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The ant fauna of Timor and neighbouring islands: potential bridges between the disjunct faunas of South East Asia and Australia

Colin R. Trainor[A,C] *and Alan N. Andersen*[B]

[A]School of Environmental and Life Sciences, Charles Darwin University, Darwin, NT 0800, Australia.
[B]CSIRO Sustainable Ecosystems, Tropical Ecosystems Research Centre, PMB 44, Winnellie, NT 0822, Australia.
[C]Corresponding author. Email: colin.trainor@cdu.edu.au

Abstract. This study examines the biogeography of the ant fauna of Timor and of stepping stone Nusa Tenggara islands to the north (Wetar, Atauro, Alor, Pantar and Lembata) that are geographically closer to continental South East Asia. Timor is of outstanding biogeographical significance because it is the second largest island within the Wallacean transitional zone between the closely approximated but geologically distinct Indo-Australasian and South East Asian continental plates. It represents a potential overlap zone between the otherwise disjunct ant faunas of Australia and South East Asia. A total of 154 ant species from 32 genera and six subfamilies were collected through a combination of systematic sampling in evergreen forest, dry forest, savanna and grassland at 23 locations in the Lautem district of Timor-Leste, and opportunistic collections at 29 sites elsewhere on Timor and on the neighbouring islands. The most species-rich genera were *Camponotus* and *Polyrhachis* (both 28 species), *Tetramorium* (14 species), *Diacamma* and *Paratrechina* (both 8 species). On Timor, 111 ant species were recorded, including 64 species in the Lautem district. The Timor ant fauna is dominated by taxa of South East Asian origin (76% of native species), and has only weak Australian affinities (18%). The latter figure is even smaller (14%) for the neighbouring islands, reflecting their closer proximity to South East Asia. In contrast to Australia, there was no clear disjunction between the ant faunas of contrasting tropical forest and savanna habitats sampled in Lautem district. This can be explained by the Timor ant fauna being dominated by South East Asian tropical forest taxa, with Australian savanna woodland taxa being poorly represented.

Introduction

The Indonesian islands of Wallacea, the biological region transitional between the Indo-Australasian (Sahul) and South East Asian (Sunda) continental plates, have been an important focus for some of the major developments in island biogeography (Wallace 1869; Holloway and Jardine 1968; Schmitt *et al*. 2000; Hisheh *et al*. 2004). Wallace's Line between Bali and Lombok, and Borneo and Sulawesi, delineates a sharp faunal boundary for mammals (Kitchener *et al*. 1990), birds (White and Bruce 1986; Clode and O'Brien 2001), frogs (Inger and Voris 2001) and snakes (How and Kitchener 1997). Dispersal across island chains and (occasional) vicariance has been a key process in the development of endemic-rich Wallacean faunas for at least birds (Norman *et al*. 2007; Jønsson *et al*. 2008; Outlaw and Voelker 2008) and reptiles (How *et al*. 1996; Schmitt *et al*. 2000).

After Sulawesi, Timor (31 459 km^2; 2963 m above sea level) is the second largest of thousands of islands in Wallacea. Timor lies 860 km east of Wallace's Line and 470 km north of north-western Australia, and was formed ~4 million years ago by the collision of the northwardly advancing Australian Plate with the Banda Volcanic Arc. It has never been in contact with either continental Australia or South East Asia, but during the last Ice Age distances to Australia were reduced by as much as 75 km and to South East Asia by even less via a range of stepping stone islands such as Atauro, Wetar and Alor, which currently lie 30–50 km north of Timor (Voris 2000).

Both South East Asia (with 155 genera and more than 4500 described species) and Australia (101 genera and ~1350 described but >5000 actual species) are hotspots of global ant species diversity (Shattuck 1999; Andersen 2007; www.antweb.org). However, despite their proximity, the two regions support remarkably disjunct ant faunas. The South East Asian fauna is predominantly forest-adapted, and although a depauperate subset of it extends into the relatively small and fragmented rain forests of northern Australia, it is totally absent from the savanna landscapes that dominate this region (Taylor 1972; Reichel and Andersen 1996; Andersen 2000). Conversely, the northern Australian fauna comprises primarily autochthonous arid-adapted elements, most of which are absent from South East Asia, even in savanna woodland habitats (Taylor 1972; Andersen 2000; Bolton *et al*. 2006).

Here we report on the first systematic study of the ant fauna of Timor and neighbouring Nusa Tenggara islands. Our specific aims were to: (1) assess the extent to which Timor and neighbouring islands represents an overlap zone between the biogeographically disjunct South East Asian and Australian ant faunas; and (2) identify patterns in the richness and composition

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of ants across a range of habitats within the Lautem district of Timor-Leste.

Methods

Study sites

Ants were collected systematically in Lautem district to examine ant/vegetation associations, and opportunistically elsewhere on Timor island and on the adjacent Nusa Tenggara islands of Wetar (3600 km^2), Alor (2125 km^2), Lembata (1270 km^2), Pantar (728 km^2) and Atauro (144 km^2) to provide a broader representation of the regional fauna. Biogeographically, Atauro and Wetar are closely associated with Timor, but the other islands are more closely associated with Flores (Stattersfield *et al*. 1998; Carstensen and Olesen 2009). Despite differences in mode of island evolution, the climate, vegetation and topography on these islands is similar. The wet season typically extends from November to April with a prolonged dry season (Regional Physical Planning Project for Transmigration 1989; Monk *et al*. 1997). Vegetation is mostly evergreen or dry (deciduous) forest, but extensive *Eucalyptus*, *Acacia*, palm and *Ziziphus* savanna woodlands are present. These islands include most of the Wallacean occurrences of *Eucalyptus alba* and the Wallacean-endemic *E. urophylla* (Martin and Cossalter 1976; Ladiges *et al*. 2003; Payn *et al*. 2007).

Lautem district (1812 km^2) is located in the far east of Timor-Leste, and maintains the most extensive tropical forests on Timor island (Trainor *et al*. 2008). The Fuiloro plateau is an upland closed catchment of 440 km^2 that includes extensive grassland, sedgeland and Lake Iralalaro, the largest freshwater wetland on the island. Mount Legumau is the highest peak at ~1200 m, with most of the district covered in lowland habitat. Almost half the district is included in Nino Konis Santana National Park (terrestrial component of 654 km^2) which was established in August 2007 (República Democrática De Timor-Leste 2007).

Mangrove, coastal strand, savannas and tropical dry (deciduous) forests occur in the lowlands below ~200 m, but with increasingly evergreen tropical forests (including montane forest) found in higher-rainfall areas such as the Paitchau range (Monk *et al*. 1997; Whistler 2001; Cowie 2006). On the south coast patches of tropical evergreen forest are found on alluvium behind the beach. Rainfall in the district is seasonal but varies substantially with elevation and aspect from 635 mm $year^{-1}$ at Laivai to 1905 mm $year^{-1}$ at Lospalos, mostly falling from November to March–April (Regional Physical Planning Project for Transmigration 1989), but the south coast and mountains also receive the south-east monsoon in May–June. Rainfall may reach 3000 mm $year^{-1}$ in the hills, but records are absent. Lautem district has a population of 55 921 people, representing the second lowest density (32 km^{-2}) of Timor-Leste's 13 districts.

Ant species records

In addition to systematic surveys in Lautem district (see below), ants were sampled opportunistically at 16 sites elsewhere on Timor (including one in West Timor), and at a total of 13 sites on Wetar (6 locations, sampled during September/October 2008), Alor, Atauro, Lembata and Pantar islands (4, 1, 1 and 1 locations respectively, sampled from November 2009 to January 2010) (Table 1, Fig. 1). Opportunistic collections targeted a wide range of habitats, but particularly the dominant *Eucalyptus* woodland, tropical forest and mangroves. At each site, the full range of ant species observed were hand collected over a 1–2-h period.

Systematic survey in Lautem district

Sampling was conducted to provide a broad overview of the composition and habitat relationships of the regional fauna, rather than to conduct comprehensive inventories at particular sites. During December 2003 to September 2006 ants were collected from 56 transects at 23 locations (Table 2) in Lautem district, with about half the sampling in the dry season (July–November) and half in the wet season (December–June). The survey covered all major natural vegetation types, with particular focus on tropical forests, but also including savannas and grasslands. At each site, ants were sampled at five points every 200 m on 1-km transects over a 48-h period. In all, 1–6 transects were sampled per location, with transects separated by 1–4 km. At each point, two (6 L, 25 cm wide by 28 cm deep) vertebrate pitfall traps were buried with their lip flush with the ground. Ants captured in the buckets, and during two 3-min active searches (at each point) were retained in a single 50-mL alcohol-filled jar over the 48 h. Sampling focussed on larger (>3 mm) readily visible ground-dwelling ants rather than the entire fauna. Transects were positioned within homogenous vegetation with data from the five points pooled for each transect. Sampling intensity was therefore low on each transect (20 pit-trap-nights and 30-min active search) but this is at least partly compensated by the large number of transects (56), and relatively comprehensive geographic and habitat coverage of the study.

All ants collected were sorted to species in the laboratory, with species nomenclature for described species following Bolton *et al*. (2006). Undescribed taxa were identified to genus, and where possible to species group, and were assigned letter codes (sp. A, sp. B, etc.) that apply to this study only. Voucher specimens of all species are held at the CSIRO Tropical Ecosystems Research Centre in Darwin.

Environmental data

For each Lautem transect a suite of landscape-scale and local habitat attributes was collected to examine the environmental relationships of ants (Table 3). Habitats were classified as evergreen forest, dry forest, savanna and grassland based on available classifications (Monk *et al*. 1997; Cowie 2006). Canopy height of evergreen forest was more than twice that of dry forest. Savanna woodland was dominated by trees ~11 m tall with less than half the extent of old-growth forest within a 3 km radius. Grassland occurred on an alluvial plain with little rock, dominated by grasses or sedges with a mean of one tree per plot (Table 3). Human population was lowest within 2 km of evergreen forest and highest near savanna and grassland habitats.

For each sample point the distance to the coast and to old-growth forest was measured. Means of the following attributes were derived from a 1-km radius of each point using ARC GIS: elevation, slope, a measure of landscape roughness (taken as the standard deviation of slope), a greenness index of vegetation density (Wide Dynamic Range Vegetation Index), area of old-growth forest, secondary forest and all tropical forest combined

Table 1. Opportunistic survey locations on Timor and adjacent islands

Island	District	Location	Habitat
Lembata	Lembata	Lewoleba	Evergreen forest/mangrove
Pantar	Alor	Baranusa	Evergreen forest/*Eucalyptus* woodland
Alor	Alor	Kalabahi	Mangrove
Alor	Alor	Mainang	Evergreen forest/*Eucalyptus* woodland
Alor	Alor	Subo	Evergreen forest/*Eucalyptus* woodland
Alor	Alor	Tanglapui	Evergreen forest/*Eucalyptus* woodland
Atauro	Dili	Manucoco	Montane forest/*Eucalyptus* woodland
Wetar	South-west Maluku	Lurang	Village
Wetar	South-west Maluku	Naumatang Gorge	Tropical forest/*Eucalyptus* woodland
Wetar	South-west Maluku	Lake Tihu	Tropical forest/*Eucalyptus* woodland
Wetar	South-west Maluku	Meron	Tropical forest/*Eucalyptus* woodland
Wetar	South-west Maluku	Napar	Tropical forest
Wetar	South-west Maluku	Redong	Tropical forest
Timor	South Central Timor	Mt Mutis	Montane forest/*Eucalyptus* woodland
Timor	Oecusse	Oesilo area	*Eucalyptus* and *Casuarina* woodland
Timor	Oecusse	Pante Makassar town	Mangroves and mudflat
Timor	Covalima	Suai Hotel	Village
Timor	Bobonaro	Maliana	*Eucalyptus* woodland and ricefields
Timor	Liquica	Lake Maubara	Saline lake and mangrove
Timor	Ermera	Railako	Coffee plantation/secondary forest
Timor	Ainaro	Hatu Builico	*Eucalyptus* woodland, grassland
Timor	Liquica	Tibar	Mangrove
Timor	Manufahi	Betano/Daisua	*Eucalyptus* and palm savanna
Timor	Dili	Dare	*Eucalyptus* woodland, secondary forest
Timor	Aileu	Remexio	*Eucalyptus* woodland, secondary forest
Timor	Dili	Cristo Rei	Mangrove and savanna
Timor	Dili	Hera	Mangrove
Timor	Viqueque	Mt Mundo Perdido	Montane forest/*Eucalyptus* woodland
Timor	Viqueque	Mt Laritame	Montane forest

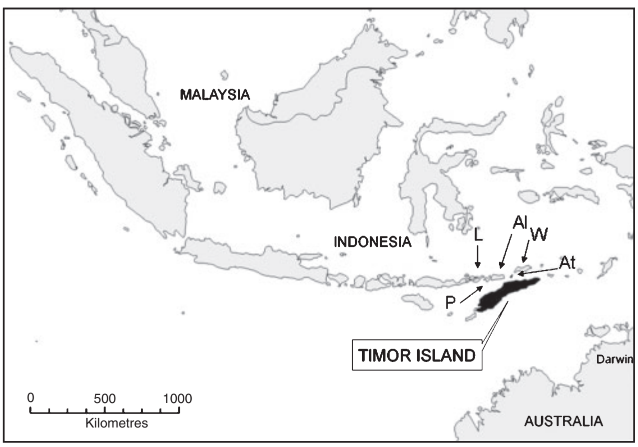

Fig. 1. Location of Timor and adjacent islands: Atauro (At), Wetar (W), Alor (Al), Pantar (P) and Lembata (L). Lautem district is located in the extreme east of Timor Island.

(within a 3-km radius of the transect), and human population (within a 2-km radius) (Table 3). The number of tree stems $\geq$10 cm was counted and tree height (m) estimated; cover (%) of bare ground, canopy, leaf litter and rock were estimated within a 20-m radius of each point (Table 3); coordinates were obtained using a global positioning system.

Analysis

A species list was compiled for all records, and the biogeographical affinity of each species was described as South East Asian, Australian, or widespread on the basis of the second author's understanding of the broader distribution of the species group to which it belongs.

Lautem transects were grouped according to habitat type, and species-accumulation curves were used to assess sampling completeness and to compare species richness among habitats (Colwell 2005). The frequency of occurrence of the 13 most abundant ant species, and of ant species richness per transect was compared among habitats with non-parametric Kruskal–Wallis ANOVA by ranks. Holm's sequential Bonferroni method (Roback and Askins 2005) was used to control for Type I error rate in the 13 tests for ant species (one test in 20 would be expected to be significant by chance at a significance level of 0.05). Patterns of ant species composition were examined using non-metric multi-dimensional scaling (NMDS) in Primer ver. 6.1.6 (Clarke and Gorley 2006) on species presence/absence data (based on a Bray–Curtis dissimilarity matrix). ANOSIM (analysis of similarity) was used to determine whether there were significant differences in ant species composition between the four habitat types. To examine factors underlying community patterns in the ordination, Spearman Rank correlation was use to test the association between ordination axis scores and local habitat variables and landscape-scale

Table 2. The 23 systematic survey locations in Lautem district, with the number of transects sampled per habitat

Village	Site	Evergreen forest	Dry forest	Savanna	Grassland
Bauro	Assalaino		4		
Bauro	Bauro	2			2
Lore II	Chin river	2			
Com	Com, Fevari		2		
Com	Com, Loikeri		1		
Com	Com, Puluru		2		
Daudere	Daudere		1	1	
Seralau	Seralau			2	
Souro	Foima	2			
Raca	Fuiloro				2
Lore II	Ili Lapa				2
Bauro	Iramalaro		1		
Muapitine	Iramimiraka	2			
Euquisi	Laivai		1	1	
Baricafa	Legumau	4			
Lore I	Lore	8			
Tutuala	Maca Beach	1			
Muapitine	Mainina	4			
Muapitine	Malahara				2
Mehara	Mehara	2			
Parlemento	Moro Parlemento			2	
Muapitine	Muapitine	1			
Parlemento	Nari		2		

factors. To assess the possible impact on the ant fauna of a commonly recorded invasive species (yellow crazy ant, *Anoplolepis gracilipes*), the mean ant species richness (subtracting yellow crazy ant from the richness variable) in tropical forest transects where it was recorded was compared with those transects where it was absent using the non-parametric Mann–Whitney *U*-test.

Results

The Timor regional fauna

A combined total of 154 ant species from six subfamilies and 32 genera were recorded on Timor Island (111 species, 32 genera), Wetar (48 species, 20 genera), Alor (36 species, 17 genera), Pantar (27 species, 11 genera), Lembata (12 species, 10 genera) and Atauro (15 species, 10 genera) (Table 4). The five most species-rich genera contributed more than half (56%) of all ant species: *Camponotus* (28 species), *Polyrhachis* (28 species), *Tetramorium* (14 species), *Diacamma* and *Paratrechina* (both 8 species). The richest subfamilies were Formicinae (68 species), Myrmicinae (43 species), Dolichoderinae and Ponerinae (both 19 species). Ten of the ant species are exotic: *Monomorium destructor* (recorded on two islands), *M. floricola* (two islands), *M. mayri* (three islands), *Solenopsis geminata* (Timor only), *Tetramorium bicarinatum* (four islands), *T. simillimum* (two islands), *Tapinoma melanocephalum* (two islands), *Technomyrmex albipes* (three islands), *Anoplolepis gracilipes* (five islands) and *Paratrechina longicornis* (four islands).

Of the 144 native species, 110 (76%) have South East Asian affinities, 23 (16%) have Australian affinities (mostly species of *Iridomyrmex*, *Rhytidoponera* and ground-nesting subgenera of *Polyrhachis*), and 11 (8%) belong to species groups that are widely distributed in the Indo-Australian region. The proportion of species with Australian affinities ranged from 17.8% on Timor, 14.6% on Wetar, 6.4% on Alor and 10% on Lembata. No Australian taxa were recorded from Atauro or Pantar.

Lautem district

During systematic survey in Lautem a total of 64 ant species (six exotic) from 25 genera and five subfamilies were collected. The most species-rich genera were *Camponotus* (10 species), *Polyrhachis* (10 species), *Tetramorium* (7 species) and

Table 3. Transect mean (±1 s.e.) landscape and environmental variables for habitats
Significance of the results is determined by Kruskal–Wallis One-way ANOVA. Significance: n.s., not significant; *, $P < 0.01$; **, $P < 0.001$

	Evergreen forest	Dry forest	Savanna woodland	Grassland	*H*
Transects	28	14	6	8	
MDS1	0.37 (0.09)	–0.11 (0.14)	–0.52 (0.22)	–0.74 (0.33)	19.4**
MDS2	0.03 (0.08)	–0.09 (0.14)	0.52 (0.29)	–0.48 (0.18)	16.3*
Greeness (WDRVI)	–0.40 (0.02)	–0.51 (0.02)	–0.67 (0.02)	–0.69 (0.06)	27.7**
Mean elevation (m)	373.1 (60.2)	310.3 (54.3)	69.4 (15.7)	384.0 (17.0)	8.9
Mean slope (°)	15.2 (2.1)	11.4 (2.2)	10.9 (1.5)	2.5 (0.5)	16.9*
Surface roughness	9.3 (1.4)	5.9 (0.9)	7.4 (1.4)	2.1 (1.1)	15.3*
Distance to coast (km)	6.1 (1.0)	4.1 (0.8)	2.2 (0.9)	10.7 (0.7)	13.6*
Distance to old-growth forest (km)	0.8 (0.4)	0.3 (0.1)	0.9 (0.2)	3.3 (0.9)	19.1**
Area of old-growth forest within 3 km (km^2)	19.5 (1.2)	16.4 (1.0)	8.3 (1.5)	6.6 (1.4)	27.8**
Population within 2 km (no.)	16.4 (7.4)	109.3 (52.5)	246.5 (72.1)	416.7 (151.6)	19.0**
Latitude	8.56 (0.02)	8.39 (0.01)	8.40 (0.02)	8.48 (0.02)	38.2**
Longitude	127.02 (0.03)	127.01 (0.03)	126.86 (0.04)	127.05 (0.03)	7.5 n.s.
Bare ground cover (%)	2.0 (0.9)	3.8 (1.6)	7.1 (3.9)	6.9 (4.3)	3.0 n.s.
Rock cover (%)	21.1 (3.6)	41.2 (6.5)	19.4 (5.1)	2.5 (2.3)	18.9**
Tree stems (≥10 cm) count	32.4 (2.8)	23.1 (2.7)	20.1 (4.2)	5.9 (4.8)	17.6*
Canopy height (m)	28.3 (1.5)	13.5 (1.3)	11.3 (2.1)	2.2 (0.9)	39.9**

Table 4. Ant species list for Lautem district (giving frequency of transect records from the four habitats), Timor Island and adjacent islands

Biogeographical affinity: SEA (South East Asia), Aus (Australia), Int (Introduced/exotic) and Wide (Widespread). 'p' denotes additional ant species collected opportunistically, but not systematically, in Lautem district. Data were pooled for Timor districts when more than one location was surveyed within a district, and pooled for Alor and Wetar where more than one location was visited

	Biogeographical affinity	Lautem					Timor District (opportunistic locations)											Island				
		Evergreen forest	Dry forest	Savanna	Grassland	Lautem present	South Central Timor	Oecusse	Liquica	Bobonaro	Covalima	Ainaro	Manufahi	Ermera	Dili	Aileue	Viqueque	Wetar	Atauro	Pantar	Alor	Lembata
Subfamily Pseudomyrmecinae																						
Tetraponera allaborans	SEA																	1			1	1
Tetraponera sp. (*nigra* group)	SEA														1							
Subfamily Ponerinae																						
Anochetus sp. A (*graeffei* group)	SEA	2		2		1																
Brachyponera sp. A	SEA	2	1	2	5	1	1		1					1		1		1	1	1	1	
Diacamma sp. A	SEA	1				1											1					
Diacamma sp. B	SEA	3	1	2		1											1					
Diacamma sp. C	SEA		2			1																
Diacamma sp. D	SEA														1							
Diacamma sp. E	SEA						1								1							
Diacamma sp. F	SEA																1					
Diacamma sp. G	SEA																	1				
Diacamma sp. H	SEA											1										
Diacamma sp. I	SEA																				1	
Diacamma sp. J	SEA																			1		
Leptogenys diminuta	SEA	4	2	2		1	1							1					1	1		
Leptogenys sp. A (*conigera* group)	Wide	1				1																
Leptogenys sp. C	SEA	5				1																
Odontoponera transversa	SEA																			1		
Platythyrea sp. A (*parallela* group)	SEA																		1			
Platythyrea sp. B (*parallela* group)	SEA																					1
Platythyrea sp. C (*parallela* group)	SEA														1							
Subfamily *Ectatomminae*																						
Rhytidoponera sp. A (*araneoides* group)	Aus	2	6		1	1										1	1					
Rhytidoponera sp. B (*araneoides* group)	Aus						1															
Rhytidoponera sp. D (*convexa* group)	Aus																				1	
Subfamily Myrmicinae																						
Cardiocondyla sp. A (*nuda* group)	SEA											1			1			1				
Cardiocondyla sp. B (*nuda* group)	SEA																1					
Cardiocondyla wroughtoni	SEA																	1				
Cataulacus sp. A	SEA		1			1																
Cataulacus sp. B	SEA					p												1				
Crematogaster ?inflata	SEA		3	1		1	1			1			1					1				
Crematogaster sp. H (*laeviceps* group)	Wide		1			1																
Crematogaster sp. C (Group A)	SEA			3		1		1	1													
Crematogaster sp. D (Group A)	Wide							1	1						1			1				
Crematogaster sp. E (*laeviceps* group)	Wide																				1	
Crematogaster sp. E (Group A)	SEA															1						
Crematogaster sp. F (Group A)	SEA									1								1				
Monomorium sp. A (*nigrius* group)	Aus																	1				
Monomorium sp. B (*nigrius* group)	Aus																	1				
Monomorium destructor	Int									1	1		1					1				
Monomorium floricola	Int			1		1				1					1	1		1				
Monomorium mayri	Int			2	1	1												1			1	
Pheidole sp. F (Group L)	SEA														1			1				
Pheidole sp. A	SEA	1				1																
Pheidole sp. B (*impressiceps* group)	SEA				1	1																
Pheidole sp. C	SEA				1	1																

(*continued next page*)

Table 4. (*continued*)

	Biogeographical affinity	Lautem					Timor District (opportunistic locations)											Island				
		Evergreen forest	Dry forest	Savanna	Grassland	Lautem present	South Central Timor	Oecusse	Liquica	Bobonaro	Covalima	Ainaro	Manufahi	Ermera	Dili	Aileue	Viqueque	Wetar	Atauro	Pantar	Alor	Lembata
Pheidole sp. D (*impressiceps* group)	SEA															1		1				
Pheidole sp. E (Group L)	SEA																	1				
Pheidole sp. E (*impressiceps* group)	SEA																				1	
Pheidologeton sp. A	SEA	12	4	1	1	1								1				1				
Rhomblonella sp. A	SEA		1			1																
Rhoptomyrmex sp. A	SEA						1															
Solenopsis geminata	Int							1		1					1							
Strumigenys ?*godeffroyi*	SEA	1				1																
Tetramorium bicarinatum	Int	1			2	1				1					1	1	1			1	1	1
Tetramorium ?*eleates*	SEA	1				1																
Tetramorium insolens	SEA																	1				
T. pacificum	SEA																	1				
Tetramorium simillimum	Int			1		1												1				
Tetramorium sp. nr *turneri*	Aus			1		1																
T. validusculum	SEA		1			1												1				
Tetramorium sp. A (*ornatum* group)	SEA	1				1										1	1					
Tetramorium sp. K (*ornatum* group)	SEA													1			1					
Tetramorium sp. B (*carinatum* group)	SEA	1				1												1				
Tetramorium sp. G (*ornatum* group)	SEA													1								
Tetramorium sp. H (*ornatum* group)	SEA																1					
Tetramorium sp. I (*bicarinatum* group)	SEA																		1		1	
Tetramorium sp. J (*ornatum* group)	SEA																				1	
Subfamily Dolichoderinae																						
Dolichoderus sp. A	SEA	9	5		2	1	1	1			1		1	1	1	1		1	1	1	1	1
Iridomyrmex sp. A (*anceps* group)	Aus					p		1				1										
Iridomyrmex sp. B (*anceps* group)	Aus									1												
Iridomyrmex sp. A (*mjobergi* complex)	Aus	1	2	2	4	1											1					
Iridomyrmex sp. B (*mjobergi* complex)	Aus			1		1																
Iridomyrmex sp. 7 (*bicknelli* group)	Aus																	1				
Iridomyrmex sanguineus	Aus							1														
Ochetellus sp. A (*glaber* group)	Aus			1		1		1				1			1						1	1
Philidris sp. A	SEA	2	1			1		1							1							
Tapinoma melanocephalum	Int									1	1		1	1	1		1	1				
Tapinoma sp. A	Wide		1	1		1									1							
Tapinoma sp. C	SEA														1							
Tapinoma sp. D	Wide														1							
Tapinoma sp. E	Wide																	1				
Tapinoma sp. F	Wide																	1				
Technomyrmex albipes	Int							1						1			1			1	1	
Technomyrmex difficilis	SEA									1								1				
Technomyrmex myops	SEA														1							
Technomyrmex sp. nr *albipes*	SEA	1				1																
Subfamily Formicinae																						
Anoplolepis gracilipes sp. A	Int	11	3		2	1		1							1	1	1	1	1		1	1
Camponotus vitreus	SEA																	1				
Camponotus sp. G	SEA					p									1		1					
Camponotus sp. J	SEA	2				1																
Camponotus sp. P	SEA											1						1	1	1	1	1
Camponotus sp. U	SEA						1													1		
Camponotus sp. X	SEA																				1	
Camponotus sp. M (*macrocephalus* group)	Aus														1							
Camponotus sp. B (*novaehollandiae* group)	SEA		1		1	1														1		

Table 4. (*continued*)

	Biogeographical affinity	Lautem					Timor District (opportunistic locations)											Island				
		Evergreen forest	Dry forest	Savanna	Grassland	Lautem present	South Central Timor	Oecusse	Liquica	Bobonaro	Covalima	Ainaro	Manufahi	Ermera	Dili	Aileue	Viqueque	Wetar	Atauro	Pantar	Alor	Lembata
Camponotus sp. F (*novaehollandiae* group)	SEA	5	3			1									1							
Camponotus sp. G (*novaehollandiae* group)	SEA																1					
Camponotus sp. I (*novaehollandiae* group)	SEA			1	1	1																
Camponotus sp. N (*reticulatus* group)	SEA															1						
Camponotus sp. R (*reticulatus* group)	SEA																				1	
Camponotus sp. S (*novaehollandiae* group)	SEA						1			1										1	1	
Camponotus sp. T (*novaehollandiae* group)	SEA																		1			
Camponotus sp. V (*novaehollandiae* group)	SEA																				1	
Camponotus sp. W (*novaehollandiae* group)	SEA																			1		
Camponotus sp. Z (*novaehollandiae* group)	SEA									1					1					1	1	
Camponotus sp. AA (*novaehollandiae* group)	SEA																			1		
Camponotus sp. A (*reticulatus* group)	SEA	1				1												1			1	
Camponotus sp. K (*reticulatus* group)	SEA	1	1			1																
Camponotus sp. L (*reticulatus* group)	SEA			1		1												1				
Camponotus sp. Q (*reticulatus* group)	SEA																	1				
Camponotus sp. Y (*reticulatus* group)	SEA							1													1	
Camponotus sp. C (*saundersi* group)	SEA	3	1			1												1				
Camponotus sp. D (*saundersi* group)	SEA	5			1	1								1				1	1	1	1	
Camponotus sp. H (*saundersi* group)	SEA					P																
Echinopla sp. A	SEA	1	1			1																
Echinopla sp. B	SEA		1			1													1	1	1	
Oecophylla smaragdina	SEA	1		2	1	1		1					1		1			1		1	1	1
Paratrechina longicornis	Int			4		1		1	1	1	1		1		1			1	1		1	
Paratrechina sp. A (*obscura* group)	SEA			1	1	1			1			1					1		1	1		
Paratrechina sp. B (*obscura* group)	Wide	2				1												1				
Paratrechina sp. C (*vaga* group)	SEA	1				1																
Paratrechina sp. D (*obscura* group)	Wide													1			1					
Paratrechina sp. F (*obscura* group)	SEA																	1				1
Paratrechina sp. G (*minutula* group)	Aus																	1				
Paratrechina sp. D	Wide																					1
Plagioloepis sp. 1.	SEA																1					
Polyrhachis (*Campomyrma*) sp. A	Aus					p																
Polyrhachis (*Chariomyrma*) sp. F (*arcuata* group)	SEA						1					1										
Polyrhachis (*Cyrtomyrma*) sp. P	SEA																			1	1	
Polyrhachis (*Hedomyrma*) sp. O (*euterpe* group)	SEA																		1			
Polyrhachis (*Myrma*) *mayri*	SEA																			1	1	
Polyrhachis (*Myrma*) sp. nr *villipes*	SEA																			1	1	
Polyrhachis (*Myrmhopla*) *acantha*	SEA																	1				
Polyrhachis (*Myrmhopla*) *argentea*	SEA	3	3			1																
Polyrhachis sp. nr *bicolor*	SEA																				1	
Polyrhachis (*Myrmhopla*) *bicolor*	SEA																					1
Polyrhachis (*Myrmhopla*) *concolor*	SEA													1				1		1	1	
Polyrhachis (*Myrmhopla*) *cryptoceroides*	SEA																			1		
Polyrhachis (*Myrmhopla*) *dives*	SEA		1			1	1					1						1	1		1	1
Polyrhachis gab	Aus			1		1												1				
Polyrhachis sp. nr *inconspicua*	Aus		1			1																
Polyrhachis mucronata	SEA	2				1								1						1	1	
Polyrhachis sp. nr *mucronata*	SEA													1						1		
Polyrhachis sp. B (*bellicosa* group)	SEA	4			1	1																
Polyrhachis sp. E	SEA		1			1																
Polyrhachis sp. E (*arcuata* group)	Aus																1					
Polyrhachis sp. F (*arcuata* group)	Aus	1	3			1									1							

(*continued next page*)

Table 4. (*continued*)

	Biogeographical affinity	Lautem					Timor District (opportunistic locations)											Island				
		Evergreen forest	Dry forest	Savanna	Grassland	Lautem present	South Central Timor	Oecusse	Liquica	Bobonaro	Covalima	Ainaro	Manufahi	Ermera	Dili	Aileue	Viqueque	Wetar	Atauro	Pantar	Alor	Lembata
Polyrhachis sp. G (*arcuata* group)	Aus		1			1																
Polyrhachis sp. J (*cupreata* group)	Aus	1				1																
Polyrhachis sp. K (*zopyra* group)	SEA																				1	
Polyrhachis sp. L (*tibialis* group)	SEA																			1	1	
Polyrhachis sp. M (*zopyra* group)	SEA														1		1		1	1	1	
Polyrhachis sp. nr *obtusa*	Aus														1			1				
Polyrhachis rixosa	SEA																	1				

Paratrechina (5 species), and the richest subfamilies were Formicinae (32 species), Myrmicinae (19 species) and Dolichoderinae (8 species) (Table 4). The most commonly recorded species (recorded from more than eight transects) were: *Brachyponera* sp. A (37 transects), *Rhytidoponera* sp. A (*araneoides* group) (26), *Pheidologeton* sp. A (18), *Dolichoderus* sp. A (16), *Anoplolepis gracilipes* sp. A (16), *Diacamma* sp. B (15) and *Iridomyrmex* sp. A (*anceps* group) (9). These seven species contributed 53% (137 of 262) of species by transect records. The great majority (74%) of the 58 native species have South East Asian origin, with only eleven (19%) representing Australian taxa (Table 2).

Indicative of low sampling intensity per transect, ant species richness and number of individuals increased with increasing survey effort (Fig. 2) for each of the habitats without reaching an asymptote. Ant species richness and individuals accumulated more slowly in grassland and reached lower final values compared with the wooded habitats. There was no significant difference in mean ant richness per transect between evergreen forest, dry forest, savanna and grassland (Kruskal–Wallis test $H = 2.98$, $P = 0.39$), although overall grassland richness was lower (Fig. 3).

Species composition varied markedly between habitat types, but there was very substantial species overlap (Tables 4, 5). Non-metric multi-dimensional scaling indicated continuous change in species composition along the gradient from evergreen forest through to grassland, without obvious disjunctions (Fig. 4). ANOSIM r-values for pairwise tests showed significant differences between the ant composition of evergreen forest and savanna woodland ($r = 0.38$, $P = 0.02$), dry forest and savanna ($r = 0.28$, $P = 0.01$) and savanna and grassland ($r = 0.35$, $P = 0.09$). The low r values show that ant species composition overlapped strongly between habitats. For example, only two of the 15 ant species recorded from grassland were restricted to that habitat.

Positive NMDS axis scores were associated with attributes characteristic of evergreen forest in the south-east of Lautem district, such as increasing distance to the nearest village, large tropical forest area, increased canopy height, high canopy cover and tree density (Table 4). Negative NMDS1 axis scores were

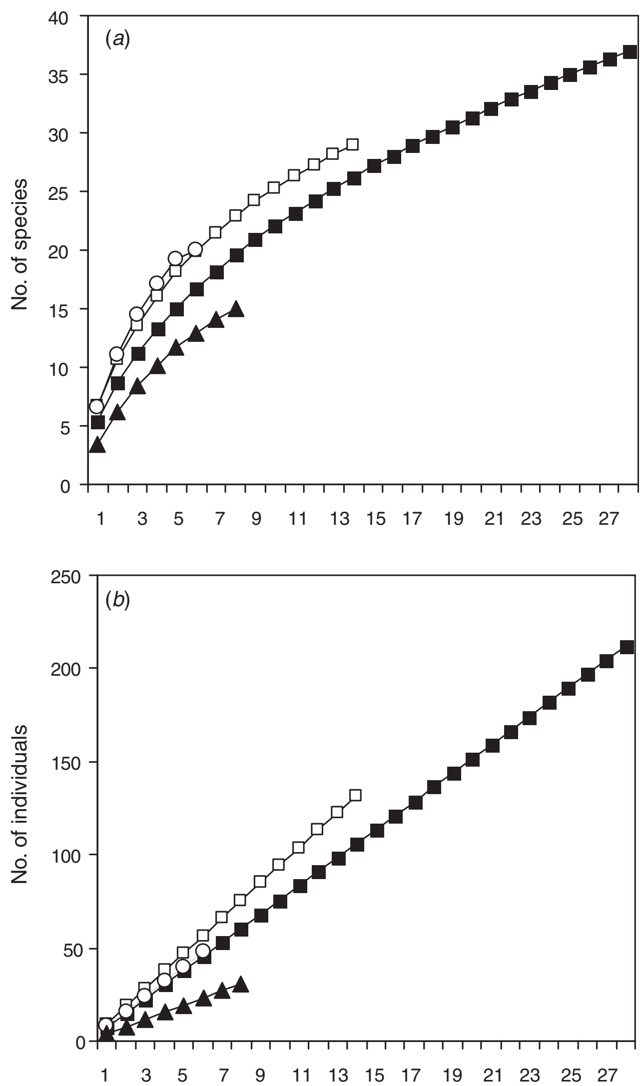

Fig. 2. Accumulation of (*a*) ant species, and (*b*) individuals for evergreen forest (closed squares), dry forest (open square), savanna (open dot) and grassland (closed diamond).

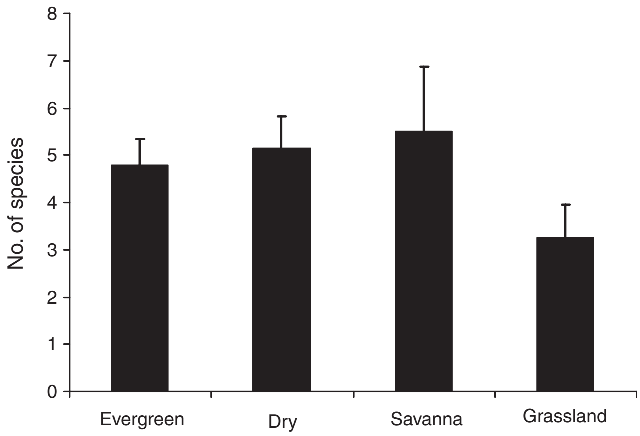

Fig. 3. Ant species richness per transect by habitat type (means ± 1 s.e.).

Table 5. Dissimilarity of ant species composition between the four habitats

Values range from 0 (no dissimilarity) to 1 (total dissimilarity). The number of species shared between habitats is shown in parentheses and the number of species unique to a single habitat is given in superscript next to the habitat name

Habitats	Dry forest[10]	Savanna woodland[9]	Grassland[2]
Evergreen forest[16]	0.69 (16)	0.86 (7)	0.68 (10)
Dry forest		0.85 (7)	0.72 (7)
Savanna woodland			0.86 (7)

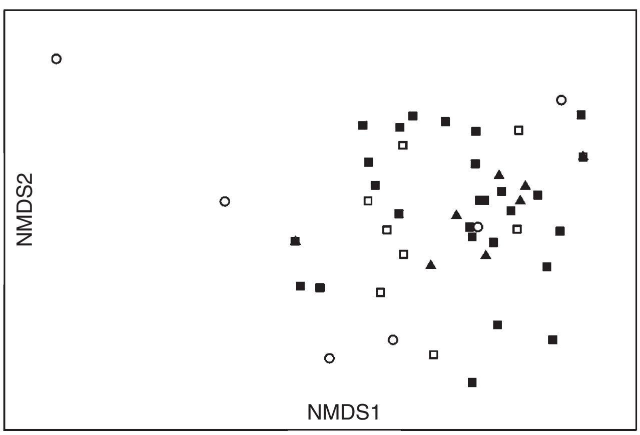

Fig. 4. Non-metric multi-dimensional scaling ordination plot of the 56 transects. Symbols: evergreen forest (solid square), dry forest (open square), savanna woodland (open dot) and grassland (closed diamond).

associated with increased disturbance typical of secondary forest, including increased population (Table 6). Positive values of NMDS2 were associated with increasing slope, increased rock cover and lower latitude typical of tropical forest and savanna on karst along the north coast.

Only three of the 13 most frequently recorded ants varied significantly in their frequency of occurrence between habitats, with *Rhytidoponera* sp. A (*araneoides* group) being recorded mostly from evergreen and dry forest, *Diacamma* sp. B mostly restricted to dry forest and savanna, and *Pheidologeton* sp. A most frequent in evergreen and dry forest (Table 7). The low abundance of many ant species weakened the statistical power of comparisons across habitats. The yellow crazy ant was recorded in 14 (33%) of evergreen and dry forest transects combined, but only two (7%) grassland transects. The occurrence of the yellow crazy ant was not significantly associated with ant species richness (Mann–Whitney $U = 281$, $P = 0.48$).

Table 6. Spearman rank correlations between landscape and habitat variables with the first two axes of the ordination

Significant correlations at $P < 0.05$ are shown in bold

	MDS1	MDS2
MDS1	1.00	–0.14
MDS2	–0.15	1.00
WDRVI 3	**0.67**	–0.14
Mean elevation (m)	0.17	0.02
Mean slope (°)	0.08	0.21
Surface roughness	0.09	0.19
Distance to coast (km)	–0.16	–0.13
Distance to old-growth forest (km)	**–0.37**	–0.23
Area of secondary forest within 3 km (km^2)	0.01	–0.25
Area of old-growth forest within 3 km (km^2)	**0.44**	0.11
Population within 2 km (no.)	**–0.65**	0.13
Latitude	**0.32**	**–0.42**
Longitude	**0.34**	–0.15
Bare ground cover (%)	0.03	–0.07
Rock cover (%)	0.14	**0.28**
Litter cover (%)	**0.56**	0.03
Tree stems (≥10 cm) count	**0.53**	–0.05
Canopy height (m)	**0.63**	–0.01
Canopy cover (%)	**0.62**	–0.08

Discussion

Our study is the first systematic examination of the ant fauna of the Timor region, which bridges the South East Asian and Australian biogeographic realms. The relatively limited sampling makes it difficult to comment on the overall richness of the ant fauna, but its biogeographic origins are clear, with ants with South East Asian affinities comprising the overwhelming majority (76%) of native Timorese species. This reflects the closer proximity of Timor to South East Asia than Australia. The proportion of species of Australian origin was slightly lower on neighbouring islands, reflecting their greater distance from Australia. The proportion of birds with Australian origins also declines on islands towards the west along the Nusa Tenggara chain (Clode and O'Brien 2001; Trainor 2010). The South East Asian ant fauna is too poorly known to assess which, if any, of the species we collected are regionally endemic.

Many of the Timorese taxa of South East Asian origin, such as *Anochetus*, *Diacamma*, *Leptogenys*, *Pheidologeton*, and the *maculatus* and *reticulatus* groups of *Camponotus*, also occur in northern Australia (Andersen 2000). Indeed, four Timor species of South East Asian origin – *Oecophylla smaragdina*, *Polyrhachis mucronata*, *Leptogenys diminuta* and *Tetramorium validiusculum* – also occur in northern Australia (Shattuck 1999;

Table 7. Frequency of occurrence (±1 s.e.) of 13 ant species recorded from five or more transects in evergreen forest, dry forest, savanna woodland and grassland

Non-parametric Kruskal–Wallis ANOVA tested for differences between habitats. Significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The smallest P value ($P = 0.0001$) was greater than 0.05/13 (significance value/n) in Holm's sequential Bonferroni method, meaning that the null hypothesis of that test, and those that follow, is not rejected

Species	Evergreen forest	Dry forest	Savanna woodland	Grassland	*H*
Transects	28	14	6	8	
Diacamma sp. B	0.11 (0.06)	0.71 (0.12)	0.33 (0.21)	0	20.6***
Rhytidoponera sp. A (*araneoides* group)	0.71 (0.09)	0.43 (0.13)	0	0.13 (0.12)	15.6**
Pheidologeton sp. A	0.43 (0.09)	0.29 (0.12)	0.17 (0.17)	0.13 (0.12)	3.5*
Brachyponera sp. A	0.71 (0.09)	0.71 (0.12)	0.33 (0.21)	0.63 (0.18)	3.4
Dolichoderus sp. A	0.32 (0.09)	0.36 (0.13)	0	0.25 (0.16)	2.9
Iridomyrmex sp. A (*mjobergi* complex)	0.04 (0.04)	0.14 (0.10)	0.33 (0.21)	0.50 (0.19)	11.2
Anoplolepis gracilipes	0.39 (0.09)	0.21 (0.11)	0	0.25 (0.16)	4.3
Camponotus sp. D (*saundersi* group)	0.18 (0.07)	0	0	0.13 (0.12)	3.8
Camponotus sp. E (*novaehollandiae* group)	0.18 (0.07)	0.14 (0.10)	0	0	2.7
Leptogenys diminuta	0.14 (0.07)	0.14 (0.10)	0.33 (0.21)	0	3.0
Leptogenys sp. C	0.18 (0.07)	0	0	0	5.4
Polyrhachis argentea	0.11 (0.06)	0.21 (0.11)	0	0	3.3
Polyrhachis sp. B (*bellicosa* group)	0.14 (0.07)	0	0	0.13 (0.12)	3.0

Andersen 2000). All these taxa are characteristic of tropical forest. In contrast, except for the *Polyrhachis cupreata* group (subgenus *Hedomyrma*) and *Camponotus macrocephalus* group (subgenus *Colobopsis*), all the taxa of Australian origin occur primarily in savanna. This includes *Polyrhachis gab*, a savanna species associated with rocky habitats throughout northern Australia (Andersen 2000); these comprise the first records outside Australia (R. Kohout, pers. comm. 2009). Similarly, *Iridomyrmex sanguineus* occurs throughout the savanna zone of northern Australia (Andersen 2000); this is the first record outside of Australia. *Iridomyrmex* sp. 7 (*bicknelli* group) is likewise widespread in Australian savanna, but it is also known from New Guinea. *Iridomyrmex* sp. B (*mjobergi* complex) is possibly the same as a very common savanna species that also occurs throughout northern Australia, but species boundaries within the *I. mjobergi* complex are yet to be resolved.

The ant fauna of Timor and its neighbouring islands includes many of the world's major pantropical invasive species. This includes the highly invasive yellow crazy ant, which has had dramatic impacts on other oceanic islands (O'Dowd *et al*. 2003; Lester and Tavite 2004; Bos *et al*. 2008). In Lautem district this species was widespread in forest but it did not occur in high densities, and at the broad scale of our sampling we could not detect any negative impact of it on the native ant fauna.

Forest and savanna habitats of Lautem supported distinct faunas, but there was very substantial overlap between them, with several of the most frequently recorded forest species (e.g. *Brachyponera* sp. A, *Diacamma* sp. B, *Pheidolegeton* sp. A) being recorded also in savannas, and nearly half the savanna and grassland species also occurring in forest. This is in striking contrast to the situation in Australia, where the forest and savanna ant faunas are remarkably disjunct (Taylor 1972; Reichel and Andersen 1996; Andersen *et al*. 2007; van Ingen *et al*. 2008). This contrast reflects the lack of arid-adapted, specialist savanna taxa in Timor, which are such dominant elements of savanna faunas in Australia (Andersen 2000). This is analogous to birds: among the 32 globally restricted-range birds of Timor, only the Timor sparrow, *Padda fuscata*, is a savanna woodland (non-forest) species (Trainor *et al*. 2007). There is also far greater floristic dissimilarity between forest and savanna in Australia compared with Timor. For example, the dominant savanna trees in northern Australia (species of *Eucalyptus*) are absent from forest, whereas some dominant savanna trees in Timor (such as *Schleichera oleosa* and *Tamarindus indica*) are common in dry forms of tropical forest (Meijer-Drees 1951; Cowie 2006).

Conclusion

The ant fauna of Timor and its neighbouring islands is overwhelmingly South East Asian in origin, with only 16% of the native species we recorded belonging to Australian taxa. This value is far less than the ~30% of more vagile resident land birds (Trainor *et al*. 2008). The dominant arid-adapted element of Australia's savanna ant fauna was virtually absent from our Timor samples, with the Timor savanna fauna mostly comprising a 'spill-over' of forest taxa. This conclusion may need to be modified somewhat with greater sampling intensity. However, the paucity of specialist savanna woodland species suggests that, historically, savanna habitats have not been as dominant as they are today on Timor, and that perhaps many have relatively recently been derived from forest due to anthropogenic clearing and burning.

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