnover (Leprieur et al. 2012).

The relative importance of turnover and nestedness of TBD and PDB was calculated as the proportion of total beta diversity explained by turnover using multiple-site dissimilarity indices (TBD_{SIM}/TBD_{SOR}, and PBD_{SIM}/PBD_{SOR}, Baselga 2010, Leprieur et al. 2012). Spatial turnover is associated with deterministic niche-based processes, while nestedness is more related to dispersal limitation (Baselga 2010). All the pairwise dissimilarity indices were calculated using R package *betapart* (Baselga and Orme 2012). The standardized effect size of all pairwise taxonomic and phylogenetic dissimilarities ($SES.TBD_{sor}$, $SES.TBD_{sim}$, $SES.TBD_{sne}$, $SES.PBD_{sor}$, $SES.PBD_{sim}$, and $SES.PBD_{sne}$) was also calculated using SES equation mentioned before. Null model assemblages for computing standardized taxonomic beta diversities were generated by using the same method ("Independent Swap") as I calculated NRI, while the random communities for calculating standardized phylogenetic diversities were generated by randomly shuffling the name of taxa across the tips of phylogeny for 1000 times following the R code in Swenson (2014).

For testing the relative role of geographic distance and environmental gradients, beta diversities between all pairwise sites were calculated. The species pool for the null model was defined as all the ant species I collected from all sites. Alternatively, in order to test the elevational connectivity, I calculated beta diversities between all the pairs that are within the 400 m elevational buffer (300 m and 500 m elevational buffers were also calculated). Species pools for each calculation were defined as the ant species that present or potentially present in each locality according to the species elevational distribution. Species elevational distribution was defined as the elevation between the lowest locality and highest locality they have been collected. For those species only been collected from one locality, I assume its elevational distribution as the elevation of that locality ± 200 m (150 m for the 300 m elevational buffer, and 250 m for the 500 m elevational buffer).

4.2.7 Statistical analyses

I evaluated whether climatic variables (precipitation, temperature) and elevation are associated with ant species richness (SR) and phylogenetic structure (NRI) using generalized additive models (GAM). GAM extends generalized linear models (GLM) by incorporating smooth functions that are more flexible in modeling nonlinear relationships (Hastie and Tibshirani 1990). GAM has been used widely in ecological studies such as species distribution modeling (Elith et al. 2006) as well as studies of alpha and beta diversity patterns (Davey et al. 2013, La Sorte et al. 2014). Since there is very high collinearity between elevation and the first principal component temperature and precipitation (Spearman's correlations, $|\rho|>0.9$), I chose elevation as the surrogate predictor of environmental conditions. Potential spatial autocorrelation was controlled by using a smoothing function on the coordinates (latitude and longitude) of sampling sites (see also La Sorte et al. 2014). For alpha diversity, the GAM was specified as:

$$g(\text{alpha diversity}) = b_0 + s(\text{lat, long}) + s(\text{elevation})$$

where g(alpha diversity) is the link function, alpha diversity is taxonomic alpha diversity (species richness) or phylogenetic alpha diversity (NRI), b_0 is the intercept, and s is a thin plate regression spline (Wood 2006). As species richness are counts, I modeled the response as a Poisson distribution using a log link function, while NRI was modeled as normal distribution with identity link function.

I also used GAM to examine the effects of two predictor variables (geographic distance and Euclidean climatic distance) hypothesized to correlate with ant taxonomic and phylogenetic beta diversities among ant assemblages in the region. A GAM was conducted separately to the three components of SES.TBD (SES.TBD_{sor}, SES.TBD_{sim}, and SES.TBD_{sne}) and SES.PBD (SES.PBD_{sor}, SES.PBD_{sim}, and SES.PBD_{sne}), using an identity link function. To determine the relative contribution of each variable to predict SES.TBD and SES.PBD, I conducted a series of partial GAM to partition the explained deviance into three fractions: explained by purely geographic distance, explained by purely climatic distance, explained by shared geographic and climatic distance. The GAM analyses were conducted using R package *mgcv* (Wood 2006). Generalized cross validation (GCV) optimization was used to choose the degree of freedom, and gamma penalty was set to 1.4 in order to reduce over-fitting (Wood 2006).

I also used GAM to examine how connectivity (cost distance), taxonomic beta diversity, and phylogenetic beta diversity among site pairs at similar elevations changes across elevation. GAM was also used to model the effect of cost distance and geographic distance on TBD and PDB within similar elevational ranges. Corrected version of Akaike information criterion (AICc) was used to test whether cost distance can predict TBD and PBD better than simple geographic distance. All statistical analyses were performed in R 3.3.1 (R Development Core Team 2016).

4.3 Results

Of the 61 localities surveyed, 127 ant species / morphospecies from 46 genera and eight subfamilies were detected across 55 sites. Six high elevation sites (above 4500m) lacked ants altogether (Appendix Table 8.2).

4.3.1 Geomorphology

In this landscape, area peaks at middle elevations, however, this peak is above the maximum elevation ants were detected (Figure 4.4B). There is complex spatial structure found at different elevational bands (Figure 4.4E-4.4I), but I did not detect a systematic correlation between connectivity and elevation in this landscape according to our 3000 randomly chosen sites (Figure 4.4C).

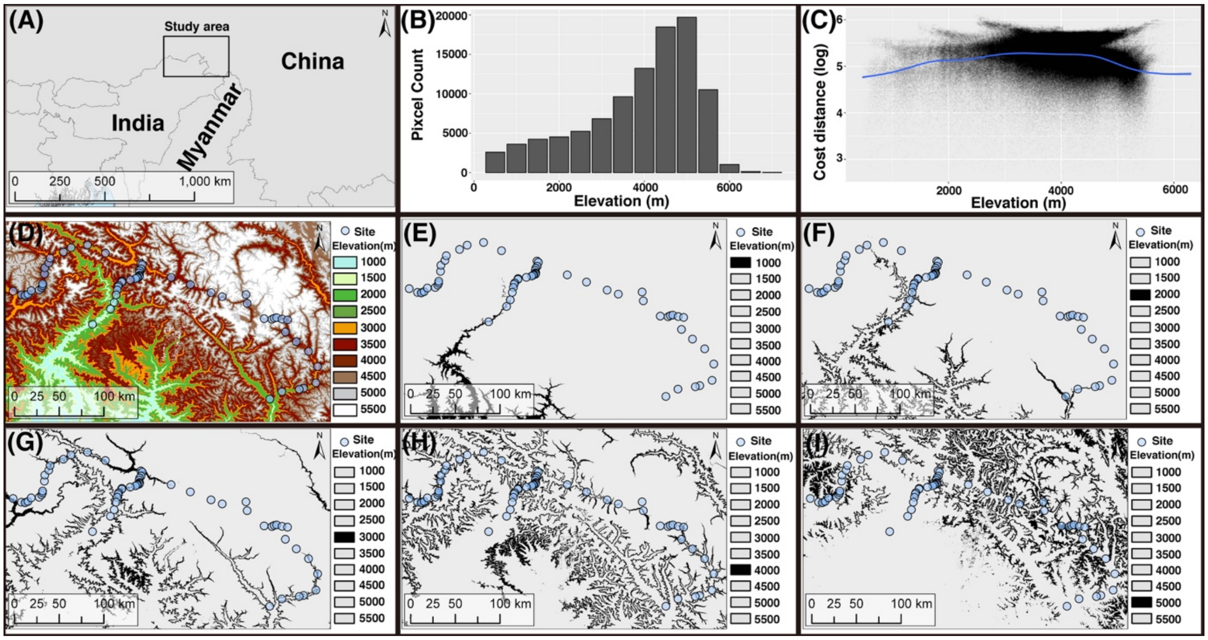

Figure 4.4 | Landscape geomorphology of the study area.
(A). Location of sampling region; **(B).** Frequency distribution of area at each elevation; **(C).** Elevational connectivity (represented by cost distance) between pairs that are within 400m elevational difference of 3000 randomly simulated sites across the landscape; **(D).** Digital elevation map (DEM) of the study area; **(E-I).** Landscape connectivity in different 400m elevational bands centered on the values in the legend. Blue dots indicate sampling localities.

4.3.2 Alpha diversity along elevation

The relationship between species richness and elevation was strong and monotonically negative (R^2=0.92, *p*<0.001, Figure 4.5A). A strong decline of phylogenetic alpha diversity (-1×NRI) was also found along the elevational gradient (R^2=0.70, *p*<0.001, Figure 4.5B). The effect of spatial autocorrelation was not significant for both taxonomic and phylogenetic alpha diversity (with *p*=0.073, and *p* =0.081, respectively). Among these ant assemblages, 19 communities with most of them below 2500 m showed phylogenetic overdispersion (with positive -1×NRI value). Of these, three communities which below 1000 m were significantly different from a null expectation at 0.05 level (Figure 4.5B). Other communities showed phylogenetic clustering (with negative -1×NRI value) with 12 that were significant at 0.05 level.

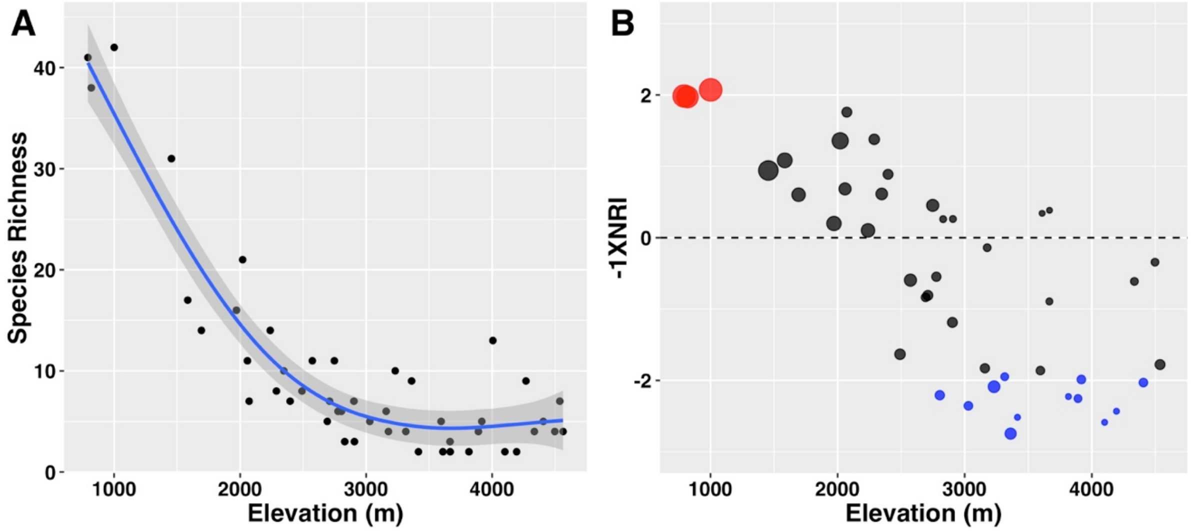

Figure 4.5 | The relationship between ant alpha diversity and elevation.
(A). species richness with elevation. **(B)**. phylogenetic alpha diversity (represented by -1X NRI) declining with elevation. The size of circle is proportional to species richness in the community. Red color indicates phylogenetic overdispersion, while the blue indicates clustering.

4.3.3 Environmental and spatial drivers of beta diversity

Taxonomic and phylogenetic beta diversity among ant assemblages in Hengduan Mountains was largely due to species and lineage replacement (TBD_{SIM} / TBD_{SOR} =0.94; PBD_{SIM} / PBD_{SOR}

=0.92). A strong relationship was found between standardized taxonomic and phylogenetic beta diversity components (SES.TBD_{sim}, SES.TBD_{sne}, SES.PBD_{sim}, and SES.PBD_{sne}) and climatic distance, while the relationship between these beta diversity components and geographic distance is not strong (Figure 4.6). The results from GAM fitting showed that climatic distance and geographic distance together explained 53%, and 72% of the variation in standardized taxonomic and phylogenetic beta diversity (SES.TBD_{sor} and SES.PBD_{sor}, respectively). Overall, climatic distance has a larger effect on the beta diversity patterns than the geographic distance (Figure 4.7).

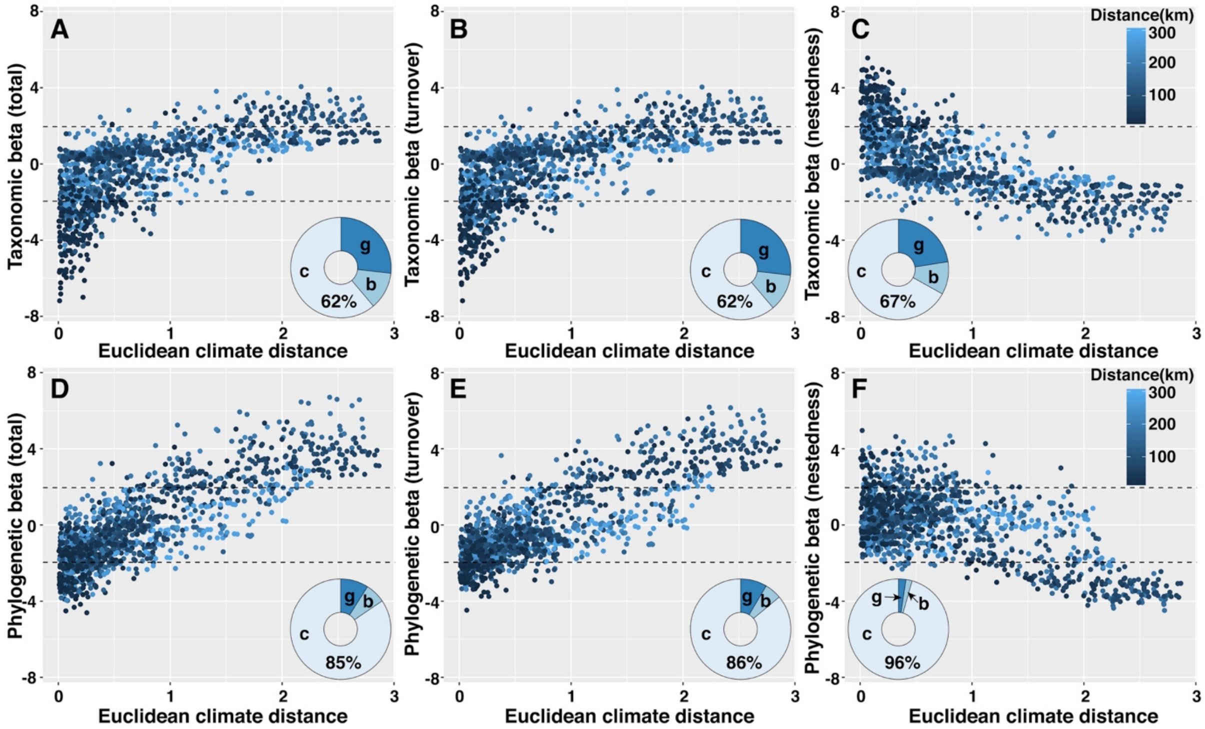

Figure 4.6 l Relationships of standardized beta diversities with climate distance and geographic distance (dot color).
(A-C). standardized taxonomic beta diversities (represented by SES.TBD_{sor}, SES.TBD_{sim}, SES.TBD_{sne}); **(D-F).** standardized phylogenetic beta diversities (represented by SES.PBD_{sor}, SES.PBD_{sim}, and SES.PBD_{sne}). The pie charts depict the fraction total explained deviance in beta diversities explained by climatic distance only, geographic distance only, and the combination of both (letter c, g, and b, respectively). The numbers indicate the deviance in beta diversities explained by climatic distance alone.

Partial GAM analyses also showed that the variance in taxonomic and phylogenetic beta diversity components (SES.TBD$_{sim}$, SES.TBD$_{sne}$, SES.PBD$_{sim}$, and SES.PBD$_{sne}$) explained by climatic distance was much larger than explained by geographic distance (Figure 4.6, Table 4.3), indicating that climatic distance between sites have played a much greater role than geographic distance in shaping taxonomic and phylogenetic composition of ant assemblages.

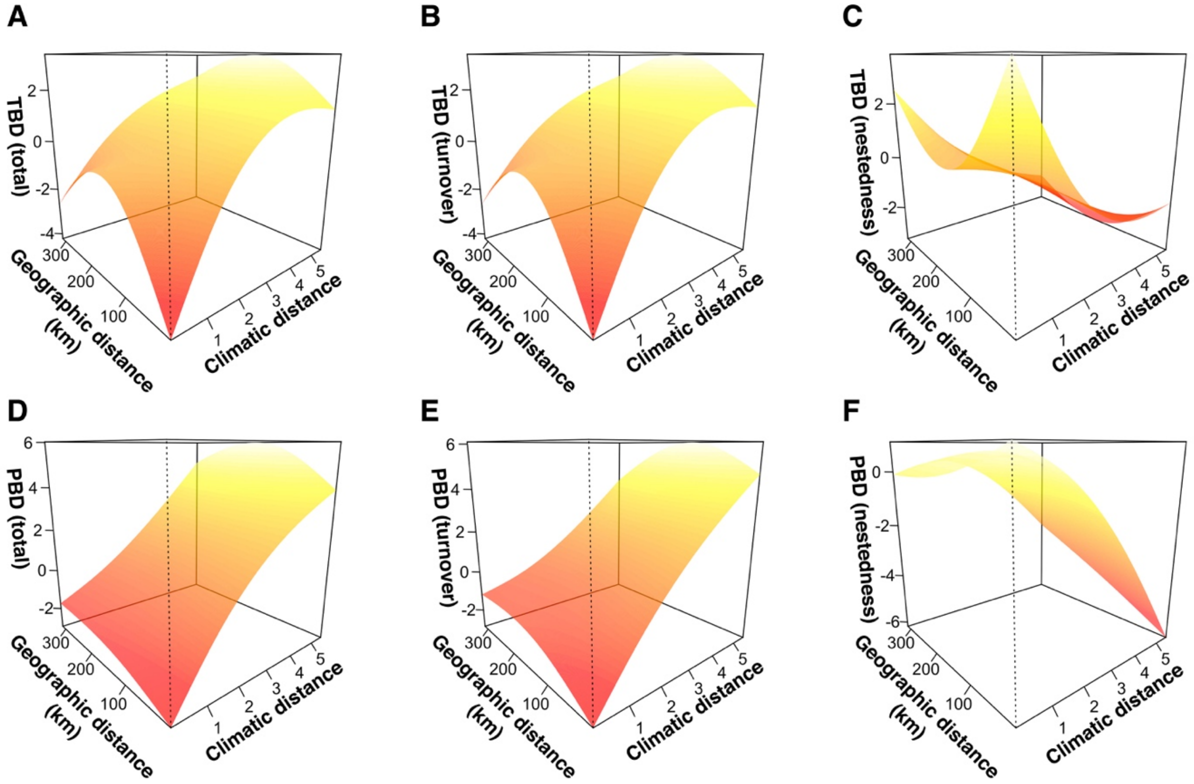

Figure 4.7 | The effects of climatic distance and geographic distance on standardized taxonomic beta diversity (TBD) and phylogenetic beta diversity (PBD) based on generalized additive models (GAM) using tensor product smooth.
(A-C). standardized taxonomic beta diversities (represented by SES.TBD$_{sor}$, SES.TBD$_{sim}$, SES.TBD$_{sne}$); **(D-F).** standardized phylogenetic beta diversities (represented by SES.PBD$_{sor}$, SES.PBD$_{sim}$, and SES.PBD$_{sne}$).

Table 4.2 | Summary of each partial generalized additive models.
Including F statistics, effective degree of freedom (edf), *P*-value and adjusted R^2 for the relationship of taxonomic and phylogenetic beta diversity components to the two variables (geographic distance and climatic distance). See Methods for details on predictors and models. *n*=1394.

Beta diversities	**Climate distance**				**Geographic distance**			
	F	edf	*P*	R^2	*F*	edf	*P*	R^2
TBD_{sor}	169.1	5.763	<0.001	0.441	51.72	8.37	<0.001	0.234
TBD_{sim}	169.2	5.819	<0.001	0.443	51.88	8.4	<0.001	0.235
TBD_{sne}	165.5	5.603	<0.001	0.445	37.26	8.49	<0.001	0.19
PBD_{sor}	410.4	7.413	<0.001	0.699	22.94	8.265	<0.001	0.119
PBD_{sim}	3275	1	<0.001	0.688	20.23	7.905	<0.001	0.105
PBD_{sne}	133.5	7.125	<0.001	0.423	4.121	6.664	<0.001	0.0191

4.3.4 Elevation connectivity

Since the results from different elevational buffers were largely consistent, I only present the results based on the 400m elevational buffer. Within the 400m elevational buffer, taxonomic and phylogenetic beta diversities were significantly correlated with cost distance (GAM, TBD_{sor}: $p<0.001$, $R^2=0.31$; PBD_{sor}: $p<0.001$, $R^2=0.23$, $n=322$; Figure 4.8A, B), indicating that elevational connectivity has an important role in shaping ant diversity patterns within similar environments. Although TBD and PBD were also correlated with geographic distance (GAM, TBD_{sor}: $p<0.001$, $R^2=0.27$, PBD_{sor}: $p<0.001$, $R^2=0.13$, $n=322$; Figure 4.8C, D), cost distance is the better predictor of species and phylogenetic composition within the similar elevational buffer (ΔAICc= -11.36 for TBD_{sor}; ΔAICc= -35.14 for PBD_{sor}). Cost distance, TBD, and PBD between each pairs within 400m elevational difference are largely consistent within elevation (GAM, Cost distance: $p<0.15$, $R^2=0.003$; TBD_{sor}: $p<0.054$, $R^2=0.008$; PBD_{sor}: $p<0.002$, $R^2=0.030$; $n=322$; Figure 4.9), indicating that the habitat connectivity was overall similar between different elevations in our study.

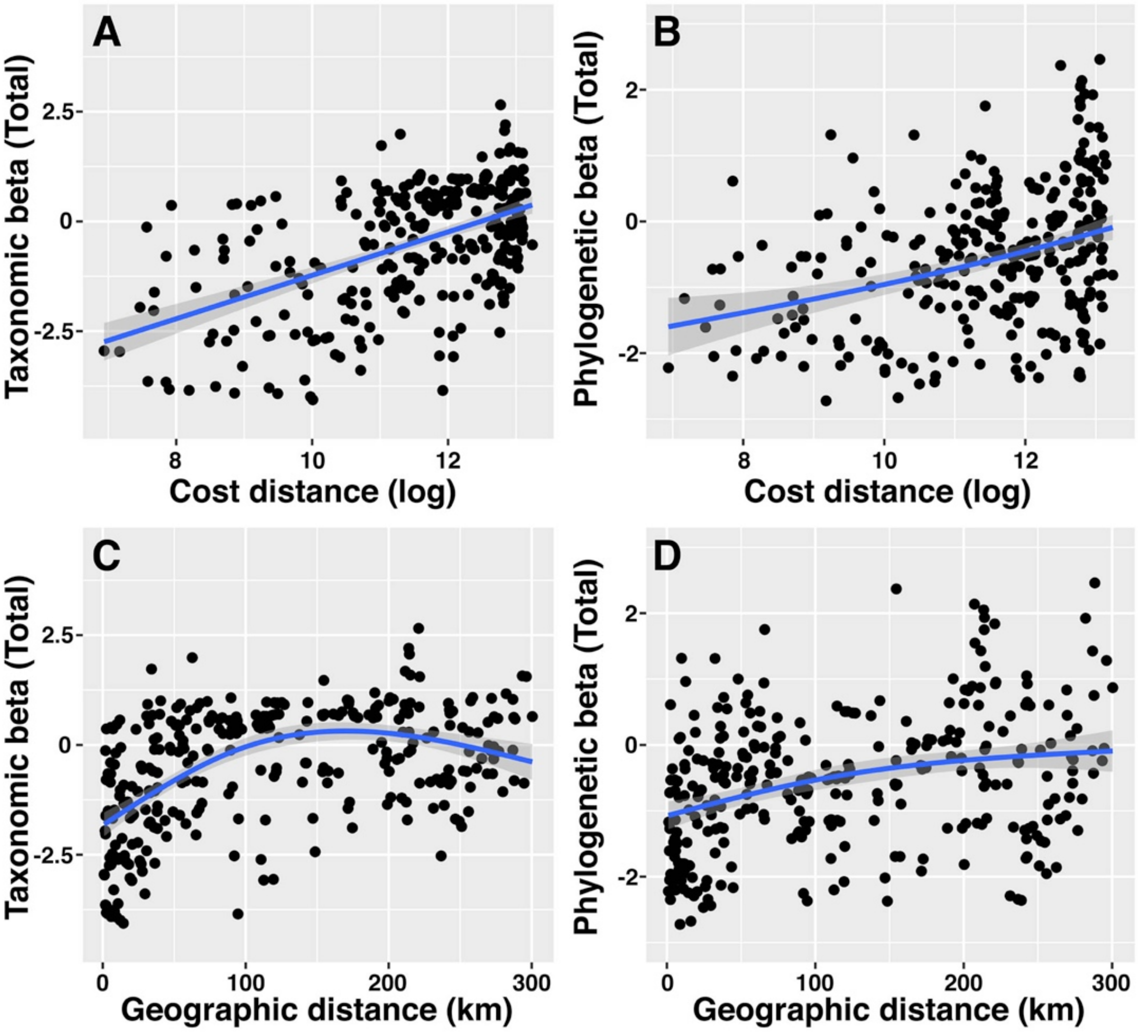

Figure 4.8 | The fit of generalized additive models (GAM) with 95% confidence interval examining the relationship between beta diversities and different distance matrices (geographic vs. cost distance).

(A, B) between standardized beta diversities and cost distance, and **(C, D)** between standardized beta diversities and geographic distance. Taxonomic beta diversity and phylogenetic beta diversity are represented by SES.TBD$_{sor}$ and SES.PBD$_{sor}$, respectively. All the pairwise comparisons are the local communities within 400m elevational buffer.

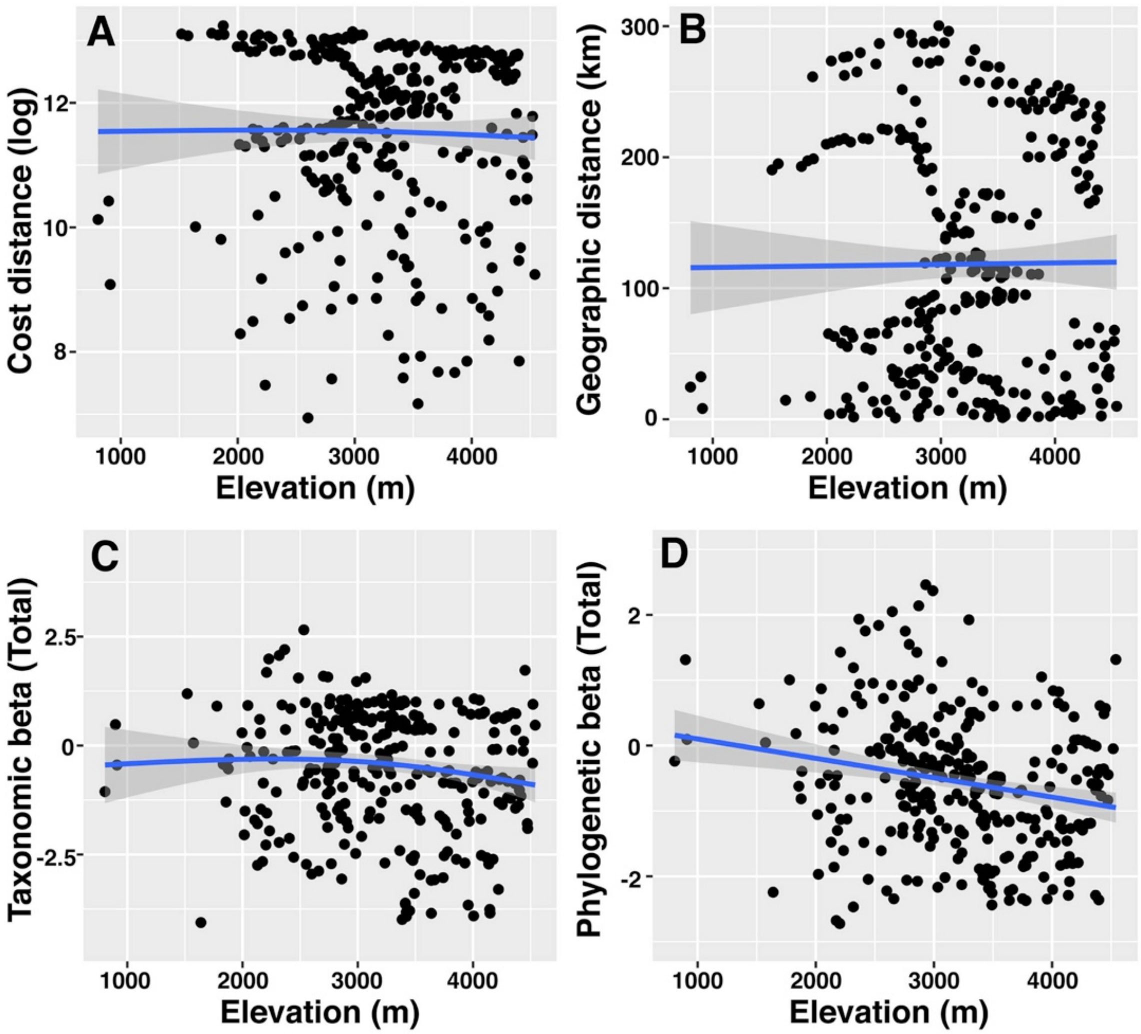

Figure 4.9 | The fit of generalized additive models (GAM) with 95% confidence interval examining the elevational changes in beta diversities and distance matrices.
(A) cost distance, **(B)** geographic distance, **(C)** standardized taxonomic and **(D)** phylogenetic beta diversities. Dots are pairs of localities located within a maximum of 400m elevational distance, with the x-axis representing the average elevation between two sites. Taxonomic beta diversity and phylogenetic beta diversity are represented by $SES.TBD_{sor}$ and $SES.PBD_{sor}$, respectively.

4.4 Discussion

Our analysis of ant communities in China’s Hengduan Mountains revealed a number of patterns that provide insight into metacommunity processes. Overall, our results highlight the predominant role of elevation-driven environmental gradients in shaping ant species distribution patterns in the region, with a secondary role for spatial connectivity detected within similar elevations. However, on the whole our findings are inconsistent with theoretical predictions, but even when theory does not match empirical patterns, it can be a useful framework for learning from empirical results.

I found a monotonic decline in local ant species richness with increasing elevation. While not an unusual finding for ant elevation-richness patterns, this result is not consistent with the theoretical prediction of a mid-elevation richness peak (Bertuzzo et al. 2016). Ant phylogenetic alpha diversity showed a shifting pattern along the elevational gradient from phylogenetic overdispersion in warm lowlands to phylogenetic clustering at cool high-elevation sites. A similar phylogenetic trend along elevation has been reported in many taxa including ants (Graham et al. 2009, Machac et al. 2011, Hoiss et al. 2012, Brehm et al. 2013). Clustered phylogenetic structure at high elevation indicates that strong environmental constraints at higher elevation influence the assembly of communities by filtering out the ant species or lineages that cannot persist there. For example, most ant species found at high-elevation sites (>4000 m) are from the genera *Formica* and *Myrmica* (Table 4.2). Phylogenetic overdispersion in lowlands has been interpreted as evidence that intense interspecific competition between species with similar traits shapes the structure of communities (Graham et al. 2009, Machac et al. 2011).

Overall, across our study region the strongest variable controlling ant taxonomic and phylogenetic beta diversity was the elevational/environmental difference between localities. Ant beta diversities were lower than the null expectation when ant assemblages are inhabiting similar environments, while higher than expected when ant communities are from more different environments. Those results highlight the role of species sorting processes (Leibold et al. 2004), where the local ant species and phylogenetic composition are largely determined by local environmental conditions rather than dispersal limitation.

Ant taxonomic beta diversity was mainly driven by species replacement along elevational gradients as demonstrated by the remarkably high proportion of the turnover component (94%), rather than nestedness component, of beta diversity. Similarly, ant phylogenetic beta diversity was largely determined by lineage replacement, with a high percentage of phylogenetic turnover (93%). These findings indicate that the ability to persist at high elevations is highly phylogenetically conserved and evolutionary history strongly limits elevational distribution of species.

While elevation was the dominant variable explaining beta diversity across all communities, within elevational bands I found a significant correlation between spatial variables and beta diversity, indicating that habitat connectivity affects the pattern of species distribution significantly within tracts of relatively homogeneous environment. The fact that cost distance (elevational connectivity) was a better predictor of beta diversities (TBD and PBD) than simple geographic distance among pairs of communities highlights the role of dispersal limitation interacting with the complex spatial geometry of the landscape. This structure, in turn, is driven by elevation-driven environmental gradients. The strength of beta diversity within elevational bands did not itself vary with elevation, a finding that is inconsistent with theoretical predictions that connectivity varies systematically with elevation and drives biodiversity patterns (Bertuzzo et al. 2016).

The theory developed by BEA is based on the well-justified premises that habitat area, dispersal limitation, and environmental gradients all contribute to biodiversity patterns in metacommunities (Leibold et al. 2004). These premises, combined with the geomorphological features of fluvial landscapes, lead to predictions about biodiversity patterns. So, what explains the discrepancy between theoretical predictions and our case study of ant metacommunities in Tibet?

First, I note that the geomorphology of our study landscape does not completely match features from idealized fluvial landscapes. In the BEA model both mountain valleys and mountain peaks are less connected than mid-elevations. In our landscape, spatial connectivity does not have a mid-elevation peak, and does not vary strongly with elevation (Figure 4.4C). This could be in part because of a general trend in elevation from south to north across the landscape (Figure 4.4D), such that corresponding geomorphological features—mountain peaks, mid-elevations, and valleys—do not correspond to the same elevations as one moves across the landscape. Second, in the BEA model habitat area also peaks at mid-elevations. This is also true in our landscape (Figure 4.4B), however the area-peak is very high at around 5000 m, which is above the maximum elevation that ants were detected (4500 m). This means that area was monotonically *increasing* with elevation within the elevational ranges that were tolerable to our study taxon, rather than declining (as would be implied by the simple mountain "cone" analogy), or peaking at mid-elevation as predicted by idealized fluvial landscapes. I also note that despite the predictions derived from idealized fluvial landscapes, a recent study found that only 39% of mountain ranges exhibited a mid-elevation peak in area after investigating the topography among 182 mountain ranges globally (Elsen and Tingley 2015).

The fact that no ant species were able to establish in high elevation habitats hints at a potential mismatch between current theory and the real-world system: the process by which species enter the metacommunity and the species pools from which they are drawn. In the BEA model, new species enter the system randomly and at the same rate at all elevations, which could be interpreted as either a speciation process and/or colonization process from outside the focal area. This assumption is the most sensible starting point for generalized theory, but there are reasons why this may not hold in our system (or others). Species enter the landscape either through speciation or colonization from the outside, but this rate may vary with elevation due to a number of factors. First, environmental tolerances are highly conserved in ants (Pie 2016, Economo et al. In Review), with high elevation habitats dominated by a few ant genera (e.g. *Formica*, *Myrmica*) that also dominate at low-elevations at high-latitudes. Physiological limits apparently preclude persistence of ant populations above 4500m in our system. The strong phylogenetic clustering found at high elevations in the Hengduan Mountains and high phylogenetic turnover across elevations implies that only a relatively few lineages are able to colonize high elevations, and overall lineages are limited in their ability to evolve across elevational ranges. This, in turn, could limit the steady-state number of species persisting at high elevations.

The issue of species pools is also intertwined with the issue of spatial scale. In the BEA model, area peaks at intermediate elevations, and this is one factor promoting high species richness at mid-elevations. This expectation assumes that the whole relevant area for the species pool is within the mountainous landscape. However, a previous study (Sanders 2002) on elevational gradients in ants made a different argument; that richness followed species-area relationships, and area declines with elevation using empirical data (e.g. not just based on a simple “mountain cone” analogy). The difference is that the latter study used entire US states (e.g. Colorado, Wyoming) to be the focal areas, where mountain ranges may be surrounded by vast expanses of low-elevation plain, and thus area has an overall declining relationship with elevation. This could be a factor in our study as well, the lower-elevation areas within the mountain landscape are essentially connected to vast expanses of the Indo-Gangetic Plain, greatly increasing the potential species pool and increasing colonization rate of species into lower elevations relative to mid-and high-elevations. The above factors could all systematically change the rate of species input into the system across elevation and affect elevational richness gradients.

Overall, despite the discrepancies between the BEA model and our empirical system, I think the former represents a promising first step toward an integrative metacommunity approach to biodiversity patterns in mountainous landscapes. The issues addressed above, particularly more explicit treatment of species pools, colonization rates, niche lability, and the issue of spatial scale, could be addressed in future extensions and iterations of theory. If such advances can be made to tie general theory more closely to empirical systems, it would facilitate a more penetrating comparison of this class of theory with other qualitatively different explanatory frameworks. For example, the BEA model is based on the more general idea in metacommunity theory, tracing back to the island biogeography theory (MacArthur and Wilson 1963) and later neutral theory (Hubbell 2001), that species input and extinction interact with habitat area and connectivity to drive diversity patterns. Environment is included, but only to limit species distributions rather than having a direct influence on community level structure. A wholly different kind of explanation would be that environmental factors such as temperature (possibly through energy and productivity) have a direct influence on local species coexistence, which provides local constraints on richness that scale up to landscape-level patterns (Currie 1991, Waide et al. 1999, Clarke and Gaston 2006, Hessen et al. 2007).

5. Comparative phylogeography, phylogenomics, and population genomics of the ant genus *Strumigenys* in the Pacific archipelago

5.1 Introduction

Current biodiversity patterns are products of historical macroevolutionary dynamics. The macroevolutionary dynamics lead to the ecological divergence across lineages, specialization for particular niches, radiation, speciation, and ultimately extinction. However, the extent to which macroevolution dynamics are the consequence of stochastic events vs. more predictable pathways in generally unclear except for a few well study cases (Losos et al. 1998, Gillespie 2004).

The biodiversity patterns can be driven by historical contingencies. These random historical events such as the appearance of new traits or colonization of new geographic region can have large effects on subsequent evolution and lead to different evolutionary outcomes (Travisano et al. 1995). For example, some biotas that evolved in a similar environment can have more differences than similarities (Orians and Paine 1983). As S. J. Gould has argued in his “replaying life’s tape” test: it would not be the same music if the tape of life can be replayed (Gould 1989). On the other hand, we might expect biodiversity dynamics to be more predictable because a certain eco-morphological trait may be favored repeatedly in the habitats with similar ecological niche (Mahler et al. 2013). E. O. Wilson has argued for the great importance of deterministic macroevolutionary dynamics in his taxon cycle hypothesis, which proposes a predictable sequence of colonization, expanding, radiation, speciation, constriction, and extinction in Melanesian ants (Wilson 1959, 1961). Recent studies have revisited and tested this theory by using modern methods in both ants (Sarnat and Moreau 2011, Economo and Sarnat

2012, Clouse et al. 2015) and other organisms (Cook et al. 2008, Jønsson et al. 2014). However, testing such a theory is still challenging due to its complexity.

Remote island archipelagos can be considered as ideal natural laboratories for understanding the fundamentals of speciation and radiation, as well as the macroevolutionary dynamics (Warren et al. 2015). For example, the Pacific archipelagoes not only provided the basic foundation for developing the original hypotheses of the notable taxon cycles (Wilson 1959, 1961), but also offered the opportunities for other studies to test those hypotheses (Sarnat and Moreau 2011, Economo and Sarnat 2012). The Fiji Islands supports a diverse terrestrial biota, with high rate of endemism. For example, there are 188 ant species from 43 genera on the islands, and more than 68% of Fijian ant species are endemic (Sarnat and Economo 2012). This high level of endemism together with low rates of colonization across oceanic islands makes Fijian ants a suitable system for studying the underlying drivers of adaptation and speciation. Recent studies have focused on the phylogenetic, geographic, morphological evolution patterns on Fiji islands for understanding the historical macroevolutionary dynamics that shaped the high endemism of Fijian ants (Sarnat and Moreau 2011, Economo and Sarnat 2012). However, those studies were based on one ant genus *Pheidole* which only represents 11% of Fijian ant fauna. It is not clear whether the evolutionary processes that drive the speciation and radiation of *Pheidole* are unified across different radiations on Fiji islands. Moreover, previous studies have only focused on the evolutionary consequences of morphological, ecological and geographic space at the level of interspecific comparison, leaving the patterns and mechanisms of intraspecific genetic structure differentiation unexplored. These population-level genetic partitions across geographic space might provide valuable information about the starting point of macroevolutionary diversification between species (Bowen et al. 2016).

In the current study, I highlight a comparative phylogeography framework that investigates microevolutionary divergence processes across an entire insular radiation to infer the underlying drivers of diversification and radiation on Fijian ant fauna. The hyperdiverse genus *Strumigenys* (Formicidae: Myrmicinae) is the ideal clade to address the mechanisms speciation and radiation. It is the third most speciose ant genus with more than 1000 described species across tropical and subtropical forest on earth (Bolton 2000). *Strumigenys* ants also have very high diversification rate compare to other insect group (Moreau et al. 2006, Pie and Tschá 2009), and the reasons promote this high diversification rate remains one of the mysteries in ant evolution. Despite the high taxonomic diversity and endemism, Fijian *Strumigenys* ants exhibit great morphological variations which might be the evidence of morphological divergence driven by ecological release. For example, Fijian endemic species *Strumigenys nidifex* has evolved exceptional large body size compared to other Fijian endemic *Strumigenys* ants, which might allow it to expand its foraging range in the absent of effective competitors (William and Wilson 1959).

Here, I revisit the radiation and speciation of Fijian ant fauna with a comparative phylogeographic perspective. There are three objectives in this study. First, I reconstruct a time-calibrated phylogeny of Fijian *Strumigenys* using restriction site-associated DNA sequencing (RADseq; Baird et al. 2008), and test whether the high endemism of Fijian *Strumigenys* was the consequence of *in situ* radiation or was the result of multiple colonization. Second, I combine the phylogenetic, morphological, as well as ecological and geographic distribution data of Fijian *Strumigenys* to test two hypotheses describing the macroevolutionary dynamics of Fijian *Strumigenys*: 1) *Dispersal assembly*: The current niche occupation of Fijian *Strumigenys* was due to the direct colonization from the similar niche of different region. For example, species from high-elevation forest in New Guinea colonize the high-elevation forest in Fiji directly. Under this hypothesis, I expect no ecological niche shift after colonization in Fijian *Strumigenys* (e.g., from lowland forest to high-elevation forest). I also expect the morphology of *Strumigenys* is highly conserved and the phenotypic differences were assembled by colonization, not *in situ* evolution. 2) *Evolutionary assembly*: Current Fijian *Strumigenys* distribution patterns were the consequences of adaptation and radiation after colonization. For example, the high-elevation forest adapted *Strumigenys* ants in Fiji evolved *in situ* from lowland forest species. This hypothesis is similar to taxon cycle hypothesis (Wilson 1959, 1961). Under this hypothesis, I expect an ecological niche shift of Fijian *Strumigenys* after colonization. I also expect morphological divergence of Fijian *Strumigenys* associated with niche shift evolve *in situ* after colonization. Finally, I use a comparative phylogeographic framework to test the predictions associated with the phylogeographic patterns of Fijian *Strumigenys* species that undergone similar or different demographic history. I expect that: a) For tramp species *S. godeffroyi* and *S. rogeri*, their high dispersal ability increase the gene flow between different islands, leading to low genetic differentiation (e.g., low F_{st}) and no clear population structure between different islands. b) All the endemic species exhibit clear population structure between different islands. c) Greater genetic differentiation (e.g., high F_{st}) will be found in the species that occupied high-elevation habitat due to the difficulty of maintaining gene flow.

5.2 Material and methods

5.2.1 Taxon sampling

I sampled 305 specimens that represent 22 *Strumigenys* (Hymenoptera: Formicidae) species (Appendix Table 8.3). Among them, 11 species are Fijian endemics, 9 are endemic to Malay archipelagos, and two are worldwide distributed. Fijian specimens were identified to species or morphospecies by Sarnat and Economo (Sarnat and Economo 2012). All sequences and voucher specimens are located in Economo's lab at Okinawa Institute of Science and Technology Graduate University, Okinawa, Japan.

5.2.2 RAD sequencing

The genomic DNA of each specimen was extracted using the non-destructively method by soaking it overnight in a chaotropic buffer (Tin et al. 2014). RAD library preparation was performed as in Tin et al. (2015) by using a Biomek® FXP Laboratory Automation Workstation (Beckman Coulter). RAD sequencing was performed on Illumina HiSeq 25000 platform. Samples were de-multiplexed, separated by individual, filtered by quality, and trimmed to 55bp using Trimmomatic (Bolger et al. 2014)

5.2.3 RAD loci assembly and genotyping

5.2.3.1 Loci assembly for phylogenetic analysis

I first assembled a dataset by selecting maximum 10 specimens with highest data coverage (raw reads) after demultiplexity from each species (Appendix Table 8.3). I then *de novo* assembled the loci from raw RAD data using ipyrad (Eaton and Ree 2013). I largely followed the default setting for the assembling parameters, except we deleted the parameter 8 ("restriction_overhang") in the parameter file since our samples were already demultiplexed. More specifically, I first filtered the reads with more than 5 ambiguous sites (Phred quality score <20). I then clustered the filtered reads within each sample using 85% sequence similarity. After the consensus sequences were called within each sample, I remove the potential paralogs by filter out the consensus loci with more than 2 alleles. Finally, I clustered the loci across samples at 85% similarity and removed the loci with low than 4X converge. The final assembled sequence and SNP datasets were exported in various formats (see ipyrad document for details).

5.2.3.2 Genotyping for comparative phylogeographic inferences

In order to examine the phylogeographic structure of Fijian *Strumigenys* ants, I applied separate ipyrad *de novo* assembly analyses on each of 7 Fijian *Strumigenys* datasets (*S. godeffroyi*, *S. rogeri*, *S. basiliska*, *S. chernovi*, *S. ekasura*, *S. nidifex*, and *S. sulcata*

; Appendix Table 8.4 – 8.10). I used the same parameter setting as above except I increased the loci converge in the final matrix to 70% across all samples.

5.2.4 Phylogenomic analysis

Because the 3' edge of loci were not well aligned and might introduce false SNP calling, I trimmed the last 5bps of each final aligned loci from .loci file, and then concatenated all loci into one supermatrix using python script. I then inferred the phylogenetic relationship using ExaBayes version 1.5 (Aberer et al. 2014). I conduct two independent runs for 2 million generations, each with two heated chains, and sampling every 1000 generations. I assessed the convergence by examining whether the ESS of all parameters were greater than 200 in Tracer version 1.6 (Rambaut and Drummond 2007), and by checking whether the average standard deviation of the split frequencies outputted from ExaBayes tool 'sdsf' was close to zero. Finally, I summarized a consensus tree (greedily refined majority-rule tree) using the 'consense' program from ExaBayes package.

I estimate the divergence dates of Fijian endemic *Strumigenys* using BEAST version 2.4.4 (Bouckaert et al. 2014) with molecular evolution model set to GTR+I, and molecular clock model set to uncorrelated lognormal relaxed clock with Yule speciation process. For the date calibration, I use the divergence date of Fijian *Strumigenys* from a separate project (Booher et al. *In preparation*). I implemented a normal distribution with a mean of 6 Ma and sigma of 1.0. I fixed the tree topology by using the phylogeny obtained from ExaBayes as starting tree. I ran the MCMC chain for 3 x 10^7 generations, sampling every 5000 generations. After checking the results in Tracer, I generated the maximum credibility clades trees using TreeAnnotator with the first 10% of posterior trees discarded as burn-in.

5.2.5 Morphological data

I assembled a morphometric dataset by measuring the head length (HL), head width (WL), scape length (SL), eye length (EL), Weber's length (WL), and pronotum height (PrH) for each sequenced Fijian *Strumigenys* specimens (281 specimens). All measurements were log-transformed, and combined as a covariance matrix for the subsequent Principle components analysis (PCA).

5.2.6 Phylomorphospace distribution

I first conduct a PCA analysis on the morphometric covariance matrix to identify the main sources of Fijian *Strumigenys* morphological divergence. I then examined the morphological diversification and occupation of Fijian *Strumigenys* across phylogeny by reconstruction a phylomorphspace using the *phylomorphospace* function in the R package *phytools* (Revell

2012). In this approach, the phylogenetic arrangement of Fijian *Strumigenys* was plotted in a two-dimensional morphospace delimited by PC1 and PC2, as well as PC1 and PC3.

5.2.7 Phylogeographic structure

5.2.7.1 SNP filtering

I applied ipyrad analyses on each of the 5 Fijian endemic *Strumigenys* species and exported the SNP data in VCF files. I first removed the SNPs that appeared at the last 5bp of each locus since they were false variants due to bad alignment. For the downstream population structure inferences such as PCA, sNMF, I randomly selected one SNP per locus to reduce the effect of linkage disequilibrium.

5.2.7.2 Population structure inference

To assess the degree of genetic clustering among the individuals that across different islands, I first examined genetic structure by conducing Principle Component Analysis (PCA) on SNP data using the Python package *scikit-allele* (Miles and Harding 2016). I then used sNMF version 1.2 (Frichot et al. 2014) to test the most likely number of genetic clusters within each species (*k*) and assign individuals to populations. I tested each *k* value (range from 1 to 10) with 20 replicated runs, and then examined their cross-entropy criterion of each *k*. sNMF results were visualized in R and the *k* value that minimizing the cross-entropy criterion was determined as optimal *k*. Finally, I used the Neighbor-Net algorithm (Bryant and Moulton 2004) implemented in the program SplitsTree version 4.14.4 (Huson and Bryant 2006) to visualize population structure by generating phylogenetic networks.

5.2.7.3 Summary statistics

Genetic diversity including nucleotide diversity and F_{st} were estimated using Python package *scikit-allele*. Pairwise F_{st} between each population was estimated at per-SNP as well as genome-average level.

5.3 Results

5.3.1 Phylogenomic analyses of Fijian *Strumigenys*

We ran ipyrad assembly on 124 specimens that include 11 Fijian endemic *Strumigenys* along with additional 11 outgroup species. The statistical summary of each sample after ipyrad can be found in Supplementary material (Appendix Table 8.3). The final concatenated super-matrix for the phylogenomic analysis contain 267715 loci and 9958618 bps. The tree topology inferenced by Bayesian method showed strong support (100% bpp) for the monophyly of Fijian endemic *Strumigenys* (Figure 5.1), indicating that the high endemism of this genus was due to *in situ* radiation not multiple colonization. The divergence dating analyzing using BEAST2 revealed the history of *Strumigenys* ant that colonized to Fiji in Miocene (10.5-7.5 Ma), followed by two independent radiations across the whole archipelago, leading to the emergence of 11 endemic species (Figure 5.2A).

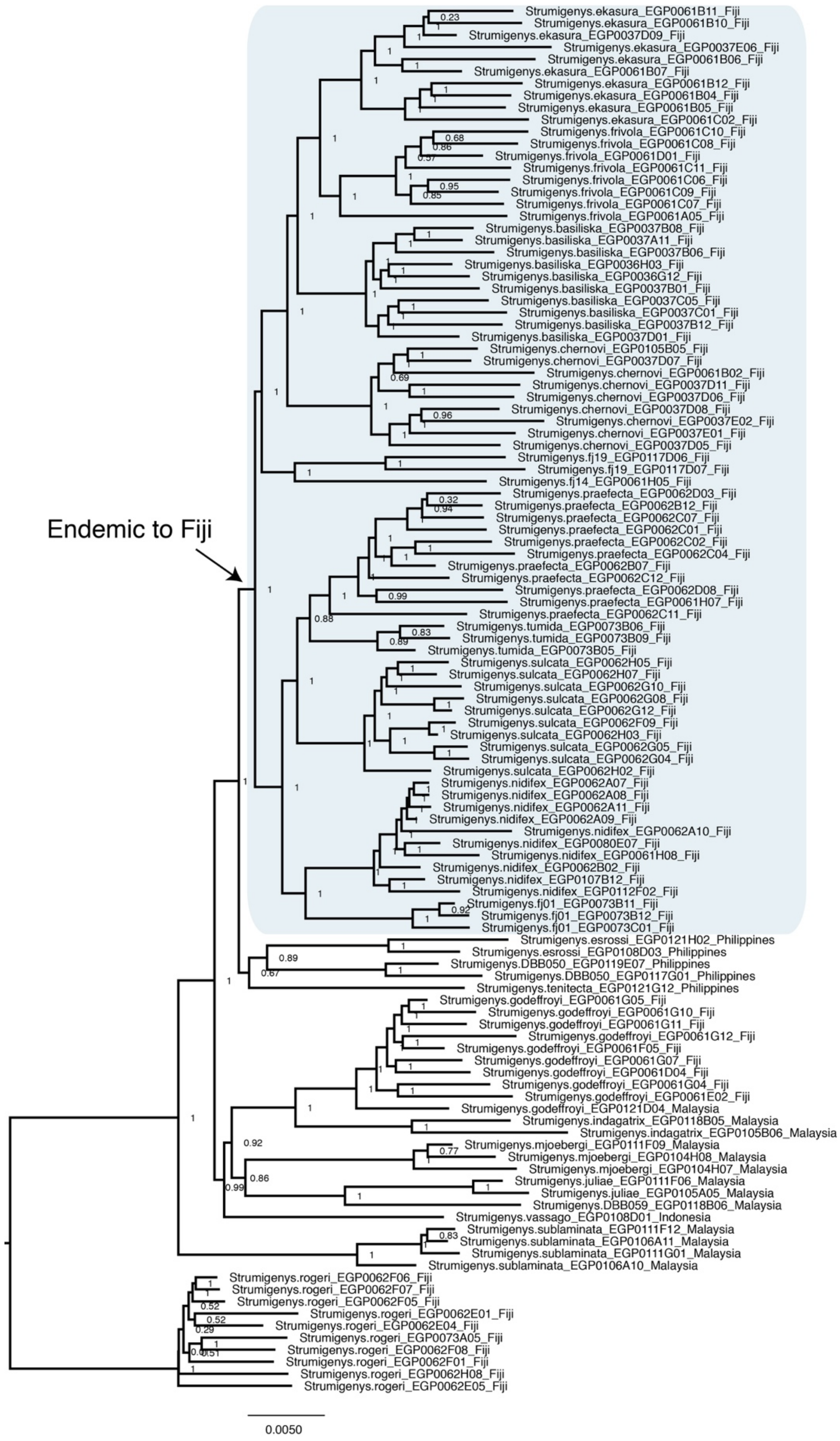

Figure 5.1 | Fijian *Strumigenys* phylogeny showing Bayesian topology.

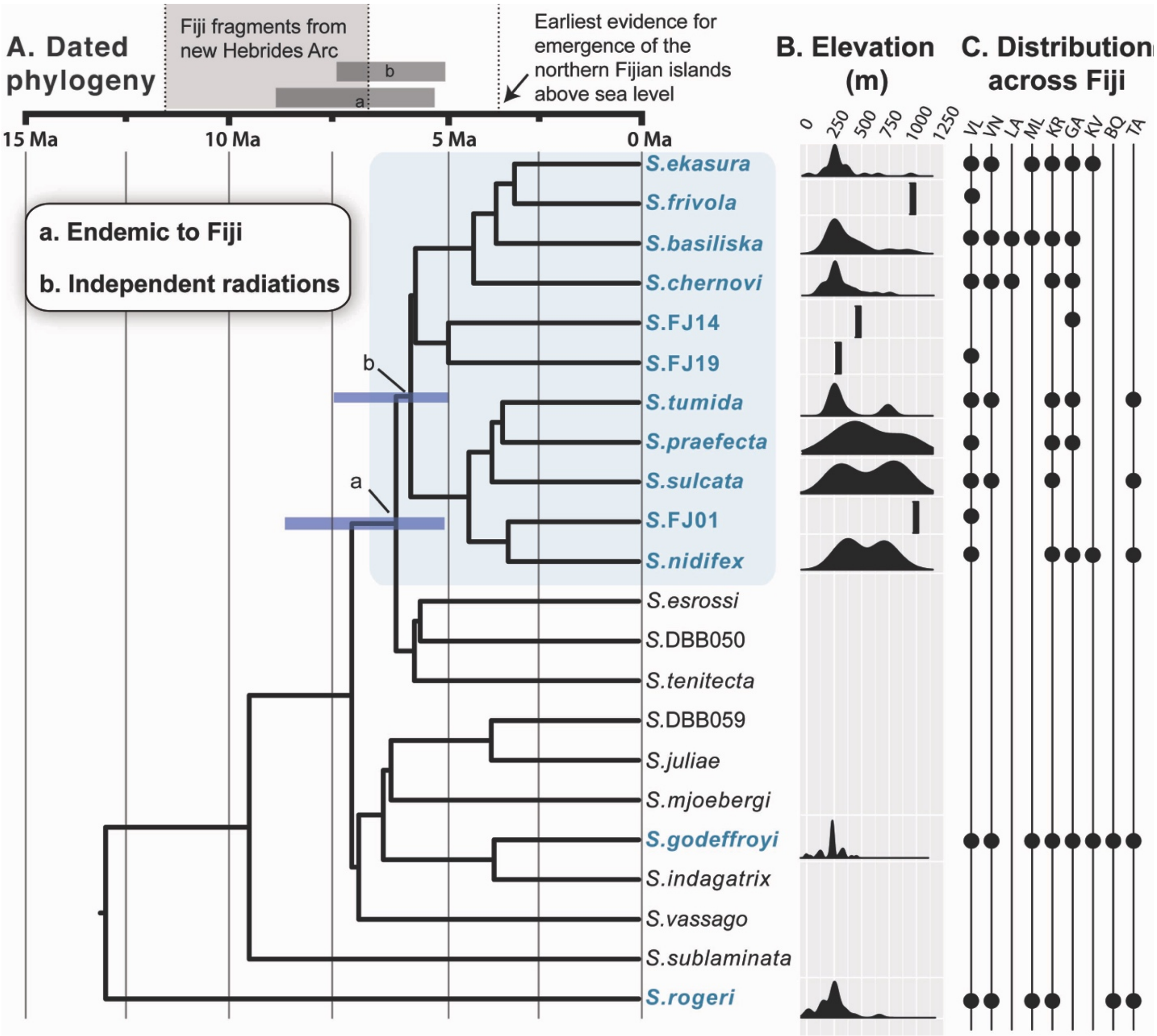

Figure 5.2 | Fijian *Strumigenys* radiation and diversification.
(A) Dated chronogram of Fijian *Strumigenys* inferred by Bayesian method based on 267715 RAD loci showing two independent radiations of *Strumigenys* in Fiji archipelago. **(B)** The elevation distribution (loess-smoothed) indicated that in general, the species in small size clade tend to live in low elevation, while large Fijian *Strumigenys* were often found in low and high elevation. **(C)** Species distribution across the whole archipelago. VL, Viti Levu; VN, Vanua Levu; LA, Ovalau; ML, Moala; KR, Koro; GA, Gau; KV, Kadavu; BQ, Beqa; TA, Taveuni.

5.3.2 Morphological divergence and phylomorphospace reconstruction

Principal component analysis of morphological measurements showed that the first three components accounted for 98.3% of total variation, 91.3% of which corresponded to PC1. All other PCs accounted for less than 2% of the variation, and were not considered further. PC1 represented general body size, while PC2 and PC3 were related to eye size and mandible size (Table 5.1). Phylomorphospace plot indicated a considerable amount of morphological divergence between the two clades of Fijian *Strumigenys* ants (Figure 5.3). PC1 separated the 2 Fijian *Strumigenys* clades into "large *Strumigenys* clade" (*Hereafter*, includes *S. nidifex*, *S.* FJ01, *S. sulcata*, *S. tumida*, and *S. praefecta*) and "small *Strumigenys* clade" (*Hereafter*, includes *S. frivola*, *S. ekasura*, *S. basiliska*, *S. chernovi*) with positive values indicating larger body size (Figure 5.3). PC2 further separated ant species within each clade related to their eye size (Figure 5.3A). It is worth noting that the two subterranean species *S.* FJ14 and *S.* FJ19 have relative small eyes compare to other species. The PC1-PC2 plot indicated that Fijian *Strumigenys* radiations with a large amount of divergences related to body size and eye size. However, the PC1-PC3 plot showed that the change in mandible size was much slower compare to body size and eye size with one expectation (*Strumigenys* FJ19, Figure 5.3B).

Table 5.1 | PCA loadings of Fijian *Strumigenys* morphological measurements.

	PC1	PC2	PC3
HL	0.385	-0.396	0.060
HW	0.372	-0.461	0.185
SL	0.388	0.061	-0.369
ML	0.375	0.180	0.718
EL	0.352	0.767	0.361
WL	0.393	-0.075	0.094
PrH	0.379	-0.022	0.413

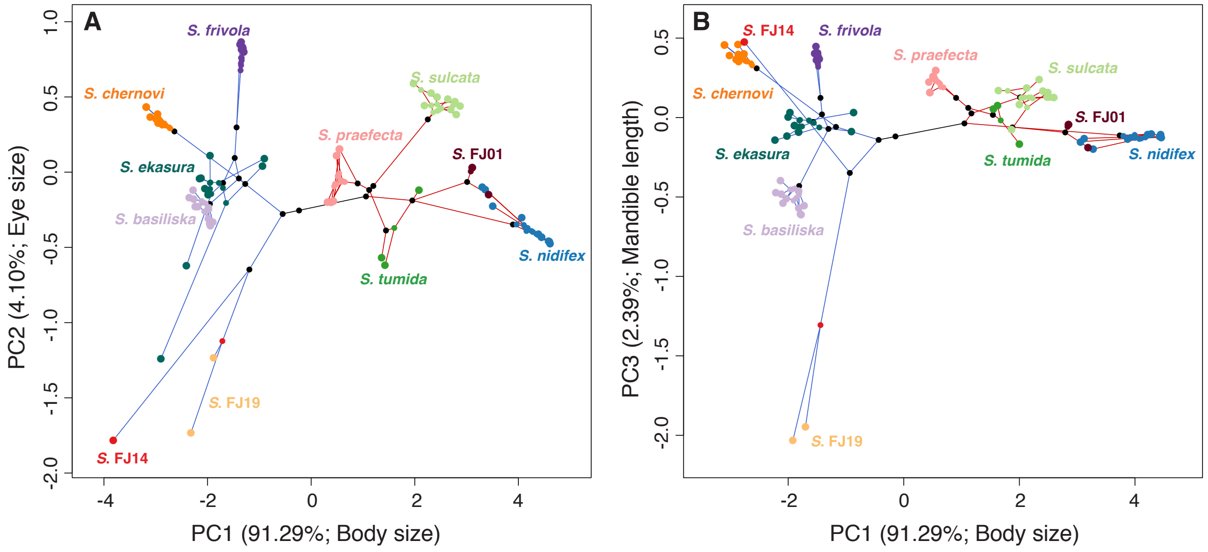

Figure 5.3 | Phylomorphospace of morphological divergence in Fijian *Strumigenys*.
(**A**) PC1 vs. PC2 and **(B)** PC1 vs. PC3. The dots in the same color indicate specimens from same species. The red branch indicates large *Strumigenys* clade (negative PC1) and the blue branch represents the small *Strumigenys* clade (positive PC1).

5.3.3 Geographic distribution and ecological niche shift in Fijian *Strumigenys*

Most Fijian *Strumigenys* species are widely distributed across the whole archipelago except *S. frivola*, *S.* FJ01, *S.* FJ14, and *S.* FJ19 which have been only collected from one locality (Figure 5.2C). Two tramp species *S. godeffroyi* and *S. rogeri* were only found in low-elevation forest. Within the endemic radiation, the ants from small *Strumigenys* clade are often found in low-elevation primary forest, while the large Fijian *Strumigenys* species were found in both low and high elevation forest (Figure 5.2B). Interestingly, all species from the large *Strumigenys* clade were found in the high mountains of the main island, Viti Levu (VL). Those results might indicate the niche shift between the two clades of endemic Fijian *Strumigenys*.

5.3.4 Phylogeographic structures of Fijian *Strumigenys*

I reconstructed the phylogeographic structure of 5 endemic *Strumigenys* species with 3 species (*S. ekasura*, *S. basiliska*, and *S. chernovi*) from the small *Strumigenys* clade, and 2 species (*S. sulcata*, and *S. nidifex*) from the large *Strumigenys* clade, as well as 2 Fijian tramp *Strumigenys* species (*S. rogeri* and *S. godeffroyi*). As expected, I did not find any population structures on the 2 tramp species (Figure 5.4A, B). PCA on SNP genotypes showed that all Fijian endemics *Strumigenys* species grouped geographically with individuals collected from the same locality clustered together (Figure 5.4C, D, E, F, G). The population clustering patterns of those species vary. For example, the individuals of *S. chernovi* and *S. ekasura* collected from each island clustered as separate population (Figure 5.4D, E), while ant samples from multiple islands were in some species clustered as a single population (KR+VN+VL+LA in *S. basiliska*, KV+VL in *S. nidifex*, and KR+VL in *S. sulcata*; Figure 5.4C, F, G). Interestingly, one population of *S. sulcata* collected from west of VL was significantly distinct from the rest of VL samples in the PCA plot (Figure 5.4G), indicating large genetic differentiation of population within the same island. In contrast, the Fijian tramp *Strumigenys* did not show any genetic structure, and had no clear cluttering patterns in the PCA (Figure 5.4A, B).

When further investigating the potential population structure, we analyzed the genotype matrices of each species using sNMF (Frichot et al. 2014). The best-supported K value of the two tramp species *S. rogeri* and *S. godeffroyi* is 1, indicating no population structure across different islands. The optimum K values as well as the population assignments on the 5 endemic species were largely consistent with the PCA (Figure 5.5).

To aid in the determination of potential population structure of Fijian *Strumigenys*, we further used phylogenetic network inference implemented in SplitsTree on our dataset. Based on the Neighbor-Net algorithm (Bryant and Moulton 2004) conducted on our SNP data, SplitsTree produced a tree for each species (Figure 5.6) that was congruent the genetic clusters inferred by sNMF and PCA.

After the population structure of each species was inferred by sNMF, we calculated the average F_{st} for pairwise comparisons of all populations for each species. The F_{st} values among all populations of different species vary from nearly 0 to 0.3 indicating the different level of genetic differentiation of different species (Figure 5.7). For example, the F_{st} values of *S. godeffroyi* and *S. rogeri* were very small suggesting little genetic differentiation in those two tramp species, while the F_{st} values in *S. sulcata* are around 0.3 indicating that populations were notably divergent from each other. It is worth noting that the 3 species from small *Strumigenys* clade (*S. basiliska*, *S. chernovi*, and *S. ekasura*) showed less genetic differentiation compared to the 2 species from large *Strumigenys* clade (*S. nidifex* and *S. sulcata*). The results proved our prediction that species that occupied in high-elevation forest (e.g., *S. nidifex* and *S. sulcata*) have greater genetic differentiation.

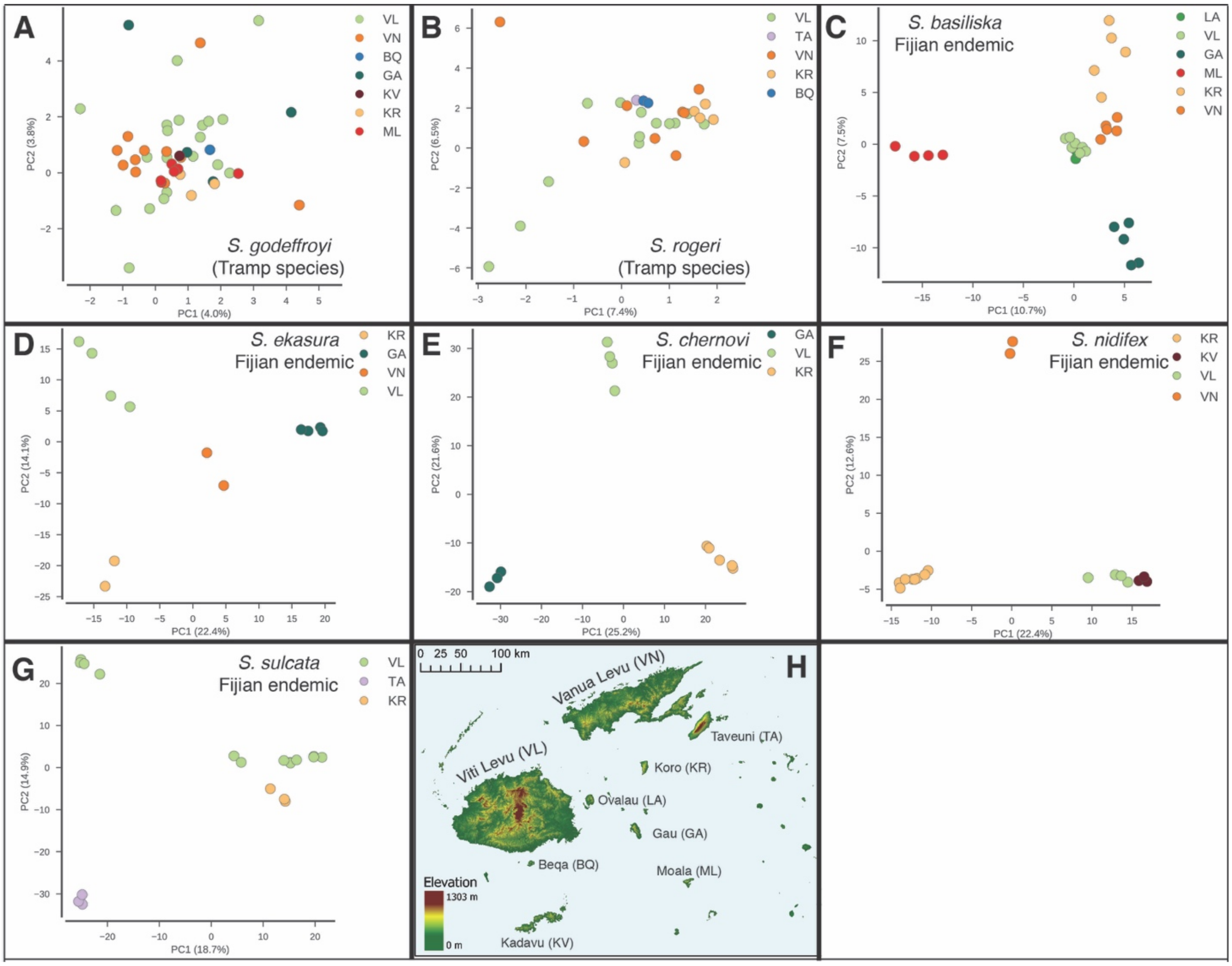

Figure 5.4 | Principal components analyses (PCA) on SNP genotypes for Fijian *Strumigenys* to characterize genetic differentiation among different islands.
No clear population structure was found in the two tramp species (A, B). All the endemic species exhibited clear population structures (C-G). (H) the map of Fiji archipelago. Colors and abbreviations correspond to different island.

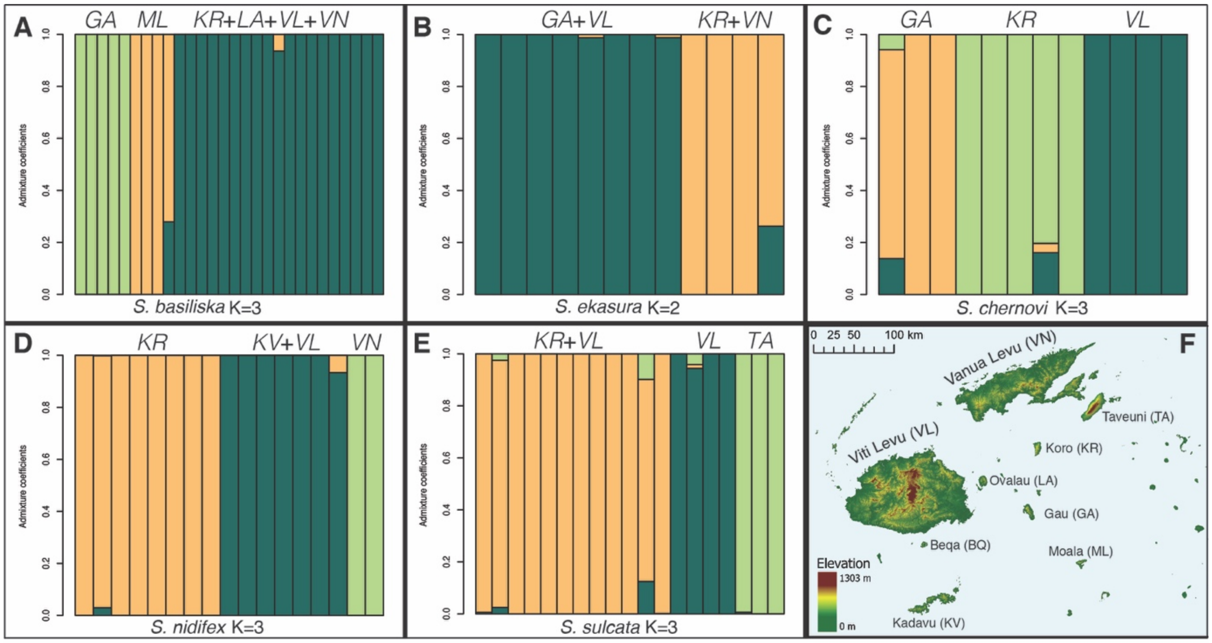

Figure 5.5 | Estimation of population structure of Fijian *Strumigenys* based on sNMF analysis on SNP genotype data from RADseq.
Different color corresponds a distinct genetic cluster and the bar corresponds to the admixture proportion of that individual's genotype assigned to each cluster. The island abbreviations above the bar indicate where the individual came from, and the k values bellow the bar are the best support k values from sNMF. (A) *S. basiliska*; (B) *S. chernovi*; (C) *S. ekasura*; (D) *S. nidifex*; (E) *S. sulcata*; (F) the map of Fiji archipelago. Please note that we did not include the two tramp species *S. godeffroyi* and *S. rogeri* since no genetic structures were found on them (best supported k values for both species are 1).

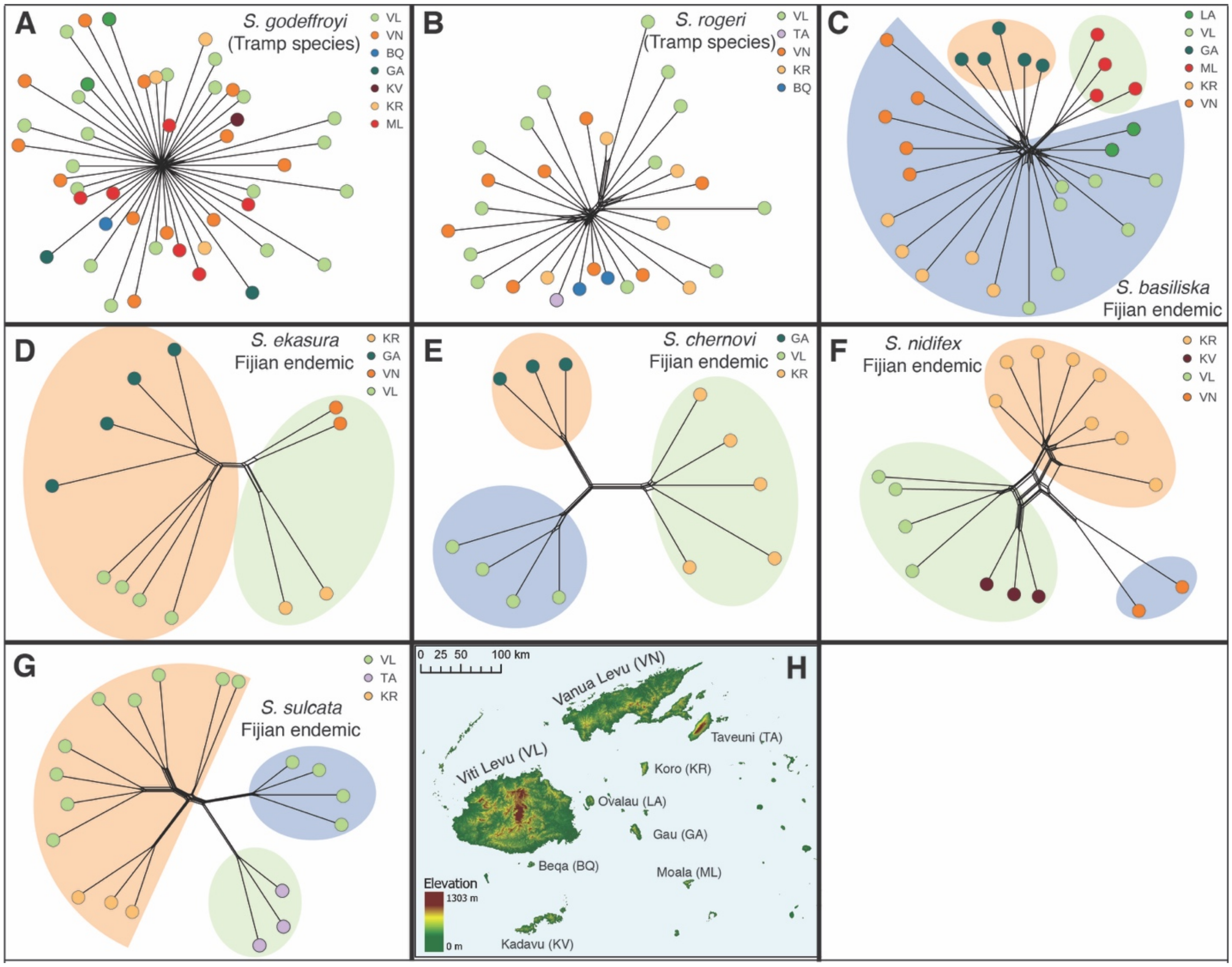

Figure 5.6 | Neighbor-net tree of Fijian *Strumigenys* inferred in SplitsTree to characterize genetic differentiation among different islands.
No clear population structure was found in the two tramp species (A, B). All the endemic species exhibited clear population structures (C-G). (H) the map of Fiji archipelago. Colored nodes at the terminal of tree correspond to the sample from different island. The colored shade indicates the genetic clusters inferred from sNMF.

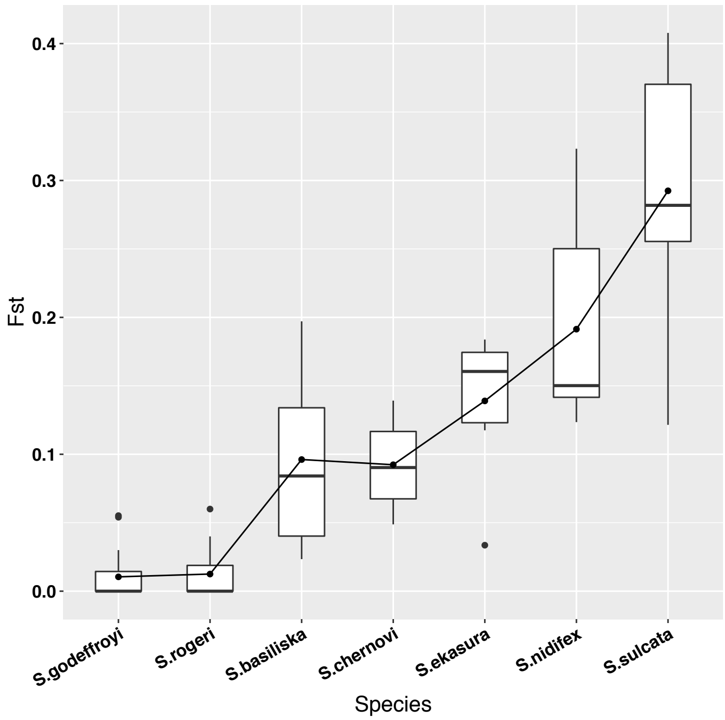

Figure 5.7 | Average F_{st} for pairwise comparisons of all populations for each Fijian *Strumigenys* species.
The number of pairwise comparisons depends on the number of populations inferred from sNMF. For *S. godeffroyi* and *S. rogeri* with no population structure, we calculated F_{st} between the samples from different islands. The box encloses the 25-75th percentiles of the values, the whisker extends to 1.5 times the interquartile range. The line connected the mean of F_{st} distribution for each species.

5.4 Discussion

Our comparative phylogeographic analysis of Fijian *Strumigenys* using RADseq revealed a number of microevolutionary and macroevolutionary patterns that provide new insights into radiation and speciation of Fijian ant fauna. Those findings recovered the biogeographic history of ant genus *Strumigenys* that colonized the Fiji Islands in Miocene followed by two independent radiations with subsequent niche shift and ecological release. Taken together, our results highlight the role of deterministic macroevolutionary processes in driving the radiation and diversification of Fijian *Strumigenys*.

5.4.1 Biogeographic history of *Strumigenys* in Fiji archipelago

There were at least three colonization events of *Strumigenys* on Fiji, and the earliest colonization event was dated back to 18-8 Ma. Those findings were consistent with other studies of Fijian ant radiations (Lucky and Sarnat 2010, Sarnat and Moreau 2011), supporting an idea a Laurasian origin of Fijian insect fauna (Balke et al. 2007, Sarnat and Moreau 2011). By approximately 8 Ma, the ancestor of all Fijian endemic *Strumigenys* had diverged, followed by two independent radiations. The monophyly of Fijian endemic *Strumigenys* revealed by our phylogenomic analysis suggests a single origin of high endemism of *Strumigenys*. According to the timing of divergence as well as the emergence time of each island, we can conclude that all the endemic species originated on Viti Levu before colonizing other islands. Indeed, Viti Levu is the oldest and largest island in Fiji and is often considered as the source of other island populations (Lucky and Sarnat 2010, Sarnat and Moreau 2011).

5.4.2 Ecological niche shift and radiation in Fijian *Strumigenys*

Within the Fijian endemic clade, our analysis recovered two independent radiations leading to the emergence of 11 endemic *Strumigenys* species. The results showed a ecological niche shift from low-land to high elevation habitat between those two endemic lineages. The species from the small *Strumigenys* clade only live in the lowland forest like the two tramp species *S. godeffroyi* and *S. rogeri*, while the large Fijian *Strumigenys* ants are more common in the high-elevation forests. This niche shift indicates a pattern of colonization and speciation towards the high-elevation habitat. In other words, high-elevation adapted species evolved *in situ* from the lowland habitat. These results are consistent with the taxon cycle prediction about ecological niche shift after colonization (Wilson 1959, 1961). Previous studies of the Fijian *Pheidole* radiation also found a similar pattern of niche shift from low and mid-elevation primary forest to high-elevation forest (Economo and Sarnat 2012).

5.4.3 Morphological shift and ecological release in Fijian *Strumigenys*

According to taxon cycle, adaptation to different habitats is often associated with morphological differences (Wilson 1959, 1961). For example, the Fijian Pheidole species that adopted to forest habitat tend to be more spinescent compare to the species live in the open habitat (Economo and Sarnat 2012). I also found morphological divergence between the two Fijian *Strumigenys* lineages. For example, the 5 species in large *Strumigenys* clade have undergone an increase in body size, while the 4 species from small *Strumigenys* clade stayed the similar size as their ancestors from the mainland (Figure 5.3). The increase of body size in island system has been considered an efficient way to reduced interspecific competition because the larger individual often has wider niche breadth, and can eat both small and large food. (Palkovacs 2003). *Strumigenys* ants are highly specialized predator that predate arthropods such as Springtails (Collembola) by using their trap jaws (Wilson 1950). Thus, for Strumigenys, increasing body size should dramatically increase their niche breadth. Although Collembola are very common and diverse in tropical forest, their abundance on a Pacific island like Fiji is still limited, and the increase of body size will allow *Strumigenys* ants to catch larger preys and expand their forage range (William L. Brown and Wilson 1959). Therefore, the body size differences between those two sister lineages of *Strumigenys* might lead to resource partitioning of prey size and facilitate species coexistence.

Those morphological divergences between the two endemic clades might also suggest an important role of adaptive radiation in historical Fijian *Strumigenys* diversification. Adaptive radiation on oceanic islands has been commonly recorded from diverse taxa such as birds, lizards, spiders, and snails (Losos et al. 1998, Chiba 2004, Gillespie 2004, Reding et al. 2009), and has also been considered as the evidence of ecological release (Gillespie 2009). Indeed, our phylogenomic analysis of Fijian *Strumigenys* revealed that larger body size of Fijian endemic *Strumigenys* ants did not inherit from other *Strumigenys* species, but resulted from the ecological release of its ancestor upon colonizing Fiji island. When the ancestral *Strumigenys* arrived in the Fiji archipelago, they quickly occupied the habitat where they are preadapted such as lowland forest and started to expand their range and species diversification. Some of them evolved larger body size enabling them to catch larger prey that was previously barred and therefore allowing them to escape from their niche constraints and expand their ecological dimensions (e.g. reaching higher elevation). Taken together, our results support a more deterministic macroevolutionary pathway in Fijian endemic *Strumigenys* radiation.

5.4.4 Implication from comparative phylogeographic partitions

By using a large number of genome-wide SNPs, our analysis revealed many phylogeographic patterns among Fijian *Strumigenys* species. First, no genetic differentiations were found across island populations in two tramp *species S. godeffroyi* and *S. rogeri.* Both species are widely distributed across Southeast Asia and Oceania, and their strong dispersal ability allows frequent gene flow between island population and prevent the divergences. Second, although all 5 endemic species from both clades showed some level of genetic differentiation among their island populations, the genetic differentiation in the small size clade was much smaller than the in the large size clade. For example, the average pairwise F_{st} in *S. basiliska* and *S. chernovi* is around 0.1, while the average pairwise F_{st} of *S. sulcata* is about 0.3. The reason for this discordant phylogeographic patterns between two endemic clades could be the low-land forests that small size *Strumigenys* inhabited facilitate oceanic dispersal between islands (Economo and Sarnat 2012), and reduce the level of genetic differentiation. The larger *Strumigenys* species have rarely been found in low-land forests across different islands. In contrast, they often have been found in the interior high-elevation forests from multiple islands. As a consequence, maintaining gene flow between interior habitats across different islands can be too much difficult of direct colonization from interior habitat in one island to another. Lastly, our findings also showed the similar phylogeographic patterns of *Strumigenys* species within each Fijian endemic clade, suggesting the shared evolutionary histories that drive the observed patterns among species in each clade. Indeed, the phylogeographic congruence we found among sister taxa within each endemic clade can provide key information about historical processes that shaping today's distribution of genetic variation within species (Papadopoulou and Knowles 2016).

Through the lens of comparative phylogeography, our results of phylogeographic patterns of Fijian endemic *Strumigenys* have significant implications for the macroevolutionary dynamics of Fijian *Strumigenys.* For the large Fijian *Strumigenys* species (*S. nidifex* and *S. sulcata*), the high genetic differentiation among populations, especially between low-land and high-elevation populations can be severed as the starting point for macroevolutionary divergences or speciation. On the other hand, the low level of genetic differentiation among island populations in the 3 small endemic species (*S. basiliska*, *S. chernovi*, and *S. ekasura*), together with their wide distribution at lowland forest suggested an early stage of population divergence.

6. Conclusions

6.1 Ant community assembly after conversion to agroecosystem

Understanding the effects of human agricultural activities on biodiversity is a pressing concern for ecology (Laurance et al. 2014). Our study found a suite of changes across different dimensions of biodiversity resulting from the conversion of natural forest to rubber plantation. Taken together, these results largely support a hypothesis of deterministic environmental filtering structuring communities in the agroecosystem. This likely reflects the strong ecological gradient formed by adjacent forest and plantation habitat. Variation in the sensitivity of ant species to habitat openness and disturbance is well documented (Economo and Sarnat 2012). This does not preclude the possibility that more stochastic, neutral dynamics dominate within similar habitats such as forests. To address such questions, it would be powerful to combine observational studies like this one with experimental manipulations, which are now increasingly common in plant community ecology (HilleRisLambers et al. 2012). Recently, researchers have started to test ant community assembly rules experimentally (Fowler et al. 2014, Fayle et al. 2015). Further research combining various approaches will benefit our understanding of the community ecology of ants in both natural habitats and agroecosystems, with consequences for basic and applied ecology.

Whether changes were consistent with null expectations, as with phylogenetic structure, or reflected deterministic reorganization, as with taxonomic and functional structure, we should not lose sight of the fact that biodiversity was much reduced in rubber plantation across all these dimensions. The links between diversity, community structure, and ecosystem functioning have long been suspected (Hooper et al. 2005) and now being demonstrated empirically through field studies in tropical environments (Ewers et al. 2015). Understanding the nature and effects of this biodiversity loss in ecologically dominant insect groups like ants remains a critical need for understanding the full consequences of the rapid emergence of agroecosystems like rubber plantation.

6.2 Ant community assembly in the complex mountains

Mountainous areas are significant centers for biodiversity, endemism, and conservation around the world (Myers et al. 2000, Fjeldså et al. 2012). Understanding the mechanisms that shape biodiversity patterns is necessary for designing effective conservation strategies as climate change alters the spatial and environmental structure of mountain landscapes worldwide (Elsen and Tingley 2015). However, inferring underlying processes from observed diversity patterns can be difficult due to the fact that multiple processes can contribute to the patterns simultaneously (e.g. environmental gradients and spatial structure, Leibold et al. 2004). By investigating ant taxonomic and phylogenetic diversity patterns in a complex mountainous landscape, this study showed that elevation-driven environmental gradients, spatial factors, as well as landscape geomorphology together affect ant biodiversity patterns in a mountainous biodiversity hotspot. Taken together, the study highlights the power of a pluralistic approach integrating field surveys with conceptual, statistical, and theoretical frameworks to understand the drivers of species distribution patterns. Future research bridging the gap between theory and the real-world systems will enhance our understanding of the mechanisms that govern biodiversity patterns.

6.3 Evolution and diversification of *Strumigenys* in Fiji archipelago

Understanding historical macroevolutionary dynamics can shed light on the debate of whether evolution follows deterministic pathways (e.g. Taxon cycle; Wilson 1959, 1961) or is driven by stochastic events, and will provide insight into the evolutionary processes that influence the community assembly. My analyses, combining phylogenomic, population genomic, morphological, geographic, and ecological data of Fijian *Strumigenys* ants investigated the evolutionary processes that generate and maintain ant community assembly in Fiji Islands. My findings recovered the biogeographic history of ant genus *Strumigenys* that colonized the Fiji Islands in Miocene followed by two independent radiations with subsequent niche shift and ecological release. These results revealed different micro- and macroevolutionary patterns between different Fijian *Strumigenys* lineages and provide new insights into radiation and speciation of Fijian ant fauna. For example, within the Fijian endemic *Strumigenys* clade, the species with larger body size shifted their niche from lowland to high-elevation forest which increased the genetic differentiation among populations, and can be considered as the early stage of speciation. Taken together, our results highlight the role of deterministic macroevolutionary processes in driving the radiation and diversification of insular ant linage.

6.4 Concluding remarks

Our understanding of the origin of biodiversity has been largely increased through two separate directions: ecologically and evolutionary. However, integration of those two directions is still difficult, and disentangling the relative importance of, and the interplay between, ecological and evolutionary processes in shaping biodiversity patterns is still a challenge. Here, I have demonstrated few different studies focused on the ecological and evolutionary processes that generate and maintain ant biodiversity patterns across multiple systems. Together, those studies provide a pluralistic framework that integrates different approaches as well as different study systems (agroecosystem, mountain landscape, and Pacific archipelago) to understanding the eco-evolutionary drivers of biodiversity patterns across scales.

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8. Appendix

Table 8.1 | Ant species (Formicidae) collected from Xishuangbanna, Yunnan in 2013.

Species	Collection record[1]
Aenictinae	
Aenictus artipus Wilson, 1964	N*
Aenictus hodgsoni Forel, 1901	N
Aenictus maneerati Jaitrong & Yamane, 2013	N*
Aenictus paradentatus Jaitrong, Yamane & Tasen, 2012	N*
Aenictus thailandianus Terayama & Kubota, 1993	N
Aenictus clm01	
Aenictus clm04	
Amblyoponinae	
Bannapone scrobiceps Guénard, Blanchard, Liu, Yang & Economo, 2013	N*
Mystrium camillae Emery, 1889	
Cerapachyinae	
Cerapachys clm2701	
Cerapachys sulcinodis Emery, 1889	
Cerapachys typhlus (Roger, 1861)	
Dolichoderinae	
Chronoxenus wroughtonii (Forel, 1985)	
Dolichoderus affinis Emery, 1889	
Dolichoderus laotius Santschi, 1920	N*
Dolichoderus squamanodus Xu, 2001	
Dolichoderus thoracicus (Smith, 1860)	
Iridomyrmex anceps (Roger, 1863)	
Tapinoma indicum Forel, 1895	
Tapinoma melanocephalum (Fabricius, 1793)	
Tapinoma clm04	
Technomyrmex albipes (Smith, 1861)	
Technomyrmex horni Forel, 1912	
Technomyrmex pratensis (Smith, 1860)	N
Ectatomminae	
Gnamptogenys costata (Emery, 1989)	N*
Gnamptogenys bicolor (Emery, 1989)	
Gnamptogenys treta Lattke, 2004	N*
Formicinae	
Acropyga nipponensis Terayama, 1985	
Anoplolepis gracilipes (Smith, 1857)	
Camponotus lasiselene Wang & Wu, 1994	
Camponotus mitis (Smith, 1858)	
Camponotus parius Emery, 1889	

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Table 8.1 (*continued*)

Species	**Collection record**[1]
Camponotus singularis Smith, 1858	
Camponotus clm02	
Camponotus clm03	
Camponotus clm04	
Camponotus clm07	
Camponotus clm08	
Camponotus clm09	
Echinopla cherapunjiensis Bharti & Gul, 2012	N
Gesomyrmex kalshoveni Wheeler, W.M. 1929	N*
Lepisiota opaca (Forel, 1892)	
Lepisiota rothneyi (Forel, 1894)	
Myrmoteras binghamii Forel, 1893	
Myrmoteras cuneonodum Xu, 1998	
Nylanderia clm01	
Nylanderia clm02	
Nylanderia clm03	
Nylanderia clm04	
Nylanderia clm05	
Nylanderia clm06	
Oecophylla smaragdina (Fabricius, 1775)	
Paraparatrechina clm01	
Paraparatrechina clm02	
Paraparatrechina clm03	
Paraparatrechina clm04	
Plagiolepis clm01	
Polyrhachis armata (Le Guillou, 1842)	
Polyrhachis bicolor Mayr, 1862	
Polyrhachis bihamata (Drury, 1773)	
Polyrhachis furcata Emery, 1889	
Polyrhachis halidayi Emery, 1889	
Polyrhachis hippomanes Smith, 1861	
Polyrhachis illaudata Walker, 1859	
Polyrhachis illaudata pauperata Emery, 1889	
Prenolepis naoroji Forel, 1902	
Prenolepis sphingthoraxa Zhou & Zheng, 1998	N
Pseudolasius cibdelus Wu & Wang, 1992	
Pseudolasius emeryi Forel, 1915	
Pseudolasius silvestrii Wheeler, 1927	
Myrmicinae	
Acanthomyrmex luciolae Emery, 1893	
Aphaenogaster beccarii Emery, 1887	
Aphaenogaster feae Emery, 1889	

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Table 8.1 (*continued*)

Species	**Collection record**[1]
Aphaenogaster clm05	
Cardiocondyla wroughtonii (Forel, 1890)	
Carebara affinis (Jerdon, 1851)	
Carebara altinoda (Xu, 2003)	
Carebara bruni (Forel, 1913)	
Carebara diversa (Jerdon, 1851)	
Carebara melasolena (Zhou & Zheng, 1997)	N
Carebara clm01	
Carebara clm05	
Carebara clm06	
Carebara clm07	
Carebara clm08	
Carebara clm09	
Carebara clm10	
Carebara clm11	
Carebara clm12	
Carebara clm13	
Cataulacus granulatus (Latreille, 1802)	
Crematogaster dohrni Mayr, 1879	
Crematogaster ferrarii Emery, 1888	
Crematogaster millardi Forel, 1902	
Crematogaster osakensis Forel, 1900	
Crematogaster politula Forel, 1902	
Crematogaster rothneyi Mayr, 1879	
Crematogaster clm05	
Crematogaster clm09	
Crematogaster clm10	
Crematogaster clm11	
Dilobocondyla fouqueti Santschi, 1910	
Kartidris ashima Xu & Zheng, 1995	
Lophomyrmex quadrispinosus (Jerdon, 1851)	
Lordomyrma idianale Taylor, 2012	
Meranoplus laeviventris Emery, 1889	
Monomorium chinense Santschi, 1925	
Monomorium pharaonis (Linnaeus, 1758)	
Monomorium clm01	
Monomorium clm02	
Monomorium clm05	
Monomorium clm06	
Myrmecina curvispina Zhou, Huang & Ma L., 2008	N
Myrmecina guangxiensis Zhou, 2001	N
Pheidole hongkongensis Wheeler, 1928	N

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Table 8.1 (*continued*)

Species	**Collection record**[1]
Pheidole noda Smith, 1874	
Pheidole pieli Santschi, 1925	
Pheidole plagiaria Smith, 1860	N
Pheidole planifrons Santschi, 1920	N
Pheidole roberti Forel, 1902	
Pheidole rugithorax Eguchi, 2008	N
Pheidole sagei Forel, 1902	
Pheidole smythiesii Forel, 1902	N
Pheidole tumida Eguchi, 2008	N
Pheidole vieti Eguchi, 2008	N*
Pheidole zoceana Santschi, 1925	N
Pheidole clm03	
Pheidole clm04	
Pheidole clm07	
Pheidole clm12	
Pheidole clm13	
Pheidole clm16	
Pheidole clm18	
Pheidole clm22	
Pheidole clm23	
Pristomyrmex brevispinosus Emery, 1887	
Pristomyrmex hamatus Xu & Zhang, 2002	
Pristomyrmex punctatus (Smith, 1860)	
Recurvidris recurvispinosa (Forel, 1890)	
Recurvidris kemneri (Wheeler & Wheeler, 1954)	N*
Solenopsis jacoti Wheeler, 1923	
Strumigenys ailaoshana (Xu & Zhou, 2004)	
Strumigenys dyschima (Bolton, 2000)	N*
Strumigenys exilirhina Bolton, 2000	
Strumigenys feae Emery, 1895	
Strumigenys kichijo (Terayama, Lin & Wu, 1996)	N
Strumigenys lyroessa (Roger, 1862)	
Strumigenys membranifera Emery, 1869	
Strumigenys mitis (Brown, 2000)	N
Strumigenys mutica (Brown, 1949)	
Strumigenys nanzanensis Lin & Wu, 1996	
Strumigenys nepalensis Baroni Urbani & De Andrade, 1994	N*
Strumigenys rallarhina Bolton, 2000	N
Strumigenys sauteri (Forel, 1912)	N
Tetramorium aptum Bolton, 1977	
Tetramorium ciliatum Bolton, 1977	
Tetramorium difficile Bolton, 1977	N*

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Table 8.1 (*continued*)

Species	Collection record[1]
Tetramorium flavipes Emery, 1893	N*
Tetramorium kheperra (Bolton, 1976)	
Tetramorium kraepelini Forel, 1905	
Tetramorium nipponense Wheeler, 1928	
Tetramorium parvispinum (Emery, 1893)	N
Tetramorium polymorphum Yamane & Jaitrong, 2011	N*
Tetramorium tonganum Mayr, 1870	N
Tetramorium clm03	
Tetramorium clm10	
Tetramorium clm18	
Tetramorium clm19	
Vollenhovia emeryi Wheeler, 1906	
Ponerinae	
Anochetus graeffei Mayr, 1870	
Anochetus mixtus Radchenko, 1993	
Anochetus myops Emery, 1893	
Anochetus clm04	
Brachyponera luteipes (Mayr, 1862)	
Diacamma clm01	
Ectomomyrmex astutus (Smith, 1858)	
Ectomomyrmex leeuwenhoeki (Forel, 1886)	
Ectomomyrmex lobocarenus (Xu, 1995)	
Ectomomyrmex clm01	
Ectomomyrmex clm02	
Ectomomyrmex clm03	
Ectomomyrmex clm04	
Emeryopone melaina Xu, 1998	
Hypoponera clm01	
Hypoponera clm02	
Hypoponera clm03	
Hypoponera clm04	
Hypoponera clm05	
Hypoponera clm06	
Hypoponera clm07	
Leptogenys birmana Forel, 1900	
Leptogenys chinensis (Mayr, 1870)	
Leptogenys crassicornis Emery, 1895	
Leptogenys diminuta (Smith, 1857)	
Leptogenys lucidula Emery, 1895	
Leptogenys mengzii Xu, 2000	
Leptogenys clm01	
Leptogenys clm02	

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Table 8.1 (*continued*)

Species	**Collection record**[1]
Leptogenys clm09	
Myopias hania Xu & Liu, 2011	
Odontomachus sp.	
Odontoponera denticulata (Smith, 1858)	N
Platythyrea parallela (Smith, 1859)	
Pseudoneoponera rufipes (Forel, 1911)	
Proceratinae	
Discothyrea clavicornis Emery, 1897	N*
Discothyrea kamiteta Kubota & Terayama, 1999	N
Probolomyrmex longiscapus Xu & Zeng, 2000	
Proceratium deelemani Perrault, 1981	N*
Pseudomyrmecinae	
Tetraponera amargina Xu & Chai, 2004	
Tetraponera allaborans (Walker, 1859)	
Tetraponera attenuata Smith, 1877	
Tetraponera concava Xu & Chai, 2004	

[1] N= New to Yunnan province; N*= New to China.

Table 8.2 | Ant species collected as well as their elevational distribution in Hengduan Mountains.

Subfamily	Genus	Species	Min elev (m)	Max elev (m)
Amblyoponinae	*Stigmatomma*	*Stigmatomma zoma*	792	819
Amblyoponinae	*Stigmatomma*	*Stigmatomma kangba*	792	1693
Dolichoderinae	*Dolichoderus*	*Dolichoderus affinis*	819	1455
Dolichoderinae	*Ochetellus*	*Ochetellus glaber*	1693	2239
Dolichoderinae	*Tapinoma*	*Tapinoma indicum*	1784	1784
Dolichoderinae	*Tapinoma*	*Tapinoma melanocephalum*	992	992
Dolichoderinae	*Technomyrmex*	*Technomyrmex antennus*	2058	3231
Dorylinae	*Cerapachys*	*Cerapachys fossulatus*	2171	2171
Dorylinae	*Cerapachys*	*Cerapachys risi*	1971	2397
Dorylinae	*Dorylus*	*Dorylus orientalis*	992	992
Ectatomminae	*Gnamptogenys*	*Gnamptogenys bicolor*	792	819
Ectatomminae	*Gnamptogenys*	*Gnamptogenys binghami*	792	1455
Formicinae	*Acropyga*	*Acropyga* sp1	992	992
Formicinae	*Camponotus*	*Camponotus crassisquamis*	1655	1655
Formicinae	*Camponotus*	*Camponotus dolendus*	1019	1019
Formicinae	*Camponotus*	*Camponotus lasiselene*	792	1455
Formicinae	*Camponotus*	*Camponotus marginatus*	2220	2220
Formicinae	*Camponotus*	*Camponotus mitis*	792	4006
Formicinae	*Camponotus*	*Camponotus nicobarensis*	1784	1784
Formicinae	*Camponotus*	*Camponotus* sp1	2220	2220
Formicinae	*Camponotus*	*Camponotus* sp2	1201	1201
Formicinae	*Formica*	*Formica candida*	2239	4537
Formicinae	*Formica*	*Formica fukaii*	3231	4406
Formicinae	*Formica*	*Formica fusca*	2020	4537
Formicinae	*Formica*	*Formica gagatoides*	2058	4537
Formicinae	*Formica*	*Formica lemani*	2020	4497
Formicinae	*Formica*	*Formica sinensis*	2573	4268
Formicinae	*Lasius*	*Lasius flavus*	1001	2397
Formicinae	*Lasius*	*Lasius himalayanus*	2258	2258
Formicinae	*Lasius*	*Lasius niger*	2072	4006
Formicinae	*Liometopum*	*Liometopum lindgreeni*	792	1001
Formicinae	*Meranoplus*	*Meranoplus laeviventris*	819	1001
Formicinae	*Myrmoteras*	*Myrmoteras cuneonodum*	792	1001
Formicinae	*Nylanderia*	*Nylanderia bourbonica*	1001	2239
Formicinae	*Nylanderia*	*Nylanderia flavipes*	792	2020
Formicinae	*Nylanderia*	*Nylanderia sakurae*	1455	3231
Formicinae	*Nylanderia*	*Nylanderia yerburyi*	1001	2748
Formicinae	*Paraparatrechina*	*Paraparatrechina sauteri*	1584	2020
Formicinae	*Paratrechina*	*Paratrechina* sp2	1655	1655
Formicinae	*Polyrhachis*	*Polyrhachis hippomanes*	1655	1655
Formicinae	*Polyrhachis*	*Polyrhachis illaudata*	792	1001
Formicinae	*Prenolepis*	*Prenolepis magnocula*	792	1455
Formicinae	*Prenolepis*	*Prenolepis* sp1	2903	3361
Myrmicinae	*Aphaenogaster*	*Aphaenogaster beccarii*	1455	2058
Myrmicinae	*Aphaenogaster*	*Aphaenogaster feae*	2272	2272
Myrmicinae	*Aphaenogaster*	*Aphaenogaster lepida*	1655	1655
Myrmicinae	*Aphaenogaster*	*Aphaenogaster* sp2	3231	3231

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Table 8.2 (*Continued*)

Subfamily	**Genus**	**Species**	**Min elev (m)**	**Max elev (m)**
Myrmicinae	*Aphaenogaster*	*Aphaenogaster tibetana*	1455	2903
Myrmicinae	*Carebara*	*Carebara affinis*	819	1455
Myrmicinae	*Carebara*	*Carebara altinodus*	792	819
Myrmicinae	*Carebara*	*Carebara rectidorsus*	1655	1655
Myrmicinae	*Carebara*	*Carebara reticapitus*	992	992
Myrmicinae	*Carebara*	*Carebara* sp1	992	992
Myrmicinae	*Carebara*	*Carebara* sp2	1019	1019
Myrmicinae	*Crematogaster*	*Crematogaster ferrarii*	1455	2239
Myrmicinae	*Crematogaster*	*Crematogaster osakensis*	792	2239
Myrmicinae	*Crematogaster*	*Crematogaster politula*	792	1001
Myrmicinae	*Crematogaster*	*Crematogaster rogenhoferi*	1019	1019
Myrmicinae	*Dilobocondyla*	*Dilobocondyla fouqueti*	1201	1201
Myrmicinae	*Leptothorax*	*Leptothorax* sp1	2977	2977
Myrmicinae	*Leptothorax*	*Leptothorax* sp2	2220	2220
Myrmicinae	*Leptothorax*	*Leptothorax* sp4	1584	2491
Myrmicinae	*Leptothorax*	*Leptothorax* sp5	2948	2948
Myrmicinae	*Leptothorax*	*Leptothorax* sp6	2020	4497
Myrmicinae	*Leptothorax*	*Leptothorax* sp7	2691	2691
Myrmicinae	*Monomorium*	*Monomorium latinode*	1455	2072
Myrmicinae	*Monomorium*	*Monomorium orientale*	1584	1693
Myrmicinae	*Myrmica*	*Myrmica bactriana*	2347	4194
Myrmicinae	*Myrmica*	*Myrmica jessensis*	1693	4543
Myrmicinae	*Myrmica*	*Myrmica margaritae*	2347	2748
Myrmicinae	*Myrmica*	*Myrmica rubra*	2020	4497
Myrmicinae	*Myrmica*	*Myrmica smythiesii*	3159	4543
Myrmicinae	*Myrmica*	*Myrmica* sp2	2058	4543
Myrmicinae	*Myrmica*	*Myrmica* sp4	4006	4268
Myrmicinae	*Myrmica*	*Myrmica sulcinodis*	2573	4543
Myrmicinae	*Pheidole*	*Pheidole bhavanae*	792	2239
Myrmicinae	*Pheidole*	*Pheidole indica*	992	992
Myrmicinae	*Pheidole*	*Pheidole nietneri*	1001	2347
Myrmicinae	*Pheidole*	*Pheidole pieli*	1455	1971
Myrmicinae	*Pheidole*	*Pheidole rhombinoda*	1201	1201
Myrmicinae	*Pheidole*	*Pheidole roberti*	1001	2020
Myrmicinae	*Pheidole*	*Pheidole sagei*	792	2397
Myrmicinae	*Pheidole*	*Pheidole* sp4	792	1455
Myrmicinae	*Pheidole*	*Pheidole spathifera*	1019	1019
Myrmicinae	*Pheidole*	*Pheidole watsoni*	792	1455
Myrmicinae	*Pristomyrmex*	*Pristomyrmex brevispinosus*	792	1001
Myrmicinae	*Stenamma*	*Stenamma kashmirense*	4737	4737
Myrmicinae	*Rhoptromyrmex*	*Rhoptromyrmex wroughtonii*	2777	2903
Myrmicinae	*Stenamma*	*Stenamma* sp1	2491	2907
Myrmicinae	*Stenamma*	*Stenamma* sp2	1019	1019
Myrmicinae	*Strumigenys*	*Strumigenys rallarhina*	1201	1201
Myrmicinae	*Strumigenys*	*Strumigenys* sp1	1201	1201
Myrmicinae	*Tetramorium*	*Tetramorium bicarinatum*	992	992
Myrmicinae	*Tetramorium*	*Tetramorium insolens*	2220	2220
Myrmicinae	*Tetramorium*	*Tetramorium laparum*	792	1455
Myrmicinae	*Tetramorium*	*Tetramorium nipponense*	792	1971

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Table 8.2 (*Continued*)

Subfamily	**Genus**	**Species**	**Min elev (m)**	**Max elev (m)**
Myrmicinae	*Tetramorium*	*Tetramorium smithi*	792	1001
Myrmicinae	*Tetramorium*	*Tetramorium* sp1	792	1584
Myrmicinae	*Tetramorium*	*Tetramorium xizangense*	792	819
Myrmicinae	*Vollenhovia*	*Vollenhovia* sp1	819	1971
Myrmicinae	*Vombisidris*	*Vombisidris* sp1	1201	1201
Ponerinae	*Anochetus*	*Anochetus subcoecus*	819	1001
Ponerinae	*Brachyponera*	*Brachyponera luteipes*	792	2804
Ponerinae	*Cryptopone*	*Cryptopone gigas*	819	2397
Ponerinae	*Cryptopone*	*Cryptopone* sp1	2439	2439
Ponerinae	*Ectomomyrmex*	*Ectomomyrmex astutus*	792	1455
Ponerinae	*Ectomomyrmex*	*Ectomomyrmex javanus*	1019	1019
Ponerinae	*Ectomomyrmex*	*Ectomomyrmex leeuwenhoeki*	792	1001
Ponerinae	*Ectomomyrmex*	*Ectomomyrmex sauteri*	819	1455
Ponerinae	*Ectomomyrmex*	*Ectomomyrmex zhengi*	792	1584
Ponerinae	*Hypoponera*	*Hypoponera sauteri*	819	1001
Ponerinae	*Hypoponera*	*Hypoponera confinis*	792	1455
Ponerinae	*Hypoponera*	*Hypoponera nippona*	792	1971
Ponerinae	*Hypoponera*	*Hypoponera sauteri*	992	992
Ponerinae	*Leptogenys*	*Leptogenys mengzii*	1201	1201
Ponerinae	*Leptogenys*	*Leptogenys yandii*	1201	1201
Ponerinae	*Myopias*	*Myopias conicara*	819	1455
Ponerinae	*Odontomachus*	*Odontomachus circulus*	1001	2020
Ponerinae	*Odontomachus*	*Odontomachus monticola*	1584	2573
Ponerinae	*Ponera*	*Ponera baka*	819	1455
Ponerinae	*Ponera*	*Ponera longlina*	1655	1655
Ponerinae	*Ponera*	*Ponera menglana*	1201	1201
Ponerinae	*Ponera*	*Ponera* sp1	2288	2748
Ponerinae	*Ponera*	*Ponera* sp2	1201	1201

Table 8.3 | *Strumigenys* specimens that used for RADseq assembly.

Specimen_code	Taxon_code	Country	Raw_reads	Total_loci	phylogeny
CASENT0185532	*Strumigenys.basiliska*	Fiji	10165852	569633	Y
CASENT0186744	*Strumigenys.basiliska*	Fiji	8780197	470231	Y
CASENT0184828	*Strumigenys.basiliska*	Fiji	5792949	324835	Y
CASENT0185612	*Strumigenys.basiliska*	Fiji	5443414	258823	Y
CASENT0185844	*Strumigenys.basiliska*	Fiji	5378912	233831	Y
CASENT0184996	*Strumigenys.basiliska*	Fiji	5312909	295863	Y
CASENT0185704	*Strumigenys.basiliska*	Fiji	4880693	288349	Y
CASENT0185702	*Strumigenys.basiliska*	Fiji	4749524	256696	Y
CASENT0185785	*Strumigenys.basiliska*	Fiji	4291101	251699	Y
CASENT0185655	*Strumigenys.basiliska*	Fiji	3517051	221359	Y
CASENT0186739	*Strumigenys.chernovi*	Fiji	7447055	351531	Y
CASENT0186767	*Strumigenys.chernovi*	Fiji	6946035	296232	Y
CASENT0184806	*Strumigenys.chernovi*	Fiji	4456496	224287	Y
CASENT0186865	*Strumigenys.chernovi*	Fiji	4117615	292164	Y
CASENT0184730	*Strumigenys.chernovi*	Fiji	3795406	226678	Y
LACM0328729	*Strumigenys.chernovi*	Fiji	3407825	232473	Y
CASENT0184994	*Strumigenys.chernovi*	Fiji	3301966	210472	Y
CASENT0184767	*Strumigenys.chernovi*	Fiji	3143794	221020	Y
CASENT0184811	*Strumigenys.chernovi*	Fiji	3136605	248323	Y
CASENT0184666	*Strumigenys.chernovi*	Fiji	2979615	214948	Y
CASENT0266464	*Strumigenys.*DBB050	Philippines	3362752	60672	Y
NA	*Strumigenys.*DBB050	Philippines	2423131	90974	Y
CASENT0747132	*Strumigenys.*DBB059	Malaysia	756959	71934	Y
CASENT0184949	*Strumigenys.ekasura*	Fiji	4086412	234805	Y
CASENT0184892	*Strumigenys.ekasura*	Fiji	3946293	185922	Y
CASENT0184963	*Strumigenys.ekasura*	Fiji	3536579	210532	Y
CASENT0184606	*Strumigenys.ekasura*	Fiji	3525319	224154	Y
CASENT0184673	*Strumigenys.ekasura*	Fiji	3123692	241165	Y
CASENT0184736	*Strumigenys.ekasura*	Fiji	2960094	157446	Y
CASENT0186618	*Strumigenys.ekasura*	Fiji	2716256	188689	Y
CASENT0186544	*Strumigenys.ekasura*	Fiji	2160088	122976	Y
CASENT0184757	*Strumigenys.ekasura*	Fiji	2017941	233438	Y
CASENT0184738	*Strumigenys.ekasura*	Fiji	1969515	128165	Y
CASENT0747539	*Strumigenys.esrossi*	Philippines	2557204	272913	Y
CASENT0267306	*Strumigenys.esrossi*	Philippines	609840	22891	Y
CASENT0747639	*Strumigenys.esrossi*	Philippines	515164	66726	Y

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Table 8.3 *(continued)*

Specimen_code	**Taxon_code**	**Country**	**Raw_reads**	**Total_loci**	**phylogeny**
CASENT0267303	*Strumigenys.esrossi*	Philippines	322367	61242	Y
CASENT0186464	*Strumigenys.*fj01	Fiji	1344852	183088	Y
CASENT0187561	*Strumigenys.*fj01	Fiji	894099	136578	Y
CASENT0187698	*Strumigenys.*fj01	Fiji	870701	137838	Y
CASENT0184710	*Strumigenys.*fj14	Fiji	1980151	166662	Y
CASENT0185843	*Strumigenys.*fj19	Fiji	4988705	182013	Y
CASENT0185576	*Strumigenys.*fj19	Fiji	4836655	131616	Y
CASENT0186995	*Strumigenys.frivola*	Fiji	2810395	127194	Y
CASENT0186834	*Strumigenys.frivola*	Fiji	2646750	134838	Y
CASENT0184581	*Strumigenys.frivola*	Fiji	1920143	180587	Y
CASENT0186684	*Strumigenys.frivola*	Fiji	1775364	116043	Y
CASENT0186628	*Strumigenys.frivola*	Fiji	1527404	178141	Y
CASENT0186829	*Strumigenys.frivola*	Fiji	1206230	85524	Y
CASENT0186907	*Strumigenys.frivola*	Fiji	1089685	55368	Y
CASENT0186934	*Strumigenys.frivola*	Fiji	885178	74473	Y
CASENT0186988	*Strumigenys.frivola*	Fiji	862607	58313	Y
CASENT0186963	*Strumigenys.frivola*	Fiji	610446	46015	Y
CASENT0185807	*Strumigenys.godeffroyi*	Fiji	4704924	223700	Y
CASENT0616621	*Strumigenys.godeffroyi*	Malaysia	3911529	204493	Y
CASENT0185838	*Strumigenys.godeffroyi*	Fiji	3823563	137035	Y
CASENT0185731	*Strumigenys.godeffroyi*	Fiji	3597740	286678	Y
CASENT0185917	*Strumigenys.godeffroyi*	Fiji	3323886	141055	Y
CASENT0185839	*Strumigenys.godeffroyi*	Fiji	3193809	175253	Y
CASENT0185815	*Strumigenys.godeffroyi*	Fiji	3167249	223340	Y
CASENT0185950	*Strumigenys.godeffroyi*	Fiji	3158906	211544	Y
CASENT0185858	*Strumigenys.godeffroyi*	Fiji	3150397	191814	Y
CASENT0185782	*Strumigenys.godeffroyi*	Fiji	3127346	168238	Y
CASENT0734231	*Strumigenys.indagatrix*	Malaysia	1698820	72356	Y
CASENT0747439	*Strumigenys.indagatrix*	Malaysia	1057649	30383	Y
CASENT0747321	*Strumigenys.juliae*	Malaysia	1361425	78028	Y
CASENT0747322	*Strumigenys.juliae*	Malaysia	742764	93727	Y
CASENT0742283	*Strumigenys.juliae*	Malaysia	632571	33921	Y
CASENT0747646	*Strumigenys.mjoebergi*	Malaysia	3435756	251021	Y
CASENT0747647	*Strumigenys.mjoebergi*	Malaysia	2933381	205381	Y
CASENT0217954	*Strumigenys.mjoebergi*	Malaysia	1718796	250203	Y
LACM0328747	*Strumigenys.nidifex*	Fiji	6206152	424753	Y
CASENT0185716	*Strumigenys.nidifex*	Fiji	5558666	332503	Y

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Table 8.3 *(continued)*

Specimen_code	Taxon_code	Country	Raw_reads	Total_loci	phylogeny
CASENT0185553	*Strumigenys.nidifex*	Fiji	5281762	225560	Y
LACM0328746	*Strumigenys.nidifex*	Fiji	4789635	321760	Y
CASENT0185985	*Strumigenys.nidifex*	Fiji	4438933	252878	Y
CASENT0185783	*Strumigenys.nidifex*	Fiji	4216469	295106	Y
CASENT0185847	*Strumigenys.nidifex*	Fiji	4205252	262654	Y
CASENT0185860	*Strumigenys.nidifex*	Fiji	3956441	293154	Y
CASENT0185829	*Strumigenys.nidifex*	Fiji	3715735	200830	Y
CASENT0185548	*Strumigenys.nidifex*	Fiji	3402203	225512	Y
CASENT0186830	*Strumigenys.panaulax*	Fiji	689699	59192	Y
CASENT0184968	*Strumigenys.praefecta*	Fiji	3988251	139642	Y
CASENT0187575	*Strumigenys.praefecta*	Fiji	3765825	156203	Y
CASENT0186724	*Strumigenys.praefecta*	Fiji	2396649	143578	Y
CASENT0186858	*Strumigenys.praefecta*	Fiji	2392377	130815	Y
CASENT0186655	*Strumigenys.praefecta*	Fiji	2356452	129237	Y
CASENT0186837	*Strumigenys.praefecta*	Fiji	2338218	161476	Y
CASENT0186704	*Strumigenys.praefecta*	Fiji	2159106	115804	Y
CASENT0186838	*Strumigenys.praefecta*	Fiji	1867836	94206	Y
CASENT0186943	*Strumigenys.praefecta*	Fiji	1724619	130240	Y
CASENT0186842	*Strumigenys.praefecta*	Fiji	1722601	92828	Y
CASENT0185947	*Strumigenys.rogeri*	Fiji	6188235	233196	Y
CASENT0185828	*Strumigenys.rogeri*	Fiji	5455481	206008	Y
CASENT0185841	*Strumigenys.rogeri*	Fiji	5392458	210614	Y
CASENT0185804	*Strumigenys.rogeri*	Fiji	4669314	170302	Y
CASENT0185938	*Strumigenys.rogeri*	Fiji	3015167	145346	Y
CASENT0185774	*Strumigenys.rogeri*	Fiji	2863508	165324	Y
CASENT0185971	*Strumigenys.rogeri*	Fiji	2495837	153210	Y
CASENT0185737	*Strumigenys.rogeri*	Fiji	2483105	152918	Y
CASENT0185877	*Strumigenys.rogeri*	Fiji	2215981	156260	Y
CASENT0185796	*Strumigenys.rogeri*	Fiji	2041523	149920	Y
CASENT0747754	*Strumigenys.sublaminata*	Malaysia	3891216	244537	Y
CASENT0735081	*Strumigenys.sublaminata*	Malaysia	3586935	555262	Y
CASENT0747134	*Strumigenys.sublaminata*	Malaysia	1182809	130932	Y
CASENT0747755	*Strumigenys.sublaminata*	Malaysia	680155	84785	Y
CASENT0185905	*Strumigenys.sulcata*	Fiji	6599085	353690	Y
CASENT0185997	*Strumigenys.sulcata*	Fiji	6593010	231561	Y
CASENT0185713	*Strumigenys.sulcata*	Fiji	6024757	279478	Y
CASENT0185729	*Strumigenys.sulcata*	Fiji	5889732	316578	Y

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Table 8.3 *(continued)*

Specimen_code	Taxon_code	Country	Raw_reads	Total_loci	phylogeny
CASENT0185715	*Strumigenys.sulcata*	Fiji	5769182	266071	Y
CASENT0185963	*Strumigenys.sulcata*	Fiji	5311669	227078	Y
CASENT0185798	*Strumigenys.sulcata*	Fiji	4935345	192350	Y
CASENT0185761	*Strumigenys.sulcata*	Fiji	4783977	278013	Y
CASENT0185705	*Strumigenys.sulcata*	Fiji	4201342	247269	Y
CASENT0185889	*Strumigenys.sulcata*	Fiji	3919740	153837	Y
CASENT0266361	*Strumigenys.tenitecta*	Philippines	667249	52299	Y
CASENT0185749	*Strumigenys.tumida*	Fiji	1541751	289510	Y
CASENT0185709	*Strumigenys.tumida*	Fiji	1394638	198239	Y
CASENT0185771	*Strumigenys.tumida*	Fiji	1234638	209953	Y
CASENT0185699	*Strumigenys.tumida*	Fiji	1017381	229166	Y
CASENT0185745	*Strumigenys.tumida*	Fiji	986281	154437	Y
CASENT0185883	*Strumigenys.tumida*	Fiji	688400	156784	Y
CASENT0185799	*Strumigenys.tumida*	Fiji	681208	153154	Y
CASENT0185474	*Strumigenys.tumida*	Fiji	654385	148374	Y
CASENT0185697	*Strumigenys.tumida*	Fiji	581995	68893	Y
CASENT0185665	*Strumigenys.tumida*	Fiji	468561	144798	Y
LACM0329744	*Strumigenys.vassago*	Indonesia	4400984	301667	Y
LACM0329743	*Strumigenys.vassago*	Indonesia	496564	64362	Y
CASENT0185769	*Strumigenys.basiliska*	Fiji	3340871	228362	N
CASENT0185805	*Strumigenys.basiliska*	Fiji	3051352	208914	N
CASENT0185507	*Strumigenys.basiliska*	Fiji	2894799	358498	N
CASENT0185920	*Strumigenys.basiliska*	Fiji	2767756	220227	N
CASENT0185834	*Strumigenys.basiliska*	Fiji	2673087	217107	N
CASENT0185767	*Strumigenys.basiliska*	Fiji	2562626	241356	N
CASENT0185760	*Strumigenys.basiliska*	Fiji	2177338	242228	N
CASENT0185752	*Strumigenys.basiliska*	Fiji	1988291	218438	N
CASENT0185873	*Strumigenys.basiliska*	Fiji	1965306	375781	N
CASENT0185801	*Strumigenys.basiliska*	Fiji	1960566	192344	N
CASENT0185735	*Strumigenys.basiliska*	Fiji	1955081	199346	N
CASENT0185695	*Strumigenys.basiliska*	Fiji	1953690	299061	N
CASENT0185482	*Strumigenys.basiliska*	Fiji	1951260	229494	N
LACM0328728	*Strumigenys.basiliska*	Fiji	1882875	142277	N
CASENT0185734	*Strumigenys.basiliska*	Fiji	1804644	292218	N
CASENT0185886	*Strumigenys.basiliska*	Fiji	1796528	327241	N
LACM0328727	*Strumigenys.basiliska*	Fiji	1783931	111157	N
CASENT0185493	*Strumigenys.basiliska*	Fiji	1714899	117039	N

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Table 8.3 *(continued)*

Specimen_code	Taxon_code	Country	Raw_reads	Total_loci	phylogeny
CASENT0185619	*Strumigenys.basiliska*	Fiji	1672301	289417	N
CASENT0185781	*Strumigenys.basiliska*	Fiji	1580044	324554	N
CASENT0185777	*Strumigenys.basiliska*	Fiji	1579905	279016	N
CASENT0185618	*Strumigenys.basiliska*	Fiji	1498290	265822	N
CASENT0185915	*Strumigenys.basiliska*	Fiji	1431770	191689	N
CASENT0185986	*Strumigenys.basiliska*	Fiji	1422076	285727	N
CASENT0185854	*Strumigenys.basiliska*	Fiji	1410626	172185	N
CASENT0185484	*Strumigenys.basiliska*	Fiji	1364913	203320	N
CASENT0185919	*Strumigenys.basiliska*	Fiji	1311807	201737	N
CASENT0185450	*Strumigenys.basiliska*	Fiji	1274435	252088	N
CASENT0185937	*Strumigenys.basiliska*	Fiji	1231453	202914	N
CASENT0185492	*Strumigenys.basiliska*	Fiji	1150811	169946	N
CASENT0185863	*Strumigenys.basiliska*	Fiji	1134967	115226	N
CASENT0185485	*Strumigenys.basiliska*	Fiji	1037276	168156	N
CASENT0185867	*Strumigenys.basiliska*	Fiji	986521	145091	N
CASENT0185862	*Strumigenys.basiliska*	Fiji	963134	186859	N
CASENT0185857	*Strumigenys.basiliska*	Fiji	942896	163666	N
CASENT0185812	*Strumigenys.basiliska*	Fiji	880586	144476	N
CASENT0185808	*Strumigenys.basiliska*	Fiji	801624	141581	N
CASENT0185865	*Strumigenys.basiliska*	Fiji	704098	128659	N
CASENT0185795	*Strumigenys.basiliska*	Fiji	696980	133854	N
CASENT0185999	*Strumigenys.basiliska*	Fiji	680115	160423	N
CASENT0185930	*Strumigenys.basiliska*	Fiji	612887	139214	N
CASENT0185849	*Strumigenys.basiliska*	Fiji	576000	135557	N
CASENT0185700	*Strumigenys.basiliska*	Fiji	556522	125207	N
CASENT0185957	*Strumigenys.basiliska*	Fiji	15193	9704	N
CASENT0184605	*Strumigenys.chernovi*	Fiji	2641551	230619	N
CASENT0184909	*Strumigenys.chernovi*	Fiji	2513673	246378	N
CASENT0184654	*Strumigenys.chernovi*	Fiji	2420017	188954	N
CASENT0184890	*Strumigenys.chernovi*	Fiji	2295988	220081	N
CASENT0184989	*Strumigenys.chernovi*	Fiji	2269726	242259	N
CASENT0186621	*Strumigenys.chernovi*	Fiji	2218931	199261	N
CASENT0184779	*Strumigenys.chernovi*	Fiji	2035421	201506	N
CASENT0184878	*Strumigenys.chernovi*	Fiji	1809615	171507	N
CASENT0184872	*Strumigenys.chernovi*	Fiji	1764986	174552	N
CASENT0186698	*Strumigenys.chernovi*	Fiji	1587944	221218	N
LACM0328730	*Strumigenys.chernovi*	Fiji	1239126	237602	N

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Table 8.3 *(continued)*

Specimen_code	Taxon_code	Country	Raw_reads	Total_loci	phylogeny
CASENT0184951	*Strumigenys.chernovi*	Fiji	874103	125683	N
CASENT0184648	*Strumigenys.ekasura*	Fiji	1959988	194532	N
CASENT0184713	*Strumigenys.ekasura*	Fiji	1868544	191150	N
CASENT0184904	*Strumigenys.ekasura*	Fiji	1818153	223121	N
CASENT0184664	*Strumigenys.ekasura*	Fiji	1814432	213306	N
CASENT0184592	*Strumigenys.ekasura*	Fiji	1680321	192345	N
CASENT0186860	*Strumigenys.ekasura*	Fiji	1516850	104956	N
CASENT0184613	*Strumigenys.ekasura*	Fiji	1237946	179589	N
CASENT0186993	*Strumigenys.ekasura*	Fiji	993729	71454	N
CASENT0184735	*Strumigenys.ekasura*	Fiji	122013	9043	N
CASENT0186956	*Strumigenys.frivola*	Fiji	574345	64585	N
CASENT0186961	*Strumigenys.frivola*	Fiji	565836	50856	N
CASENT0186945	*Strumigenys.frivola*	Fiji	368928	32611	N
CASENT0185887	*Strumigenys.godeffroyi*	Fiji	3106966	190934	N
CASENT0185770	*Strumigenys.godeffroyi*	Fiji	3094116	158399	N
CASENT0185809	*Strumigenys.godeffroyi*	Fiji	2947731	156561	N
CASENT0185946	*Strumigenys.godeffroyi*	Fiji	2839671	140810	N
CASENT0185820	*Strumigenys.godeffroyi*	Fiji	2834889	137571	N
CASENT0185733	*Strumigenys.godeffroyi*	Fiji	2793178	138068	N
CASENT0185718	*Strumigenys.godeffroyi*	Fiji	2755194	216887	N
CASENT0185932	*Strumigenys.godeffroyi*	Fiji	2644450	150538	N
CASENT0185954	*Strumigenys.godeffroyi*	Fiji	2631358	139015	N
CASENT0185916	*Strumigenys.godeffroyi*	Fiji	2536524	196770	N
CASENT0185983	*Strumigenys.godeffroyi*	Fiji	2524754	145852	N
CASENT0185500	*Strumigenys.godeffroyi*	Fiji	2494541	204534	N
CASENT0185870	*Strumigenys.godeffroyi*	Fiji	2452433	229293	N
CASENT0185765	*Strumigenys.godeffroyi*	Fiji	2421469	204442	N
CASENT0185823	*Strumigenys.godeffroyi*	Fiji	2369153	140614	N
CASENT0185560	*Strumigenys.godeffroyi*	Fiji	2350677	105247	N
CASENT0185753	*Strumigenys.godeffroyi*	Fiji	2350235	176617	N
CASENT0185988	*Strumigenys.godeffroyi*	Fiji	2067203	164359	N
CASENT0185620	*Strumigenys.godeffroyi*	Fiji	1993316	173837	N
CASENT0185913	*Strumigenys.godeffroyi*	Fiji	1980078	184827	N
CASENT0185900	*Strumigenys.godeffroyi*	Fiji	1958381	153802	N
CASENT0185757	*Strumigenys.godeffroyi*	Fiji	1897678	191133	N
CASENT0185972	*Strumigenys.godeffroyi*	Fiji	1846352	119084	N
CASENT0185833	*Strumigenys.godeffroyi*	Fiji	1845519	125489	N

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Table 8.3 *(continued)*

Specimen_code	Taxon_code	Country	Raw_reads	Total_loci	phylogeny
CASENT0185813	*Strumigenys.godeffroyi*	Fiji	1820087	163060	N
CASENT0185967	*Strumigenys.godeffroyi*	Fiji	1769429	133555	N
CASENT0185884	*Strumigenys.godeffroyi*	Fiji	1760872	112207	N
CASENT0185965	*Strumigenys.godeffroyi*	Fiji	1749218	162646	N
CASENT0185959	*Strumigenys.godeffroyi*	Fiji	1672161	104366	N
CASENT0185822	*Strumigenys.godeffroyi*	Fiji	1527976	131803	N
CASENT0185934	*Strumigenys.godeffroyi*	Fiji	1452987	86136	N
CASENT0185817	*Strumigenys.godeffroyi*	Fiji	1401832	180301	N
CASENT0185788	*Strumigenys.godeffroyi*	Fiji	1258881	98197	N
CASENT0185960	*Strumigenys.godeffroyi*	Fiji	1169954	128405	N
CASENT0185912	*Strumigenys.godeffroyi*	Fiji	1132736	91401	N
CASENT0185674	*Strumigenys.godeffroyi*	Fiji	1057760	121728	N
CASENT0185904	*Strumigenys.godeffroyi*	Fiji	1047388	72930	N
CASENT0185872	*Strumigenys.godeffroyi*	Fiji	1008567	96627	N
CASENT0185948	*Strumigenys.godeffroyi*	Fiji	920571	58685	N
CASENT0185982	*Strumigenys.godeffroyi*	Fiji	897233	84732	N
CASENT0186996	*Strumigenys.nidifex*	Fiji	2762974	250606	N
CASENT0185721	*Strumigenys.nidifex*	Fiji	2341335	206026	N
CASENT0185764	*Strumigenys.nidifex*	Fiji	2273041	211678	N
CASENT0186612	*Strumigenys.nidifex*	Fiji	2199717	256794	N
CASENT0185800	*Strumigenys.nidifex*	Fiji	2164443	208034	N
CASENT0185641	*Strumigenys.nidifex*	Fiji	2160284	280727	N
CASENT0185742	*Strumigenys.nidifex*	Fiji	1619897	175727	N
CASENT0185783	*Strumigenys.nidifex*	Fiji	1377699	225401	N
CASENT0185744	*Strumigenys.nidifex*	Fiji	809636	119110	N
CASENT0186762	*Strumigenys.praefecta*	Fiji	1556824	84513	N
CASENT0186954	*Strumigenys.praefecta*	Fiji	1412571	131688	N
CASENT0186966	*Strumigenys.praefecta*	Fiji	1403741	81299	N
CASENT0186679	*Strumigenys.praefecta*	Fiji	1323594	86257	N
CASENT0187611	*Strumigenys.praefecta*	Fiji	1294891	99999	N
CASENT0187690	*Strumigenys.praefecta*	Fiji	1248817	66562	N
CASENT0186799	*Strumigenys.praefecta*	Fiji	1218612	154471	N
CASENT0187790	*Strumigenys.praefecta*	Fiji	1092407	54301	N
CASENT0186625	*Strumigenys.praefecta*	Fiji	1048883	75020	N
CASENT0186642	*Strumigenys.praefecta*	Fiji	1028523	128363	N
CASENT0186935	*Strumigenys.praefecta*	Fiji	1020063	71838	N
CASENT0187784	*Strumigenys.praefecta*	Fiji	1019471	51654	N

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Table 8.3 *(continued)*

Specimen_code	Taxon_code	Country	Raw_reads	Total_loci	phylogeny
CASENT0186629	*Strumigenys.praefecta*	Fiji	936687	55664	N
CASENT0186798	*Strumigenys.praefecta*	Fiji	896327	100596	N
CASENT0186794	*Strumigenys.praefecta*	Fiji	779172	48414	N
CASENT0186831	*Strumigenys.praefecta*	Fiji	762200	69114	N
CASENT0186980	*Strumigenys.praefecta*	Fiji	735748	84927	N
CASENT0186555	*Strumigenys.praefecta*	Fiji	617406	81102	N
CASENT0186957	*Strumigenys.praefecta*	Fiji	446716	42572	N
CASENT0187680	*Strumigenys.praefecta*	Fiji	61589	8698	N
CASENT0185738	*Strumigenys.rogeri*	Fiji	1725774	134291	N
CASENT0185926	*Strumigenys.rogeri*	Fiji	1372368	138029	N
CASENT0185676	*Strumigenys.rogeri*	Fiji	1355499	90295	N
CASENT0185690	*Strumigenys.rogeri*	Fiji	1106624	127756	N
CASENT0185664	*Strumigenys.rogeri*	Fiji	1079912	126421	N
CASENT0185717	*Strumigenys.rogeri*	Fiji	1061495	83147	N
CASENT0185880	*Strumigenys.rogeri*	Fiji	1039896	105310	N
CASENT0735643	*Strumigenys.rogeri*	Fiji	910290	92568	N
CASENT0185555	*Strumigenys.rogeri*	Fiji	852451	112110	N
CASENT0185561	*Strumigenys.rogeri*	Fiji	852248	120946	N
CASENT0185526	*Strumigenys.rogeri*	Fiji	850308	71378	N
CASENT0185952	*Strumigenys.rogeri*	Fiji	773155	105675	N
CASENT0185973	*Strumigenys.rogeri*	Fiji	772428	57819	N
CASENT0185975	*Strumigenys.rogeri*	Fiji	742197	57653	N
CASENT0185711	*Strumigenys.rogeri*	Fiji	732410	56493	N
CASENT0185935	*Strumigenys.rogeri*	Fiji	535477	68275	N
CASENT0185871	*Strumigenys.rogeri*	Fiji	516968	47436	N
CASENT0185969	*Strumigenys.rogeri*	Fiji	505352	36919	N
CASENT0185692	*Strumigenys.rogeri*	Fiji	451039	72252	N
CASENT0185910	*Strumigenys.rogeri*	Fiji	443579	66936	N
CASENT0185868	*Strumigenys.rogeri*	Fiji	441325	41338	N
CASENT0185648	*Strumigenys.rogeri*	Fiji	432876	107115	N
CASENT0185925	*Strumigenys.rogeri*	Fiji	408100	70218	N
CASENT0185756	*Strumigenys.rogeri*	Fiji	344902	71206	N
CASENT0185518	*Strumigenys.rogeri*	Fiji	274441	48707	N
CASENT0185911	*Strumigenys.rogeri*	Fiji	234658	55238	N
CASENT0185447	*Strumigenys.rogeri*	Fiji	191304	56843	N
CASENT0185939	*Strumigenys.sulcata*	Fiji	3687731	208794	N
CASENT0185694	*Strumigenys.sulcata*	Fiji	3210820	232675	N

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Table 8.3 *(continued)*

Specimen_code	Taxon_code	Country	Raw_reads	Total_loci	phylogeny
CASENT0185818	*Strumigenys.sulcata*	Fiji	3114520	214276	N
CASENT0185944	*Strumigenys.sulcata*	Fiji	3105049	223189	N
CASENT0185581	*Strumigenys.sulcata*	Fiji	2691123	164717	N
CASENT0185768	*Strumigenys.sulcata*	Fiji	2659326	185564	N
CASENT0185892	*Strumigenys.sulcata*	Fiji	2456388	282518	N
CASENT0185909	*Strumigenys.sulcata*	Fiji	2244970	221934	N
CASENT0185748	*Strumigenys.sulcata*	Fiji	1909230	159778	N
CASENT0185557	*Strumigenys.sulcata*	Fiji	1688700	170085	N
CASENT0185953	*Strumigenys.sulcata*	Fiji	1685434	183729	N

Table 8.4 | *S. basiliska* specimen's information for population genomic analysis

Taxon code	Specimen code	Locality code	Island	Raw read	Loci#
Strumigenys.basiliska	CASENT0185734	Levuka 400	LA	1804644	2464
Strumigenys.basiliska	CASENT0186744	Levuka 400	LA	8780197	2711
Strumigenys.basiliska	CASENT0185450	Nabukavesi 300	VL	1274435	2125
Strumigenys.basiliska	CASENT0185873	Korobaba 300	VL	1965306	2543
Strumigenys.basiliska	CASENT0185986	Nabukavesi 300	VL	1422076	2447
Strumigenys.basiliska	CASENT0185507	Nabukavesi 300	VL	2894799	2350
Strumigenys.basiliska	CASENT0185937	Korobaba 300	VL	1231453	1224
Strumigenys.basiliska	CASENT0185655	Navukailagi 505	GA	3517051	2605
Strumigenys.basiliska	CASENT0185702	Mt. Korolevu 300	ML	4749524	2553
Strumigenys.basiliska	CASENT0185801	Mt. Korolevu 300	ML	1960566	2016
Strumigenys.basiliska	CASENT0185769	Mt. Korolevu 300	ML	3340871	2574
Strumigenys.basiliska	CASENT0185484	Mt. Korolevu 300	ML	1364913	2221
Strumigenys.basiliska	CASENT0185844	Navukailagi 575	GA	5378912	2563
Strumigenys.basiliska	CASENT0185805	Navukailagi 475	GA	3051352	2526
Strumigenys.basiliska	CASENT0185612	Navukailagi 505	GA	5443414	2633
Strumigenys.basiliska	CASENT0185854	Navukailagi 490	GA	1410626	2096
Strumigenys.basiliska	CASENT0184996	Nasoqoloa 300	KR	5312909	2413
Strumigenys.basiliska	CASENT0185704	Nasoqoloa 300	KR	4880693	2426
Strumigenys.basiliska	CASENT0185752	Nasoqoloa 300	KR	1988291	1916
Strumigenys.basiliska	CASENT0185834	Nasau 465 a	KR	2673087	2412
Strumigenys.basiliska	CASENT0184828	Nasoqoloa 300	KR	5792949	2588
Strumigenys.basiliska	CASENT0185482	Nakasa 300	VN	1951260	1578
Strumigenys.basiliska	CASENT0185760	Yasawa 300	VN	2177338	1951
Strumigenys.basiliska	CASENT0185785	Mt. Vatudiri 570	VN	4291101	2634
Strumigenys.basiliska	CASENT0185915	Rokosalase 180	VN	1431770	2080
Strumigenys.basiliska	CASENT0185492	Rokosalase 180	VN	1150811	1526
Strumigenys.basiliska	LACM0328727	Monasavu 1000	VL	1783931	892
Strumigenys.basiliska	LACM0328728	Monasavu 1000	VL	1882875	1638

Table 8.5 | *S. chernovi* specimen's information for population genomic analysis

Taxon code	Specimen code	Locality code	Island	Raw reads	Loci#
Strumigenys.chernovi	CASENT0184806	Navukailagi 475	GA	4456496	3111
Strumigenys.chernovi	CASENT0184730	Navukailagi 490	GA	3795406	3017
Strumigenys.chernovi	CASENT0184811	Navukailagi 300	GA	3136605	2755
Strumigenys.chernovi	CASENT0184779	Navukailagi 490	GA	2035421	2849
Strumigenys.chernovi	CASENT0186767	Tavua 220	KR	6946035	3184
Strumigenys.chernovi	CASENT0186865	Nasoqoloa 300	KR	4117615	2977
Strumigenys.chernovi	CASENT0184605	Korobaba 300	VL	2641551	2765
Strumigenys.chernovi	CASENT0184994	Korobaba 300	VL	3301966	2895
Strumigenys.chernovi	LACM0328729	Suva 150	VL	3407825	2944
Strumigenys.chernovi	LACM0328730	Suva 150	VL	1239126	2896
Strumigenys.chernovi	CASENT0186621	Yasawa 300	VN	2218931	2357
Strumigenys.chernovi	CASENT0184951	Yasawa 300	VN	874103	1275

Table 8.6 | *S. ekasura* specimen's information for population genomic analysis

Taxon code	Specimen code	Locality code	Island	Raw reads	Loci#
Strumigenys.ekasura	CASENT0184673	Navukailagi 408	GA	3123692	8117
Strumigenys.ekasura	CASENT0184736	Navukailagi 300	GA	1868544	7357
Strumigenys.ekasura	CASENT0184892	Navukailagi 300	GA	1237946	5190
Strumigenys.ekasura	CASENT0184949	Nasoqoloa 300	KR	4086412	7781
Strumigenys.ekasura	CASENT0184606	Nasoqoloa 300	KR	3525319	8066
Strumigenys.ekasura	CASENT0186544	Tavua 220	KR	2017941	7746
Strumigenys.ekasura	CASENT0186860	Tavua 220	KR	2960094	7172
Strumigenys.ekasura	CASENT0186618	Tavua 220	KR	3946293	7751
Strumigenys.ekasura	CASENT0184713	Korobaba 300	VL	2160088	5969
Strumigenys.ekasura	CASENT0184613	Naikorokoro 300	VL	1516850	4170
Strumigenys.ekasura	CASENT0184757	Naikorokoro 300	VL	2716256	5907
Strumigenys.ekasura	CASENT0184904	Naikorokoro 300	VL	1818153	7240

Table 8.7 | *S. nidifex* specimen's information for population genomic analysis

Taxon code	Specimen code	Locality code	Island	Raw read	Loci#
Strumigenys.nidifex	CASENT0185829	Navukailagi 356	GA	3715735	5915
Strumigenys.nidifex	CASENT0185548	Nasau 470; 3.7 km	KR	3402203	5730
Strumigenys.nidifex	CASENT0185847	Nasau 420 b	KR	4205252	6016
Strumigenys.nidifex	CASENT0185985	Nasau 420 b	KR	4438933	6009
Strumigenys.nidifex	CASENT0185860	Nasau 420 b	KR	3956441	5998
Strumigenys.nidifex	CASENT0185716	Nasau 420 b	KR	5558666	6001
Strumigenys.nidifex	CASENT0185800	Nasau 420 b	KR	2164443	4944
Strumigenys.nidifex	CASENT0185783	Mt. Kuitarua 440 b	KR	4216469	5955
Strumigenys.nidifex	CASENT0185783	Mt. Kuitarua 440 b	KR	1377699	5474
Strumigenys.nidifex	CASENT0185721	Mt. Washington 760	KV	2341335	4717
Strumigenys.nidifex	CASENT0185641	Mt. Washington 760	KV	2160284	5750
Strumigenys.nidifex	CASENT0185764	Mt. Washington 700	KV	2273041	5677
Strumigenys.nidifex	CASENT0186612	Monasavu Dam 600	VL	2199717	5607
Strumigenys.nidifex	CASENT0185744	Nasoqo 800 d	VL	809636	3802
Strumigenys.nidifex	CASENT0185742	Naikorokoro 300	VL	1619897	4848
Strumigenys.nidifex	CASENT0186996	Monasavu Dam 600	VL	2762974	5745
Strumigenys.nidifex	LACM0328747	Mt. Delaikoro 699	VN	6206152	5887
Strumigenys.nidifex	LACM0328746	Mt. Delaikoro 699	VN	4789635	5595

Table 8.8 | *S. sulcata* specimen's information for population genomic analysis

Taxon code	Specimen code	Locality code	Island	Raw read	Loci#
Strumigenys.sulcata	CASENT0185953	Mt. Kuitarua 440 b	KR	1685434	4693
Strumigenys.sulcata	CASENT0185713	Nasau 420 b	KR	6024757	5796
Strumigenys.sulcata	CASENT0185761	Mt. Kuitarua 380	KR	4783977	5827
Strumigenys.sulcata	CASENT0185798	Mt. Devo 734	TA	4935345	5507
Strumigenys.sulcata	CASENT0185997	Mt. Devo 734	TA	6593010	5644
Strumigenys.sulcata	CASENT0185694	Mt. Devo 734	TA	3210820	5726
Strumigenys.sulcata	CASENT0185889	Mt. Batilamu 840 c	VL	3919740	5562
Strumigenys.sulcata	CASENT0185557	Mt. Batilamu 840 c	VL	1688700	5286
Strumigenys.sulcata	CASENT0185818	Monasavu Dam 800	VL	3114520	4922
Strumigenys.sulcata	CASENT0185892	Monasavu Dam 800	VL	2456388	5412
Strumigenys.sulcata	CASENT0185944	Monasavu Dam 800	VL	3105049	4741
Strumigenys.sulcata	CASENT0185748	Mt. Tomanivi 950	VL	1909230	4249
Strumigenys.sulcata	CASENT0185909	Mt. Tomanivi 950	VL	2244970	5285
Strumigenys.sulcata	CASENT0185729	Mt. Tomanivi 950	VL	5889732	5695
Strumigenys.sulcata	CASENT0185939	Mt. Tomanivi 950	VL	3687731	5053
Strumigenys.sulcata	CASENT0185705	Mt. Batilamu 840 c	VL	4201342	5837
Strumigenys.sulcata	CASENT0185768	Mt. Batilamu 840 c	VL	2659326	5570
Strumigenys.sulcata	CASENT0185715	Korobaba 300	VL	5769182	5795
Strumigenys.sulcata	CASENT0185905	Naikorokoro 300	VL	6599085	5809

Table 8.9 | *S. godeffroyi* specimen's information for population genomic analysis

Taxon code	Specimen code	Locality code	Island	Raw read	Loci#
Strumigenys.godeffroyi	CASENT0185858	Dukuibeqa 50	BQ	3150397	6723
Strumigenys.godeffroyi	CASENT0185946	Navukailagi 300	GA	2839671	4296
Strumigenys.godeffroyi	CASENT0185884	Navukailagi 356	GA	1760872	4114
Strumigenys.godeffroyi	CASENT0185917	Navukailagi 300	GA	3323886	5049
Strumigenys.godeffroyi	CASENT0185932	Navukailagi 300	GA	2644450	4106
Strumigenys.godeffroyi	CASENT0185731	Mt. Kuitarua 380	KR	3597740	7363
Strumigenys.godeffroyi	CASENT0185817	Nasoqoloa 300	KR	1401832	4340
Strumigenys.godeffroyi	CASENT0185950	Nasoqoloa 300	KR	3158906	6517
Strumigenys.godeffroyi	CASENT0185900	Moanakaka 60	KV	1958381	5187
Strumigenys.godeffroyi	CASENT0185753	Mt. Korolevu 300	ML	2350235	6199
Strumigenys.godeffroyi	CASENT0185757	Mt. Korolevu 300	ML	1897678	6308
Strumigenys.godeffroyi	CASENT0185839	Mt. Korolevu 375	ML	3193809	6447
Strumigenys.godeffroyi	CASENT0185838	Mt. Korolevu 300	ML	3823563	6355
Strumigenys.godeffroyi	CASENT0185913	Mt. Korolevu 300	ML	1980078	5753
Strumigenys.godeffroyi	CASENT0185960	Mt. Korolevu 300	ML	1169954	3907
Strumigenys.godeffroyi	CASENT0185870	Colo-i-Suva 200	VL	2452433	5819
Strumigenys.godeffroyi	CASENT0185872	Abaca 525	VL	1008567	2473
Strumigenys.godeffroyi	CASENT0185815	Nakavu 300	VL	3167249	6199
Strumigenys.godeffroyi	CASENT0185620	Naikorokoro 300	VL	1993316	4502
Strumigenys.godeffroyi	CASENT0185916	Naboutini 300	VL	2536524	6316
Strumigenys.godeffroyi	CASENT0185500	Naboutini 300	VL	2494541	6047
Strumigenys.godeffroyi	CASENT0185887	Naikorokoro 300	VL	3106966	5412
Strumigenys.godeffroyi	CASENT0185813	Nabukavesi 300	VL	1820087	4033
Strumigenys.godeffroyi	CASENT0185948	Mt. Rama 300	VL	920571	1603
Strumigenys.godeffroyi	CASENT0185988	Colo-i-Suva 220	VL	2067203	5698
Strumigenys.godeffroyi	CASENT0185733	Colo-i-Suva 186d	VL	2793178	5275
Strumigenys.godeffroyi	CASENT0185770	Colo-i-Suva 186d	VL	3094116	4688
Strumigenys.godeffroyi	CASENT0185782	Colo-i-Suva 186d	VL	3127346	4869
Strumigenys.godeffroyi	CASENT0185912	Colo-i-Suva 200	VL	1132736	2071
Strumigenys.godeffroyi	CASENT0185765	Colo-i-Suva 200	VL	2421469	5701
Strumigenys.godeffroyi	CASENT0185972	Colo-i-Suva 200	VL	1846352	3501
Strumigenys.godeffroyi	CASENT0185967	Colo-i-Suva 186 d	VL	1769429	4392
Strumigenys.godeffroyi	CASENT0185674	Colo-i-Suva 186 d	VL	1057760	2647
Strumigenys.godeffroyi	CASENT0185904	Colo-i-Suva 186 d	VL	1047388	2401
Strumigenys.godeffroyi	CASENT0185820	Nakanakana 300	VL	2834889	4439
Strumigenys.godeffroyi	CASENT0185959	Mt. Wainibeqa 152c	VN	1672161	3315

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Table 8.9 (*continued*)

Taxon code	Specimen code	Locality code	Island	Raw read	Loci#
Strumigenys.godeffroyi	CASENT0185934	Mt. Wainibeqa 152c	VN	1452987	3284
Strumigenys.godeffroyi	CASENT0185823	Vusasivo Village 400	VN	2369153	4291
Strumigenys.godeffroyi	CASENT0185809	Rokosalase 94	VN	2947731	5922
Strumigenys.godeffroyi	CASENT0185982	Drawa 270	VN	897233	3173
Strumigenys.godeffroyi	CASENT0185983	Vusasivo Village 400	VN	2524754	5770
Strumigenys.godeffroyi	CASENT0185833	Kasavu 300	VN	1845519	3271
Strumigenys.godeffroyi	CASENT0185965	Lagi 300	VN	1749218	5407
Strumigenys.godeffroyi	CASENT0185954	Yasawa 300	VN	2631358	4710
Strumigenys.godeffroyi	CASENT0185788	Yasawa 300	VN	1258881	2821
Strumigenys.godeffroyi	CASENT0185560	Mt. Delaikoro 391	VN	2350677	4822

Table 8.10 | *S. rogeri* specimen's information for population genomic analysis

Taxon code	Specimen code	Locality code	Island	Raw read	Loci#
Strumigenys.rogeri	CASENT0185877	Dukuibeqa 50	BQ	2215981	5030
Strumigenys.rogeri	CASENT0185971	Dukuibeqa 50	BQ	2495837	4989
Strumigenys.rogeri	CASENT0185796	Nasoqoloa 300	KR	2041523	4346
Strumigenys.rogeri	CASENT0185975	Kuitarua 480	KR	742197	1580
Strumigenys.rogeri	CASENT0185711	Kuitarua 480	KR	732410	754
Strumigenys.rogeri	CASENT0185692	Kuitarua 480	KR	451039	839
Strumigenys.rogeri	CASENT0185925	Kuitarua 480	KR	408100	1061
Strumigenys.rogeri	CASENT0185926	Qacavulo Point 300	TA	1372368	4587
Strumigenys.rogeri	CASENT0185717	Nabukavesi 300	VL	1061495	1739
Strumigenys.rogeri	CASENT0185561	Nabukavesi 300	VL	852248	3134
Strumigenys.rogeri	CASENT0185690	Lami 200	VL	1106624	3545
Strumigenys.rogeri	CASENT0185871	Naikorokoro 300	VL	516968	1059
Strumigenys.rogeri	CASENT0185935	Colo-i-Suva 200	VL	535477	1630
Strumigenys.rogeri	CASENT0185737	Nakavu 300	VL	2483105	4014
Strumigenys.rogeri	CASENT0185555	Nadakuni 300	VL	852451	4213
Strumigenys.rogeri	CASENT0185738	Colo-i-Suva 200	VL	1725774	3822
Strumigenys.rogeri	CASENT0185676	Colo-i-Suva 200	VL	1355499	2955
Strumigenys.rogeri	CASENT0185880	Nabukavesi 300	VL	1039896	2932
Strumigenys.rogeri	CASENT0185526	Naikorokoro 300	VL	850308	1232
Strumigenys.rogeri	CASENT0185648	Nabukelevu 300	VL	432876	2009
Strumigenys.rogeri	CASENT0185664	Naboutini 300	VL	1079912	3599
Strumigenys.rogeri	CASENT0185774	Vuya 300	VN	2863508	4754
Strumigenys.rogeri	CASENT0185756	Mt. Delaikoro 391	VN	344902	1917
Strumigenys.rogeri	CASENT0185910	Rokosalase 180	VN	443579	2862
Strumigenys.rogeri	CASENT0185973	Yasawa 300	VN	772428	1208
Strumigenys.rogeri	CASENT0185947	Rokosalase 180	VN	6188235	5108
Strumigenys.rogeri	CASENT0185938	Mt. Delaikoro 391	VN	3015167	4301
Strumigenys.rogeri	CASENT0185952	Rokosalase 180	VN	773155	2248
Strumigenys.rogeri	CASENT0735643	Rokosalase 180	VN	910290	2073