

The Community Ecology of Ants (Formicidae) in Indonesian Grasslands with Special Focus on
the Tropical Fire Ant, *Solenopsis geminata*.

By

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Abstract

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Invasive species and habitat destruction are considered to be the leading causes of biodiversity decline, signaling declining ecosystem health on a global scale. Ants (Formicidae) include some of the most widespread and impactful invasive species capable of establishing in high numbers in new habitats. The tropical grasslands of Indonesia are home to several invasive species of ants. Invasive ants are transported in shipped goods, causing many species to be of global concern. My dissertation explores ant communities in the grasslands of southeastern Indonesia. Communities are described for the first time with a special focus on the Tropical Fire Ant, *Solenopsis geminata*, which consumes grass seeds and can have negative ecological impacts in invaded areas. The first chapter describes grassland ant communities in both disturbed and undisturbed grasslands. The second chapter narrows in focus to describe the utilization of grass seeds as a food resource for *S. geminata* and the potential for spread of this invasive ant given an unlimited food supply. The third, and final, chapter describes competition between ant species at food resources. *Solenopsis geminata* competes with several native and introduced ant species. These interactions are analyzed and I report on the ability of invasive ants to dominate invaded habitats.

Chapter 1 includes a large-scale diversity survey across eight islands in and around Komodo National Park, Nusa Tenggara Timur, Indonesia. Invasive ants are able to disrupt native habitats and the communities of ants found in them. Land use plays a role in invasion as human-mediated disturbances facilitate the introduction of non-native species. Biogeography, land use, climate, and habitat structure help to shape local communities. We surveyed eight islands using pitfall trap transects. Transects were placed in undisturbed and disturbed grasslands. Data on ant species counts and identification was used to test four hypotheses related to species distribution and abundance. 1. Introduced species will have broader distributions than native species across space, habitat, and seasons. 2. Habitat structure (grass and trees) influences ground-dwelling ant species abundance, diversity, and composition. 3. Grassland disturbance is associated with an increase in introduced species richness and abundance. 4. Development (human-made landscape elements) and distance from a port (measures of connectivity) have a greater influence on diversity than island size. We found that introduced species are generally more numerous than native species, but that some introduced species present in the region were fairly restricted both spatially and numerically. Season and vegetation structure were related and influenced by land use. Differences are linked to differences in ant community compositions. In addition to

differences related to habitat structure, species richness and diversity was influenced by the distance between the site and the port of Labuan Bajo.

The second chapter of my dissertation focuses on fire ant diets. The Tropical Fire Ant consumes large quantities of grass seeds. We described the diet of *S. geminata* in populations that inhabit grasslands and villages with comparisons to other ant species. Omnivorous ants are able to utilize a wide range of food resources, and this can enable invasion and even dominance in novel landscapes. Dietary specialization has evolved numerous times and can confer competitive advantages, optimal nutrition, and reduced cognitive needs in foraging. The Tropical Fire Ant, *Solenopsis geminata*, is a globally distributed invasive species. *Solenopsis geminata* has evolved a major worker caste for seed milling and granivory while the species is largely a dietary generalist. Here we used stable isotope analyses and behavioral assays to describe dietary shifts in *S. geminata* during range expansion from villages into disturbed grassland. These methods were used to question the benefits and draw-backs of dietary specialization in range expansion across habitat types with seemingly unlimited seed resources. We analyzed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in four ant species in adjacent village, disturbed grassland, and undisturbed grassland habitats on one island in Nusa Tenggara Timur, Indonesia. Isotope analysis was coupled with behavioral assays that delineated preferences for some grasses over others. Seed-size was manipulated to assess the influence of a worker's ability to move a seed relative to its attractiveness. *Solenopsis geminata* shifts from a diet of animal-based foods and C3 plants in villages to a largely C4 grass seed-based diet in grasslands. Co-occurring ant species are within the same trophic level but show lower utilization of C4 plants in savannas. *Solenopsis geminata* collects seeds from exotic grasses common in disturbed Indonesian grasslands at higher rates than larger seeds of native grasses. When the larger native seeds are cut to smaller sizes, they are collected at a higher rate. Foraging assays show that large seed size in native grasses may pose a barrier to seed consumption and expansion into undisturbed grasslands with otherwise similar structure and environmental conditions.

In chapter 3 I look at competition between ant species at food resources. Competition for food resources within a community of native and invasive ant species was investigated in disturbed and undisturbed grassland ecosystems on islands in Komodo National Park. Several species of invasive ants have established populations across the region, threatening endangered ground-nesting wildlife. Invasive ants are generally very abundant and may have negative impacts on local flora and fauna. Competition with dominant native ant species may limit access to resources for introduced ants offering some level of biotic resistance to the impacts of invasion. We examine intraspecific competition between ants at food resources in disturbed and undisturbed grasslands. Our approach examines forager abundance, temporal resource partitioning, and dominance-discovery tradeoffs, three concepts related to foraging behavior and access to resources that sustain ant colonies. We test the following hypotheses to describe competitive interactions. 1. Introduced species will be more abundant and widespread than native species. 2. Common and widespread species partition resources by foraging at different times of day. 3. Dominance-discovery tradeoffs exist between dominant species and weaker competitors. Tuna baits were observed at five sites on three islands in Nusa Tenggara Timur, Indonesia. Observations were made during morning, mid-day, and evening hours of the wet and dry seasons. A total of 81,188 ants were observed. Ants were collected at the end of each observation period for identification. Two invasive ant species, *Solenopsis geminata* and *Trichomyrmex destructor*, dominated baits in all disturbed habitat types. In undisturbed grassland, native ants were as common as invasive ants, though they did not exclude invasive ants from baits. We did

not find evidence of temporal partitioning of the food resource within a 24-hour period, but results suggest that there may be seasonal partitioning between the top competitors. *Solenopsis geminata* was able to outcompete *T. destructor* but could be resisted by a native species, *Iridomyrmex sp 2*. No evidence of a discovery-dominance tradeoff was found between top competitors though *Nylanderia vaga* and, to a lesser extent, *Paratrechina longicornis* may benefit from earlier arrival and departure when dominant species arrive. Interspecific competition between a network of dominant species may prevent any one species from becoming overly abundant and excluding less successful competitors. Complex interactions between dominant species and asymmetric foraging behaviors most likely create opportunities for weak competitors to access resources and may further limit resource access for invaders.

Dedicated to

Jonathan, my conscience and my inspiration to make a positive difference,
keep my eye on the prize,
and do what makes me happy.

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Chapter 1 The ant communities in grassland habitats on islands in southeastern Indonesia

1.1 Introduction

Ants account for 10 to 15 percent of terrestrial animal biomass and include some of the most pervasive and damaging invasive species (Hölldobler and Wilson 1990). In addition to providing a wide range of ecosystem services (Hölldobler and Wilson, 1990; Parr et al., 2016), ants are abundant, ubiquitous, extremely diverse, easily collected, and have a wide range of habitat and dietary needs. Studies of ant communities can signal climactic shifts and quantify land use impacts, providing a powerful tool in monitoring ecosystem health (Arcoverde et al., 2017; Agosti et al., 2000; Costa, 2010; Hoffman, 2010). The impacts of ant invasions are well documented in developed, economically important, and affluent regions (Daane et al., 2007; Hölldobler and Wilson 1990; Parr et al., 2016; King et al., 2008) and have proven to be very costly. The imported fire ant, *Solenopsis invicta*, is estimated to cause \$1 billion to \$6 billion in damages in the United States each year (Pimentel et al., 2005; Lard et al., 2006). The primary causes of species invasion are disturbance of native ecosystems and increased connectivity through global shipping routes (McGlynn, 1999; Holway et al., 2002; Suarez et al., 2001). Islands in the Indonesian Archipelago have been exposed to global trade since the early 1600's (Bertelsmeier et al., 2017; McGlynn, 1999; Rizali et al., 2010; Rizali et al., 2011). The Strait of Malacca lies between Indonesia, Singapore and Malaysia connecting Africa, Europe, Southeast Asia, and East Asia as the second busiest global shipping route (Rusli, 2010). Indonesia is considered a biodiversity hotspot within the “biological realm”, referred to later as “region”, of Indomalaya. There is a total of 8 “biological realms” or regions. Indomalaya encompasses India to Southern China and south through Indonesia. It is adjacent to the Afrotropic (Africa and Arabian Peninsula), Palearctic (Europe to China and south to Northern Africa), and Australasian (Papua, Australia and south through New Zealand) regions. Despite its importance in global shipping (Rusli, 2010) and potential as a source population for economically important pest species, the influence of the Indonesian Archipelago on global species migration is not well understood and most islands have not been surveyed.

Land use plays a major role in determining a habitat's susceptibility to invasion (King and Tschinkel, 2008). As invasive species eliminate native species, they create opportunities for introduced species to establish (Stachowicz and Tilman, 2005). Depletion of vegetation, soil compaction, and erosion promote invasion by changing local conditions (Leopold and Hess, 2017), leading to changes in community composition (Milchunas and Lauenroth, 1993). It is common for invasive ants to co-occur with disturbances in plant communities (O'Loughlin, 2016) even benefitting invasive plant species (Loch et al., 2010). Grasslands are expanding (Bourliere and Hadley, 1970; White et al., 2000), receive little protection (Hoekstra et al., 2005), and can be heavily invaded (D'Antonio and Vitousek, 1992). Grasslands store carbon (Jones and Donnelly, 2004), harbor highly diverse plant communities (Wilson et al., 2012), and provide a majority of food consumed by humans (White, 2000). Human-mediated habitat destruction causes grassland expansion and threatens native grasslands (White et al., 2000). Grazing impacts an estimated 40 percent of the Earth (Havstad, 2008; White et al., 2000) and often replaces fire in providing the required regular disturbance. Impacts of disturbance in grasslands is mixed,

highlighting the importance of locally conducted research in management decisions. Studies show that disturbances impact ant abundance and diversity less than species composition, typically favoring generalist species (Bestelmyer and Weins, 1996; Hoffman and Andersen, 2003; Hoffman, 2010). Often the degree and direction of impact is dependent on disturbance intensity (Bestelmyer and Weins, 1996). An underlying theme is that ant species composition is correlated with habitat structure, vegetation type, and soil characteristics, creating interactions with activities such as grazing and fire (Hoffman, 2010). Savanna trees may play an important role in insect invasion by increasing habitat heterogeneity and acting as refuges that can buffer the effects of exposure in open grasslands (Dunn, 2000).

Understanding how a large number of factors influences island communities is complex. Groups of numerous islands with geographic and climatic similarity reduce environmental variation allowing research to highlight anthropogenic impacts in comparable closed systems. GENERALIZED MYRMECINE and DOMINANT DOLICHODERINE functional groups make up a large proportion of the ant communities found in Indonesian tropical savanna grasslands. These groups along with the CRYPTIC and OPPORTUNIST groups, are the source of all tramp species (McGlynn, 1999) which are a large component of both the native and introduced ant communities on oceanic islands (Wilson and Taylor, 1967). Examining the invasion process in island ecosystems often utilizes key concepts of biogeography. At a regional scale, colonization of a closed island system is influenced by its proximity to source populations and the size of the island (Jonsson et al., 2009; Badano, 2005), and the diversity of habitat on the island (Hubbel, 1997). In addition to environmental factors, development and disturbance can alter communities (Nakamura et al., 2009; Rizali et al., 2010). These concepts can be applied at larger scales, as well. At the global scale, research in the Lesser Sunda Islands fills a gap in knowledge of global ant distribution, native or introduced affiliations, and migration.

We provide an in-depth analysis of the ant community on eight islands in southeastern Indonesian grasslands across seasons and land-use types. Pitfall data is used to address four global themes that produce varied findings across savanna grasslands to describe local conditions. 1. Introduced species will have broader distributions than native species across space, habitat, and seasons. 2. Habitat structure (grass and trees) influences ground-dwelling ant species abundance, diversity, and composition. 3. Grassland disturbance is associated with an increase in introduced species richness and abundance. 4. Development and distance from a port (measures of connectivity) have a greater influence on diversity than island size. This study addresses a lack of biogeographical knowledge in the Indomalayan-Australasian transition zone using species records, known native ranges, and local distribution patterns. Records of introduced and native tramp species provide useful information for developing local research projects specific to understanding invasiveness at a localized, rather than regional, scale. The impact of grassland disturbance as a potential promoter for introduced ant populations is evaluated. Local study of grassland dynamics is necessary to development of effective local management practices given the variability and wide global distribution of the grassland biome. Analyses highlight seasonally-driven structural changes in vegetation under differing disturbance levels. Analysis of ant communities in savanna tree understories versus open grassland is included for a robust assessment of how vegetation structure can influence ant species composition and diversity. For regions with limited economic resources available to control invasion, preventative actions focusing on land management are an inexpensive and effective approach. The goal of this work is to provide baseline data and correlative analyses to support further research in biogeography, invasion biology, natural history and land management.

1.2 Methods

Site description

Study sites were located on eight islands at the western edge of the Manggarai Barat Regency in the Indonesian province of Nusa Tenggara Timur located in southeastern Indonesia. The study area includes the island of Komodo and other islands within and adjacent to Komodo National Park, a World Heritage Site. The southeastern region of Indonesia supports large areas of tropical savanna grasslands. The West Manggarai Regency is climactically similar to Northern Australia and most likely represents a transition zone for the two major diversity regions (Trainor et al., 2010).

Nusa Tenggara Timur has a seasonally dry climate with a monsoonal rainfall pattern. On average, the region receives 200-1,500mm of rainfall during the wettest months lasting from November to March (Pet, 2000). Islands receive an average of 15mm of rainfall in September, the driest month. The wettest month is January when rainfall on Papagarang and Komodo averages 269mm. Labuan Bajo, Flores receives a more even distribution of rainfall throughout the year with an average of 75mm of rain in October, the driest month, and 118mm in June, the wettest month.

Soils in the region are complex and consist of andesite, tuff, clay, and others (Pet, 2000). The terrain is rugged and typical of a topography formed by recent and ongoing volcanic activity. The islands in the study area were probably connected by land as recently as 18,000 years ago when sea levels were low, allowing species to move freely where deep water and strong currents now separate islands (Pet, 2000). *Chrysopogon subtilis*, *Heteropogon contortus*, and *Agrostris infirma* are native species that co-occur with large patches of *Brachiaria reptans*, *Dactyloctenium sp.*, and *Panicum delicatulum*, the most common exotic grass species. Forbs and *Lantana sp.* are common under tree canopies in disturbed areas and can also be found in some undisturbed sites. Native savanna grasslands occur in two main forms; tallgrass savanna is the most common native grassland type in the region. These grasslands are dominated by *C. subtilis* and *H. contortus* growing in thick, continuous mats. Low densities of small legumes, forbs, sedges, and other grasses are typical in these habitats and plant diversity can be fairly high though a small number of species dominate the landscape. The second local savanna type is steppe. Steppe habitat tends to be found on hilltops and areas with high wind exposure. Grasses and forbs are shorter with exposed soil and rocks. Trees are rare or absent in these grasslands and though the dominant grasses are the same species, they are often stunted. Often the two forms do not have clearly defined boundaries and intermediate types can be found. Coastal savanna grasslands are found adjacent to beaches and a small number of species are unique to this savanna type. *Spinifex littorues*, *Themeda frondosa*, *Chloris barbata*, and various sedges (Cyperaceae) are characteristic of costal grasslands. Patches of coastal savanna are generally small or narrow making them less common than tallgrass and steppe savanna habitats.

Human populations

Eight islands were selected for study based on the presence of both disturbed and undisturbed grassland habitat and a combination of permanently inhabited and uninhabited islands. Islands have varying combinations of the following criteria: size, presence of human settlement, grazed savanna, and undisturbed/native savanna (Table 1.1, Fig. 1.1).

Sampling

Sampling was conducted on five islands at the end of the dry season (August-October 2011) and on eight islands following the wet season (March-May 2012). Passive sampling techniques were employed using pitfall trap transects placed in open savanna grasslands and under single savanna trees for 48 hours. Pitfall trap containers were 50ml conical centrifuge tubes with tapered bottoms and an opening diameter of 27mm, buried in the soil with the lip of the tube flush with the soil surface. Traps were each filled with 20ml of a 95% water, 5% ethanol solution with a small amount of scent-free soap added to reduce surface tension.

An open-grassland transect consisted of 5 traps placed 10 meters apart in a straight line (Fig. 1.2A). Transect locations were selected in such a way that the natural variation in grassland and land use types was represented and included sites on slopes, on flat ground, in areas with sparse vegetation, on hilltops, and near human settlements. Where a tree was present within 30 meters of a transect, an additional two traps were placed 2.5 meters from the center trap, perpendicular to the main transect (Fig. 1.2B). This 3-trap line in the center of the open grassland transect was paired with a 3-trap transect located directly under the nearest tree (Fig. 1.2C). Traps under trees were separated by 2.5 meters; this distance ensured that all traps were under the tree canopy during some or all parts of the day. Tree transects and paired open grassland traps allowed for comparisons of ant communities experiencing different levels of exposure, insolation, and vegetation structure. The closely spaced traps under trees and their paired grassland traps could not be considered independent samples and were pooled in all analyses.

Vegetation and ground cover variables were recorded within a one-meter square area centered on each trap. Vegetation cover was defined as any standing vegetation live or dead, bare soil and rock cover were combined for a bare ground value, and leaf litter was defined as any area covered by fallen vegetation including woody plant materials. Maximum vegetation height was recorded as the tallest point of vegetation and minimum vegetation height as the shortest point located at the top of vegetation within the square meter quadrat at each trap. Distance from settlement and distance from a major port were measured as a straight line using the ruler tool in Google Earth.

Sampling effort and rarefaction

In total, 67 transects and 710 individual traps were recovered. Dry season sampling recovered 218 traps and wet season sampling recovered 492 traps. Sampling efforts differed seasonally as Komodo, Padar, and Tetawa could only be sampled during the wet season. Species accumulation curves were constructed for each island in the EstimateS 9.0.1 (Colwell, 2014) software and extrapolated to 125 samples. Analysis was performed using wet season data, as numerous studies show ants are most abundant in the wet season and sampling covered more sites and islands during the wet season. Accumulation curves included all open grassland and under-tree samples in both disturbed and undisturbed sites. Abundance based and incidence-based coverage estimators (ACE and ICE respectively) were computed in EstimateS 9.0.1 (Colwell, 2014) as estimations of the total number of species present. ACE best estimated richness in communities with rare species. The number of species collected on each island was divided by the number predicted by each estimator to calculate the estimated percentage of total diversity captured. Maximum richness was predicted for each island in EstimateS software using all available data. Islands were analyzed separately and then rarefied to 40 samples for comparison.

Sorting and identification

Ants were stored in 70% ethanol in the field then sorted by morphospecies and identified to species where possible at Lembaga Ilmu Pengetahuan (LIPI), Cibinong, Java, Indonesia. Pinned voucher collections are located at LIPI, Cibinong, Indonesia and in the Essig Museum of Entomology at the University of California, Berkeley. Thirty of the 46 species were identified to species level according to Bolton 1994 and use of the collection at CSIRO, Darwin, Australia. Identifications were confirmed by Dr. Eli Sarnat at the California Academy of Sciences, San Francisco, California.

Status as a native or introduced ant species was primarily determined by distribution data, literature review, and AntWeb records (AntWeb, 2013) along with recommendations of Dr. Alan Andersen of CSIRO, Darwin, Australia. The study area represents a unique climactic region within the Indomalaya region with seasonally dry forests and grasslands similar to those found in Australasia. Ants considered native to both the Indomalayan and Australasian regions were always considered native to the study region as both geographic location and climate type of the study area are characteristics of their native ranges. This applies to *Nylanderia vaga*, and *Monomorium floricola* which are considered globally invasive tramp species but are geographically and climactically within their native ranges (AntWeb, 2013; McGlynn, 1999). *Anoplolepis gracilipes* is considered native to the Indomalaya region, however, it is considered to be introduced in Indonesia (ISSIG, 2011), particularly when found east of Wallace's line (Wetterer, 2005), as well as being invasive in climactically similar areas of Australasia. *Brachyponera sp.* is considered native based upon the geographical native range of the genus being Asia and the Indomalaya regions. The genus also includes a prominent widespread invasive species, *Brachyponera chinensis*. Our designation as a native species is with some hesitation as it is not native in the climactically similar Australasian region and can have high localized abundances in the study area.

Abundance and spatial distributions

Introduced ants often have large colony sizes and we hypothesized that native species would have lower abundances than introduced species when present at the same frequency. Pitfall data was used and each sample represented an abundance or density at a point in space ($n = 718$). Samples were a minimum of ten meters apart and treated independently to highlight potential differences in the relationship between abundance and range with trap frequency being an indicator of range. Species were grouped as native or introduced and the three species with unknown designation, *Monomorium sp. 1*, *Pheidole sp. 1* and *Tapinoma sp.*, were excluded. Distribution was measured as a response to the total abundance and designation of each species as native or introduced. Spatial distribution was represented by the number of traps each species appeared in. The full model tested frequency as a response to total abundance and status as native or introduced along with the interaction term for status and total abundance. Linear regressions were performed for pooled data (Fig. 1.5) followed by Breuch-Pagan tests of linear fit and heteroskedasticity of the data. The ANCOVA function of the 'vegan' package in R was applied to nested regression models to confirm difference in slope between native and introduced populations. The relative importance of each main effect and their interaction was assessed using the 'relaimpo' package in R which produces a decomposition of the full model as non-negative contributions for each term.

Habitat and seasonal specialization in ant species

Differences in median values of abundance between seasons, land use types, and habitat types were tested for each species using paired, Wilcoxon signed-rank tests in the ‘*exact ranks*’ package in R (Table 1.4). Data from traps in each transect were pooled for each of the three comparisons and $n = 1$ represents one complete transect. Complete transects were those without missing data, i.e. a lost trap.

Seasonal data included complete paired wet season/dry season transects. Komodo, Padar, and Tetawa are absent from the analysis because they were only sampled in the wet season. Analysis was limited to transects that were successfully recovered in both wet and dry seasons. An open grass transect included traps 1-5 (Fig. 1.2); each separated by ten meters for a total length of 40 meters. A tree transect included traps 8, 9, and 10, placed under the tree canopy and separated by 2.5 meters. In the seasonal analysis, traps 1 through 5 were used as a grass transect, rather than traps 6,7, and 11 as in the land use analysis, to include transects that were not located near a tree. Shorter grassland transects pair specifically with beneath tree transects of the same length and sampling effort and were used for habitat preference analyses.

Land use comparisons used data only from complete transects on islands that had both disturbed and undisturbed/native grassland sites. Islands matching the criteria were: Flores, Komodo, Papagarang, and Seraya Kecil. Disturbed and undisturbed/native transects were randomly paired within islands, and not across islands, to minimize the effect of island distance from port and species absences not associated with local habitat characteristics but by migration patterns and distance between islands. Grass transects included traps 1 through 5 and tree transects included traps 8, 9 and 10. Transects in land use comparisons were always paired within habitat (tree compared to tree) but across land use (disturbed compared to undisturbed/native).

Habitat preference by species for grasslands under tree canopies versus open grasslands was calculated using paired Wilcoxon method testing differences in median abundances at trees compared with median abundances in open grassland. Habitat comparisons used paired data from open grassland traps 6, 7, 11 (Fig. 1.2) and data from transects placed beneath the nearest tree not more than 30 meters away, traps 8,9, and 10.

Vegetation differences in open grasslands

Density plots were used to show the distribution of frequencies of measured vegetation characteristics in samples within and across season and land use. Analysis was done in R. Boxplots were used to display the distribution of vegetation data for each land use and season combination (dry, disturbed; wet disturbed; dry undisturbed; wet, undisturbed). Statistical analysis was performed only on pooled samples from the five islands sampled in both seasons, allowing for seasonal comparisons to be made. Komodo and Padar were only sampled in the wet season and had few disturbed areas making sample sizes for land use types exceedingly uneven. Tetawa was only sampled in the wet season and had no disturbed sites. Transects were excluded by random selection where sample sizes were uneven or data was missing and traps were treated as independent samples. Vegetation data from each season/land use group were compared using standard t-tests with a Bonferroni correction applied for multiple tests. Percent vegetation cover, minimum vegetation height, and maximum vegetation height were selected for analysis to describe both coverage and structure. Bare soil and litter were excluded to simplify the comparison and because these measures were correlated to percent vegetation cover.

Vegetation structure and ant communities

We hypothesized that sites with greater similarity in vegetation structure would also have greater similarity in ant community composition. Jaccard's, and Bray-Curtis indices of community dissimilarity were calculated using the '*vegdist*' function with binary standardization in the Vegan package in R. For ant species composition, the Jaccard method was used to analyze presence/absence data and Bray-Curtis was used as the method applied to abundance data. Vegetation data was analyzed using the Bray-Curtis method. Abundance data included all species found in the study. Vegetation dissimilarity included percent cover of live vegetation, leaf litter, bare soil and rock, vegetation height maximum and vegetation height minimum. Transects were randomly selected for inclusion in the analysis where sampling between seasons and land use was uneven. The resulting data set included sites used in seasonal and land use comparisons of distance from port, island size, and human structures with additional data from Sebayur Besar and Bajo which were sampled in both seasons but had only native/undisturbed grassland.

An ant community dissimilarity value and a vegetative structure dissimilarity value was calculated for every combination of two sites within land use type and island using species abundance (Bray-Curtis) or presence/absence (Jaccard) data and vegetation data. Islands were analyzed separately to avoid including any potential island effects on species composition. Land use types were analyzed separately to focus on physical vegetation structure and ant communities. Linear regression was then applied to each island-land use data set allowing us to examine the relationship between ant communities and vegetation structure.

bray djc = $\frac{1}{2} \sum_i |x_{ij} - x_{ik}| / (x_{ij} + x_{ik})$ binary: $A+B-2J$ $A+B$

Jaccard index is computed as $2B/(1 + B)$, where B is Bray-Curtis dissimilarity

Non-metric multidimensional scaling (NMDS) was applied to species abundance data to draw out any associations between individual species and land use as well as visually identifiable patterns in the grouping of transect-based ant communities. NMDS analyses were performed on seasonally paired data from islands with both undisturbed habitat and disturbed habitat. NMDS was performed using a maximum of 100 iterations and selecting the resulting plot with the lowest run stress at the final iteration out of 5 tests. Solutions were reached for each test and stress was between 0.04 and 0.14. ANOSIM was applied to the same data set using the '*Vegan*' package in R to compare ant community similarities between land uses. Paired t-tests were used to compare ant communities in open grasslands to communities found beneath savanna tree canopies by pooling below-tree pitfalls and open grassland pitfalls in each five-meter transect. Analysis was repeated excluding data for *P. longicornis* in order to assess the degree to which *P. longicornis* drove observed patterns.

Seasonal and land use influences on ant community characteristics

Differences in mean total abundance, introduced proportion of abundance, and Shannon-Weiner diversity were assessed using Wilcoxon signed-rank tests for nonparametric samples with ties. Analysis was performed using sites on Flores, Papagarang, and Seraya Kecil, all of which had native and disturbed habitat and were sampled in both wet and dry seasons. Seasonal and land use excluded samples with missing seasonal pairs and, in the case of uneven sampling effort, transects were randomly selected using a random number generator to obtain even sample sizes. Paired tests were used to compare wet season and dry season samples. Native and

disturbed land use treatments were analyzed using even sample numbers, but were not treated as paired samples.

Island size, distance, and human settlement

Mean richness and Shannon-Weiner diversity indices from rarefied results in EstimateS were used in linear regression analyses to determine the influence of distance from the mainland port, size of the island, and measures of human settlement on species diversity and richness. As in accumulation analyses, regressions were run for wet season data only to include islands only sampled once and exclude resampling at sites surveyed twice. *Tapinoma sp.* was the only ant occurring only during the dry season and in low abundance and therefore was assumed not to impact overall results.

Mean species richness and Shannon-Weiner diversity were analyzed separately with each of the explanatory variables after multiple regression analysis revealed no interactions between the model terms. Three explanatory variables were included: the minimum distance between the island and the port of Labuan Bajo, island size, and the number of types of human structures present on the island. The port of Labuan Bajo is the primary destination or origin for inter island travel and there are no other ports along the local coast of Flores. Island size was log transformed due to the large difference in size between Flores, the “mainland”, and the other islands. Human structures were categorized in one of three groups: docks, village residences, and hotels.

The first set of analyses were performed using rarefied data for open grass samples (20 samples per island) and excluded samples taken beneath trees. A second set of analyses were performed in the same manner on a rarefied data set (40 samples per island) that included open grass samples as well as samples collected under trees. All analyses were Bonferroni corrected for multiple comparisons of three variables.

1.3 Results

Sampling effort and rarefaction

Pooled wet season survey data from all islands estimated total regional richness to be 61.41 species (ACE) and 59.42 species (ICE). The total species estimates include open grasslands and grassland habitat under tree canopies. According to coverage estimators, we captured 73.3% (ACE) and 75.6% (ICE) of the total savanna grassland ant diversity present in the region. Rarefied data shows that Flores is the most diverse island with 19.82 observed species and a maximum estimated 24.87 species (Table 1.2). Bajo and Seraya Kecil are the closest islands to the port of Labuan Bajo, Flores and had 18.41 and 16.79 observed species, respectively and estimated maximum richness of 22.05 and 22.49 species.

Description of species diversity

In total, 25,548 individual ants from 46 species and 6 subfamilies were collected from transects in open grassland and vegetation directly below tree canopies (Table 1.3). Thirty-seven native species comprised 80.4% of the total richness and 54.6% of the total abundance. Six introduced species made up 13.0% of species richness and 44.1% of the total abundance of individuals. Two species, *Pheidole sp.1* and *Tapinoma sp.*, do not have known native ranges and, combined, made up 1.5% of the total abundance. The subfamily Myrmicinae was the most speciose with 20 species, followed by Formicinae with 13 species and Dolichoderinae with seven

species. Together, these three subfamilies comprise 97 percent of the total abundance of ants collected in our study.

We were able to confirm the native range for 34 species. The majority of species with known origin (KO), 82.4%, were native to the Indomalaya region. Almost half of the KO species, 41.2%, were native to both the Indomalaya and Australasia regions. No recorded KO species were native to Australasia but not Indomalaya. The Palearctic and Oceania regions were included in the native ranges of 14.7% and 2.9% of KO species respectively. The native ranges of 13 species of the 46 recorded species were unknown, however, ants in the genera *Brachyponera*, *Camponotus*, *Crematogaster*, and *Iridomyrmex* were assumed to be native to at least the Indomalaya region based on genus origin and likelihood of successful migration.

Six species occurred on all eight islands sampled. Of these cosmopolitan species, four are considered global tramp ants. Three native ants, *Nylanderia vaga*, *Iridomyrmex sp.1*, and *Iridomyrmex sp.2* had widespread distributions and were found on all islands sampled. *Iridomyrmex sp.2* was the most common species, followed by *Paratrechina longicornis* and *Trichomyrmex destructor* (formerly *Monomorium destructor*). In addition to *Iridomyrmex* (4 species), the most speciose genera were *Camponotus* (4 morphospecies), *Polyrhachis* (5 species), *Monomorium* (4 species), and *Tetramorium* (6 species). *Tetramorium sp.1* is an undescribed species that may be endemic to the study region.

Abundance and spatial distributions

Native and introduced populations tended to be more widely distributed as abundance increased. Introduced species were more densely populated; abundance per sample was higher than that of native ants (Fig. 1.5). Breuch-Pagan heteroscedasticity tests conducted for introduced and native ant data indicated that a linear-shaped model was appropriate for our data sets (BP = 0.74313, df = 1, p -value = 0.3887; BP = 1.6738, df = 1, p -value = 0.1957). The resulting linear relationships showed strong correlation between frequency (the number of samples the species was found in) and total abundance with R-squared for introduced species = 0.64 and for native species = 0.77. When status as introduced or native was included as an explanatory term, status alone was not correlated with frequency but showed a significant interaction with total abundance (adj. R-squared = 0.7742, $F = 47.85$, $DF = 3$, p -value = 5.593e-13) indicating that introduced species are associated with higher abundances and thus, wider distributions. Total abundance, status as “native”, and the interaction between total abundance and native status were ranked in their contributions to the model fit (0.876, 0.070, and 0.054 respectively) using the ‘*relaimpo*’ package in R. Nested models were compared using ANCOVA confirming that relationships between frequency and total abundance (slopes) were significantly different between native and introduced ant populations ($F = 4.0952$, p -value = 0.0243).

Model 1 : frequency ~ total abundance + status

Model 2 : frequency ~ total abundance * status

In addition to difference in slope, the y-intercept of the introduced ant community was higher (38.07) than the intercept value for the native community (11.62).

Habitat and seasonal specialization in ant species

We found no evidence of seasonality in species abundances. There was no significant community-level difference between wet season (mean = 185 ants per trap) and dry season (mean = 446 ants per traps) abundance ($t = -1.5666$, $df = 57.926$, p -value = 0.1226). Species-level abundances did not fluctuate significantly between seasons for 44 of 46 species recorded. *Crematogaster sp. 1* (p -value = 0.0458) and *Pheidole sp. 1* (p -value = 0.0049) were exceptions.

Creumatogaster sp. 1 increased in the wet season and *Pheidole sp. 1* was more abundant in the dry season, but both occurred in low numbers and frequencies throughout the entire study (Table 1.1). Fourteen species were recorded only during the wet season, but in fairly low abundances or as singletons, therefore, these results are not considered to be indicative of seasonal specialization (Table 1.3).

Ant species varied with habitat type and land use. *Brachyponera sp.* were more common at undisturbed grassland sites, along with two additional native species, *Iridomyrmex angusticeps* and *Iridomyrmex sp.4*. *Solenopsis geminata* was the only species more common in disturbed grasslands than in undisturbed grasslands (p -value = 0.0464). Differences were more marked in habitat choice; several species occurred more often under a tree canopy or in open grassland. All four species of *Iridomyrmex* favored open grasslands (Table 1.4) along with the single species collected in the genus *Brachyponera*. *Iridomyrmex sp.2*, the dominant native species, was found in 11% of all samples collected at trees and 57% of all open grassland samples, occurring across land uses. In Wilcoxon signed-rank comparisons of paired samples, median values of *Iridomyrmex sp.2* abundance was higher in open grasslands than near trees (p -value = 0.0000)(Table. 1.2). *Paratrechina longicornis* was the dominant introduced species and its overall abundance was similar to *Iridomyrmex sp. 2*, however, the two species prefer different habitat types with *P. longicornis* being far more common under trees (p -value = 0.0000)(Table 1.4). *Paratrechina longicornis* was found in 51% of all tree samples and 12% of all open grassland samples. Additionally, *Tetramorium simillimum*, an introduced ant, had a strong preference for grasses below tree canopies (p = 0.0002) and *Pheidole sp. 1* was also more common at trees (p = 0.0156).

Vegetation differences in open grasslands

Percent vegetation cover did not differ between native and disturbed sites in the wet season (df = 60.551, p -value = 0.6765)(Fig. 1.6) with undisturbed and disturbed sites having averages of 71% and 69%, respectively. In the dry season cover at disturbed sites was significantly lower than cover in undisturbed/native sites (df = 86.222, p -value = 3.761e-07). Dry season, undisturbed sites averaged 55% vegetation cover compared to disturbed sites in the same season which averaged 30% cover. Seasonal differences in vegetation cover within land use type differed significantly for both native and disturbed grassland sites (disturbed, df = 75.83, p -value = 1.791e-11; undisturbed, df = 136.17, p -value = 0.0001) with both land use types having more coverage in the wet season. Seasonal differences are less pronounced in undisturbed habitats with a mean dry season coverage of 55% and mean wet season coverage of 71%. In disturbed grasslands, seasonal differences were more pronounced with mean dry season coverage of 30% and mean wet season coverage of 69%.

Maximum vegetation height across five islands sampled in both seasons followed a similar pattern as percent vegetation cover. Maximum height did not differ between land uses in the wet season. Maximum height was significantly higher in undisturbed sites when compared to disturbed sites in the dry season (df = 114.29, p -value = 3.323e-09). Wet season undisturbed grasslands were taller than dry season undisturbed grasslands (df = 141.55, p -value = 0.0047) and this difference was larger between seasons in disturbed grasslands (df = 59.547, p -value = 5.773e-12). Minimum vegetation height was on average 4.37cm in disturbed sites and 6.96cm in undisturbed sites in the dry season (df = 115, p -value = 1.108e-05). Minimum vegetation height was lower in disturbed sites than in undisturbed sites in the wet season, with averages being 16.48cm and 30.23cm, respectively (df = 100.78, p -value = 0.0001). Differences were also

significant across seasons in both disturbed sites ($df = 40.34$, p -value = $1.583e-05$) and undisturbed sites ($df = 82.982$, p -value = $2.59e-15$).

Vegetation structure and ant communities in open grasslands

Dissimilarity in vegetation characteristics (percent bare ground, percent litter cover, percent vegetation cover, and maximum vegetation height) was related to dissimilarity in ant community composition in undisturbed habitats, but not disturbed habitats, on each of the five islands sampled in both the wet and dry season. Flores, Papagarang, and Seraya Kecil had both native and disturbed savanna grasslands. Sebayur Besar and Bajo did not have disturbed grassland. The observed pattern holds in both the Bray-Curtis dissimilarity index and the Jaccard dissimilarity index (Table 1.5), though r-squared values indicating model fit were fairly low (Fig. 1.7).

NMDS was applied to paired wet and dry season, open grassland data for species abundances at disturbed and undisturbed sites (Fig. 1.8). There were no clear species associations with a particular land use type, but sites (pooled transects) with more similar ant community compositions grouped together based on undisturbed or disturbed habitat designations (Fig. 1.8). ANOSIM analyses supported these findings. Ant communities differed between disturbed and undisturbed grassland in both the dry and wet seasons on Papagarang ($r = 0.226$, p -value = 0.007 ; $r = 0.282$, p -value = 0.002) and Seraya Kecil ($r = 0.16$, $p = 0.006$; $r = 0.196$, p -value = 0.005).

Total abundances of native and introduced ants varied significantly between samples from under tree canopies (referred to as “tree” samples) and paired samples from open grassland in both undisturbed and disturbed sites during the wet season but not in the dry season. At disturbed sites, native species were more abundant in open grassland than under trees (p -value = 0.0464). At undisturbed sites, introduced species were far more abundant at trees, averaging 161.34 ants per tree compared to 34.41 ants per open grass sample (p -value = 0.0082). During the dry season, total abundance of native versus introduced species was not significantly different in either disturbed or undisturbed grasslands.

Trees had proportionally higher abundances of introduced species (proportion I) than open grasslands (Table 1.6). At dry, undisturbed sites, 62% of ants collected at trees were introduced species, but they were only 12% of all ants in the open grassland ($p = 0.0001$). At wet, undisturbed sites, 64% of ants collected under trees were introduced species and 23% of ants collected in open grass were introduced species ($p = 0.0000$). At wet, disturbed sites, 64% were introduced species at trees but were 26% percent of all ants in open grassland ($p = 0.0053$). Removal of *Paratrechina longicornis* from the analysis (proportion I nP) reduced the statistical significance of a greater proportion I in all conditions except wet, undisturbed habitat, though raw measurements of proportion I were still higher at trees. Shannon-Weiner diversity was similar between paired tree and grass samples across islands.

Seasonal and land use influences on abundance and diversity

Total abundance of ants was strongly influenced by both land use and season in open grasslands (Fig. 1.9). Mean abundance was significantly higher in undisturbed grasslands than in disturbed grasslands in three of the six cases; no cases of disturbed sites having greater abundance than undisturbed sites were found. On Flores ($Z = -2.7399$, p -value = 0.0021 , dry season), Papagarang ($Z = -2.9262$, p -value = 0.0013 , wet season), and Seraya Kecil ($Z = -2.5323$, p -value = 0.0051 , dry season), undisturbed site total abundance was higher than disturbed site

total abundance within season. When comparing abundances within land use and across seasons, Wilcoxon signed-rank analysis results showed significant seasonal differences in undisturbed grasslands. Total abundance at undisturbed sites was higher in the wet season than in the dry season on Flores ($Z = -2.1198$, p -value = 0.0167) and Papagarang ($Z = -2.78$, p -value = 0.0022). Disturbed grasslands did not differ in total abundance between seasons.

When comparing land use types within seasons, PROPINT was higher in undisturbed grassland sites on Papagarang ($Z = -2.3182$, p -value = 0.0102) and Flores ($Z = -1.7005$, p -value = 0.0465). After applying a Bonferroni correction for eight tests these results were not significant. No significant seasonal comparisons of PROPINT within land use type were found.

Comparisons of overall Shannon-Weiner diversity between land management types within season suggested higher diversity in undisturbed grassland habitats in the dry season on Flores ($Z = -2.3072$, p -value = 0.0102) which did not meet the critical alpha level of 0.008. Within land use type, undisturbed, wet season grasslands on Papagarang were significantly more diverse than dry season grasslands ($Z = -2.1861$, p -value = 0.0140). No seasonal difference was seen within each land use type at disturbed sites.

When native and introduced ant diversities were analyzed separately, rather than looking at overall diversity, mean diversity of native and introduced ants differed between land uses in open grasslands, but not under tree canopies. On Flores, native ant diversity in open grasslands was higher at undisturbed sites in the dry season ($t = -2.7438$, $df = 9$, p -value = 0.0227) but no significant differences were found between land uses under tree canopies. On Papagarang, native ant diversity was statistically similar between land uses in both open grasslands and under tree canopies. Introduced ant diversity was higher in disturbed open grasslands than undisturbed open grasslands in the wet season ($t = 2.4327$, $df = 14$, p -value = 0.0300) and no differences were found under tree canopies.

Island size, distance from port, and human settlement

Island size and number of structure types had no significant relationship to mean species richness or Shannon-Weiner diversity whether samples from beneath trees were excluded or included. Both Shannon-Weiner diversity and mean species richness had the strongest relationship with distance between the port of Labuan Bajo (DP) and the island sampled in both open grassland and in grasses beneath tree canopies. The general trend was a decreasing diversity and richness with increasing distance from the port of Labuan Bajo, though not all results were significant. In rarefied analysis of open grassland samples (20 samples per island) Shannon-Weiner diversity and DP had the strongest linear relationship of the three explanatory variables tested (r -squared = 0.6284, p -value = 0.0116). Linear regression results for mean species richness and DP yielded an r -squared value of 0.5224 and a p -value of 0.0259, but this result was not significant after applying a Bonferroni correction. When samples taken from beneath trees were included in linear regressions of rarefied data (40 samples per island), none of the explanatory variables were significantly related to diversity.

1.4 Discussion

Grassland ant species richness in the Komodo region, with 46 species, is similar to diversity measures in savanna focused literature from around the globe and to a study conducted on the nearby island of Timor (Trainor et al., 2010). South African grasslands in the southern region of Rietvlei Nature Reserve supported 36 ant species in one recent study (Jamison et al.,

2016). In another study, Kunai grasslands in Papua had 39 ground-foraging ant species (Room, 1975). Ant communities shared broad community characteristics with communities on the climatically similar island of Timor, approximately 430km from the port of Labuan Bajo and 890km from the northern tip of Australia. The relatively high number of species and high abundances in the subfamily Dolichoderinae diverge from global patterns and reflect a distinctly Australasian component of the local ant community (Andersen, 2000). Dolichoderines dominate savanna biomes (Andersen, 1995) and, often times, the communities they are introduced to, as in the case of the Argentine ant (*Linepithema humile*; Holway, 1999). In Indonesia, the dominance of Dolichoderines most likely extends through the entirety of the Lesser Sunda Islands, including Sumbawa (Sandidge, unpublished data) where seasonal grasslands are commonplace.

The majority of the species in Komodo grasslands can be found across broad geographical ranges. One species, *Tetramorium sp. 1*, may be endemic to the region. An apparent lack of regional endemism suggests that the islands have either been colonized by native ants relatively recently or that the prevalence of introduced species has led to the extirpation and replacement of rarer native species. Many islands are entirely or mostly uninhabited, fisherpeople making regular stops to these islands are the most likely source of introductions. A large majority, over 82% of species with known origin, were native to the Indomalaya region, with over 41% being native to both Indomalaya and Australasia. Relatively few species, 14.7%, had origins including the Palearctic region. Notably, no species were introduced migrants from Australasia or the Palearctic region, suggesting that migration happens primarily from west to east. Further analysis of species found in Australasia and the Palearctic would be helpful in determining the frequency of movement from Indomalaya to the east.

Six species were collected on all eight islands. *Paratrechina longicornis* (Formicinae), *Solenopsis geminata* (Myrmicinae), and *Trichomyrmex destructor* (Myrmicinae) were introduced cosmopolitan species and all fall under the tramp species designation. *Iridomyrmex sp. 1* (Dolichoderinae), *Iridomyrmex sp. 2* (Dolichoderinae), and *Nylanderia vaga* (Formicinae) were native cosmopolitan species with *N. vaga* being considered a tramp species. Myrmecines and Formicines were the most speciose subfamilies in our study, reflecting global patterns in speciation (Fig. 1.4). Tramp species arise from the CRYPTIC, DOMINANT DOLICHODERINE, GENERALIZED MYRMICINE, and OPPORTUNISTIC functional groups as defined by Andersen in a study of Australian ant communities (McGlynn, 1999; Andersen, 1995). *Monomorium floricola*, *Nylanderia vaga* and *Tetramorium walshi* are native tramp species. The Komodo region offers an opportunity to look at behaviors and impacts of tramps on variable closed island systems where the species evolved. Research on global invaders within their native ranges can provide insight into the conditions that must arise for these ants to become invasive. *Nylanderia vaga* was very common and may behave in a way that could be considered locally invasive. This study did not address this question directly and closer study of *N. vaga* in comparison to species such as *Iridomyrmex sp. 2* would be helpful in understanding what characteristics give rise to global success.

Survey results showed that the six introduced species (including 4 tramp species) collected make up 13.0% of total richness and 44% of the total abundance of ants. Global success as an invader is linked to large colony size and high abundance, hallmarks of introduced species. While introduced species did not have an impact on overall richness or diversity, their high proportional abundances may have significant ecological impacts. In our findings, two of the three most abundant ants were the invasive species, *Trichomyrmex destructor* and *Paratrechina longicornis*. These two species are known to dominate ant communities (Wetterer

et al., 1999), impacting other groups of insects (Koch et al., 2011) and plant communities. *Trichomyrmex destructor* has previously been considered a small component of ant communities outside of urban areas (Harris et al., 2005) but is very abundant in both disturbed and undisturbed grasslands in the Komodo region.

As expected, when the abundance of a species increased, its distribution became broader (Fig. 1.5). But differences were seen in the density of introduced populations versus native populations. Higher densities of invasive ants may give them a competitive advantage over less dense species with similar spatial distributions. Denser occupation of habitats may increase the likelihood of introduced species crowding out native species even if no direct aggression is present.

The influence of season and land use on abundance, PROPINT, and diversity were mixed across the three islands analyzed. Total ant abundance in Indonesian grasslands increased in the wet season, as is common in myrmecological surveys, but only at undisturbed sites (Fig. 1.9). In two of three cases, abundances were higher at undisturbed sites when compared to disturbed sites in the same season. Diversity was seasonally higher in one case, also in undisturbed grasslands. NMDS and ANOSIM community analyses indicate that individual species are not associated with one another or clearly associated with a land use type, despite community level differences between land use types (Fig. 1.8). A third analysis of dissimilarity measures linked ant community dissimilarity and vegetative community dissimilarity in undisturbed grasslands but not in disturbed grasslands (Table 1.5, Fig. 1.7). Community-wide differences were able to take uncommon species into account. As is common for grassland ant communities (Hoffman, 2010), 59% of recorded species in our study, had an abundance and too low for species-level, statistical analysis of seasonal, land use, and/or habitat type preference. This trend results in exclusion of low-abundance specialists, thus potentially underreporting specialization overall.

The seasonal increased abundances and diversity are most likely correlated with higher abundances of prey, availability of seeds, greater vegetation cover (Fig. 1.6), and softer soils. The most visually striking difference between seasons in Nusa Tenggara Timor grasslands is grass height. Grasses grow quickly during the wet season, produce an enormous quantity of seed, and then go dormant after rains subside. Grazing may dampen the seasonal effect on abundances at disturbed sites by compacting soils and directly reducing vegetation (Fig. 1.6) and seed availability. The impact of grazing on vegetation structure (height) is more pronounced outside of the growing season and this might be enough to exclude more sensitive species all together. Additionally, seasonal changes may have varying effects on native and introduced grass species (Wainwright et al., 2012) and preferential grazing (Ash and Corfield, 1998) could further contribute to measured seasonal variation in disturbed plant communities. Despite larger seasonal differences in vegetative structure at disturbed sites (Fig. 1.6), these sites had a lower community response to vegetative differences (Table 1.5, Fig 1.7). Interestingly, all undisturbed grassland sites showed a significant linear relationship between vegetation change and ant community changes. Species living in disturbed habitats are generally known to be better adapted to change (Holway et al., 2002; Sakai, 2001), which might allow them to maintain a more even distribution across seasonal and vegetative conditions.

Past work in grasslands points to vegetation and land systems being more impactful on community structures than grazing intensity (Arcoverde, 2017; Hoffman, 2010). Disturbance-adapted native species in would naturally occur in grasslands; the habitat type is created and maintained by regular disturbance. Our findings fit well with other grassland studies and bring up important questions regarding the relationship between faunal communities and vegetative

communities. Our results imply that seasonal vegetative shifts related to grazing disturbance may homogenize ant communities. A more heterogeneous ant community may be able to exist in undisturbed grasslands where seasonal shifts in vegetative structure are less pronounced. The rarity of many species, particularly environmentally sensitive ones, makes it difficult to statistically analyze their populations. Additionally, absence of a species altogether at some sites may not reflect land use-related affinities, but rather immigration patterns, confounding the results when data are pooled across ecologically or physically distant sites. Many times, as is the case here, these species are left out of analysis of individual species. As a result, their changes are sensed at the community level but have little impact on abundance and diversity. We expected a large proportion of native species to respond negatively to disturbance. Three of eight native species common enough to be statistically analyzed were less common with disturbance and none were more common with disturbance (Table 1.4), however, eight species accounted for less than 23 percent of native richness.

The numerical dominance of *Iridomyrmex sp.2* on Papagarang had a strong effect in grouping sites dominated by that species (Fig. 1.8). NMDS results suggested that despite mean abundance per trap of *Iridomyrmex sp.2* being lower at disturbed sites than at undisturbed sites (Table. 1.4), they were frequently the only species or the dominant species at disturbed open grassland sites on Papagarang due to generally low diversity. This pattern was not seen across islands, but exemplifies the impact a small number of dominant species can have on mapping communities, particularly when pooling “native” and “introduced” species in the analysis.

When assessing habitat preference across the ant community, three species were found to significantly prefer habitat beneath trees, *Paratrechina longicornis*, *Tetramorium simillimum*, and *Pheidole sp.1*. Trees harbor high diversity in open landscapes (Dunn, 2000; Majer and Delabie, 1999) and have been considered important diversity refuges. Our findings suggest that trees may also provide a refuge for introduced species. Introduced ants were collected in every pitfall trap set below a tree canopy. Pitfall from under tree canopies contained one (46.7%), two (43.7%) or three (9.6%) introduced species. The pattern of high abundances and proportions of total abundances of introduced ants near trees was driven in part, but not entirely, by high frequencies of *Paratrechina longicornis* combined with a relative scarcity of *Paratrechina longicornis* in open grassland (Table. 1.2). *Tetramorium simillimum* contributes to the heightened introduced proportion, but its less pervasive than *P. longicornis* and *T. destructor*. The impact of introduced ant colonization of trees on the arboreal ant community was not assessed but it is an important area of ecological study. High numbers of introduced species at trees may reduce their efficacy as a refuge from insolation for native species. These comparisons could not be made in our study as all trees had been invaded.

Competitive exclusion and inter species aggression may explain the proportionally high incidence of introduced species at trees. *Paratrechina longicornis* and *Iridomyrmex sp.2* had a notably inverse relationship in habitat preference and frequency in traps. Both species were found in over half of the samples collected in their respectively favored habitats and *Paratrechina longicornis* was found in every sample collected below tree canopies. Like *Paratrechina longicornis*, *Iridomyrmex* diets are primarily sugar based and they collect large amounts of honeydew from aphids and other insects (Wetterer et al., 1999). *Iridomyrmex sp.2* is an aggressive ant that may be competitively or physically excluding other species from open habitat, even dominant invasive ants.

A dominant, ubiquitous ant such as *Iridomyrmex sp. 2* can aid in preventing invasion by fully occupying a niche (Kennedy et al., 2002; Wilson and Taylor, 1967). Protecting undisturbed

habitat that favors these species may provide some level of protection in adjacent disturbed habitats. Less common or more highly sensitive native ants are useful in monitoring programs. We identified *Iridomyrmex sp. 1* as a good candidate for monitoring programs. It occurred in relatively high abundance on all surveyed islands and shows a clear preference for undisturbed habitat. *Solenopsis geminata*, the only introduced species with land use preference, preferred disturbed sites, a pattern well documented across their range (Carroll and Risch, 1984; Way, 1998). *S. geminata* is unique, utilizing seeds of introduced grasses as a major food source where other introduced species may be associated with diverse food sources, such as insect prey and honeydew, that are not necessarily dependent on disturbance. Native grasses form dense mats in undisturbed grassland with very little open space for establishment of new grass species and other introduced species that may co-occur with them. Specialized dietary characteristics, such as seeds in *S. geminata* diets, make it another useful species in monitoring habitat with its presence being an indicator of damage to native grass ecosystems.

Oceanic islands commonly support large numbers of invasive ants in part because they have ports hosting vessels from around the globe. Labuan Bajo on the island of Flores acts as the major port connecting the islands offshore. Island biogeography concepts explain diversity as a function of patch or island size, connectivity to other patches, distance to a main source, and extinction/colonization rates (Badano et al., 2005; Hubbel, 1997; MacArthur and Wilson, 1967). On nearby Java, human-built structures and distance from the major port of Jakarta most strongly predicted the abundance of introduced species (Rizali et al., 2010), overshadowing island size. Our findings show distance between the island of focus and the main port having the greatest influence on diversity and species richness. If we assume that closer islands are visited more frequently, this pattern indicates that frequency of visits to islands plays a larger role in introductions than infrastructure development and island size, though other factors contribute. Often, ecological studies focus on connectivity as a necessary component of managing land that allows species to migrate, sharing genes and repopulating patches. The potential for repeated introduction of invasive species is a function of connectivity that relies on human modes of transportation. Fishing, travel to Labuan Bajo for goods, and tourism activity provide frequent opportunities for introduced species to leave a major port and establish on outer islands.

Grasslands are a major part of landscapes around the world, providing humans with most of their food and sequestering large amounts of carbon. Designation of a portion of the area between Flores and Sumbawa as a World Heritage Site and National Park has limited development and protected large areas of grassland from invasion by non-native grasses and insects. Few studies have focused on local flora and fauna other than large macro fauna, mainly ground-nesting *Veranus komodoensis*, the Komodo dragon. Ant communities in southeastern Indonesia should be incorporated into monitoring the degradation and recovery of native grassland systems. Localized research is critical to development of management plans as grassland communities across the world have varied ecological responses. Furthermore, ecological patterns can be over-generalized, particularly in public forums for people with no scientific training. For example, the belief that disturbance leads to habitat destruction and diversity decline is common. Cultural practices around grazing may seem under attack if discouraged when, in fact, practices can be developed that enable grazing and grassland protection. Local surveys, such as this one, provide distribution information on invasive ants. *Solenopsis geminata*, can impact ground-nesting species (Plentovich et al., 2009) such as the Komodo Dragon. Understanding how land use and development influence species distributions is critical to species preservation and preventing further invasion. Many invasive and tramp

species originate in Asia (McGlynn, 1999) and are considered native to Indonesia based on regional affiliation. However, little is known about the impacts and invasiveness of tramp species, such as *Nylanderia vaga*, when they are introduced to new areas within their native range (Tilman, 2004). The Komodo region of Nusa Tenggara Timur in the Lesser Sunda Islands is currently under great development pressure from tourism and investment industries. The variable development and environmental factors present on each island make this an excellent system for investigating invasion. Local management would be improved by a larger body of local research. Preliminary results show that disturbance to grasslands will alter species composition and enable the spread of introduced species, however, the direct impacts of these species on local flora and fauna have not yet been studied.

1.5 Acknowledgements

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1.6 Figures

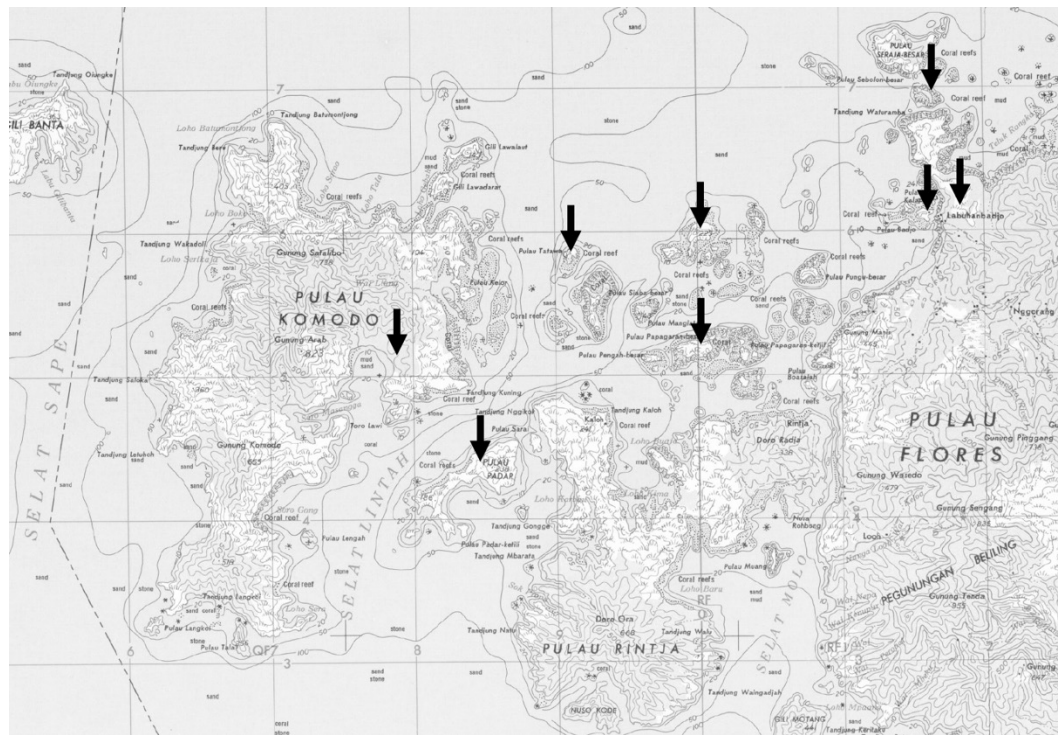


Fig. 1.1. Map of the study region. Black arrows point to islands included in survey.

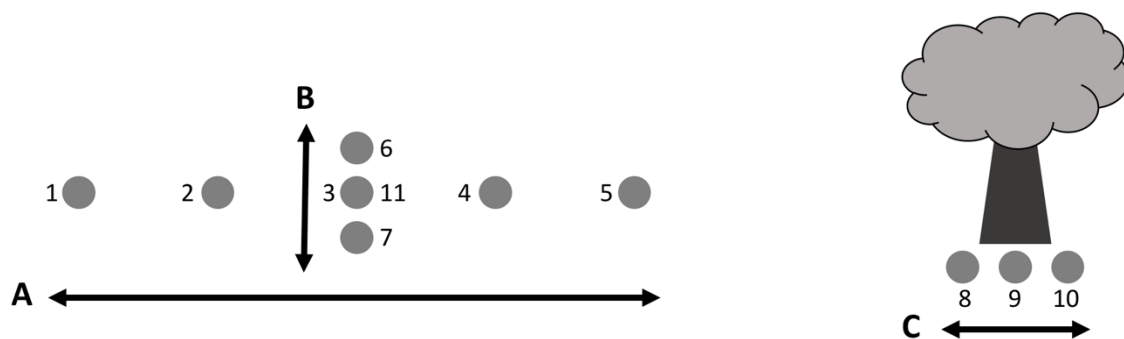


Fig. 1.2. Pitfall transect layout. A. Open grassland long transect, 40m total length. B. Open grassland short transect, 5m total length, paired with tree transect beneath nearby tree. C. Tree transect, 5m total length, placed in ground beneath tree canopy.

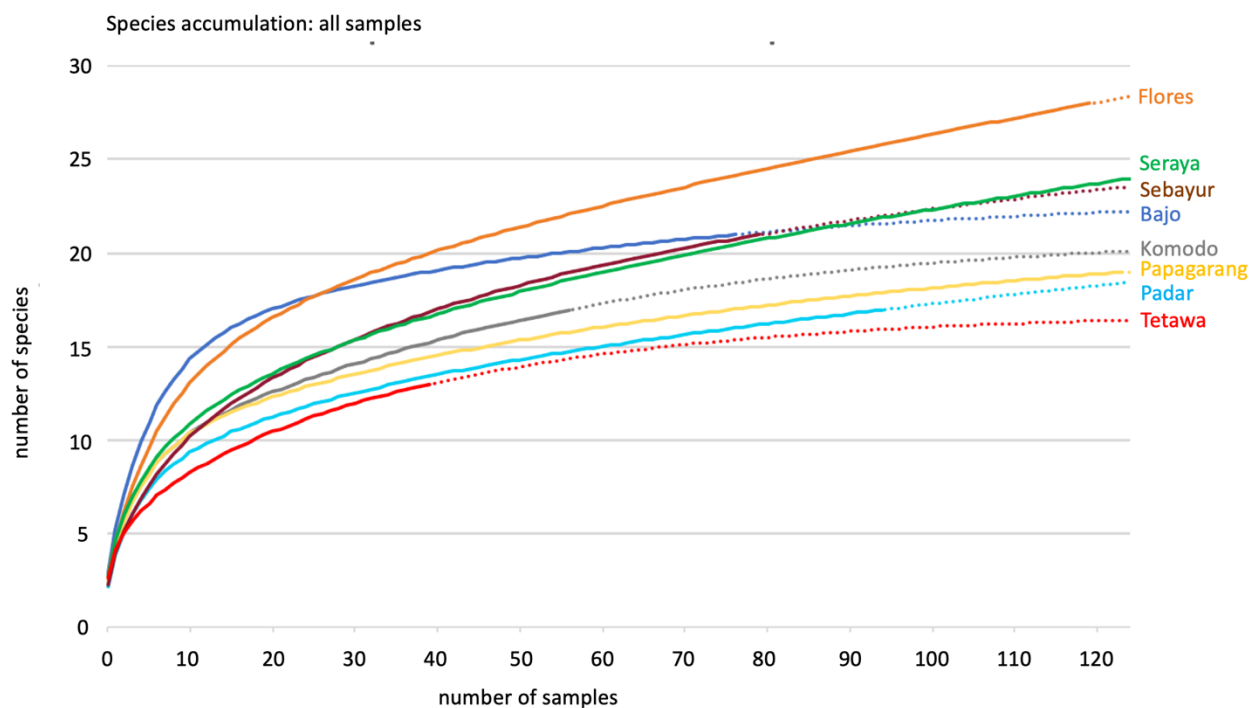


Fig 1.3. Species accumulation curves utilized all samples from each island and were extrapolated to 125 samples. Extrapolation is represented by the dashed portion of each line.

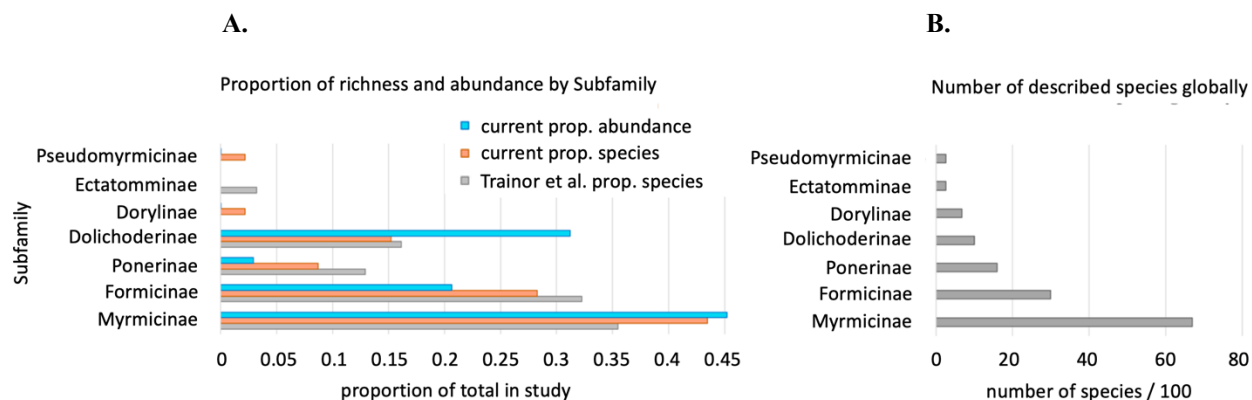


Fig. 1.4. A. Proportion of total abundance (25,548 ants) and proportion of total number of species (46 species) by subfamily. Results for the proportion of total number of species by subfamily found in Trainor et al. 2010 are included for comparison. B. The global number of described species in each subfamily found in regional surveys.

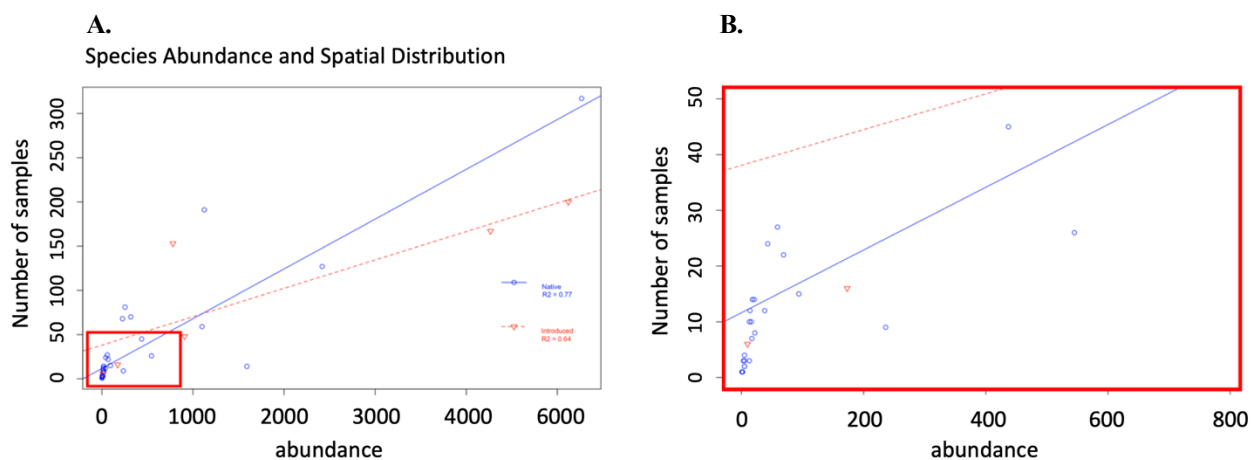


Fig. 1.5. A. Linear regressions for introduced and native species looking at number of individuals of each species collected and the number of traps in which it was found. B. Enlarged image of area marked by red box in A.

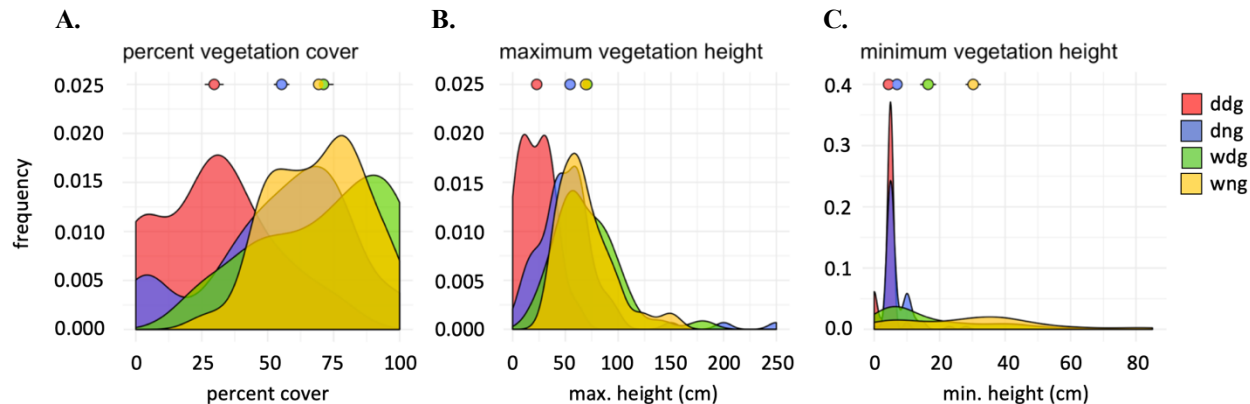


Fig. 1.6. Density plots of the frequency of vegetation coverage and height measurements. Averages are presented as colored circles. A. percent vegetation cover, B. minimum vegetation height, and C. maximum vegetation height by habitat and by season in grassland sites. Pooled data includes islands sampled in wet and dry seasons (Bajo; Flores; Papagarang; Sebayur Besar; Seraya Kecil). ddg = dry, disturbed grassland, $n = 38$; wdg = wet, disturbed grassland, $n = 40$; dng = dry, undisturbed/native grassland, $n = 79$; wng = wet, undisturbed/native grassland, $n = 78$ where n = number of samples (individual traps) per season and land use group.

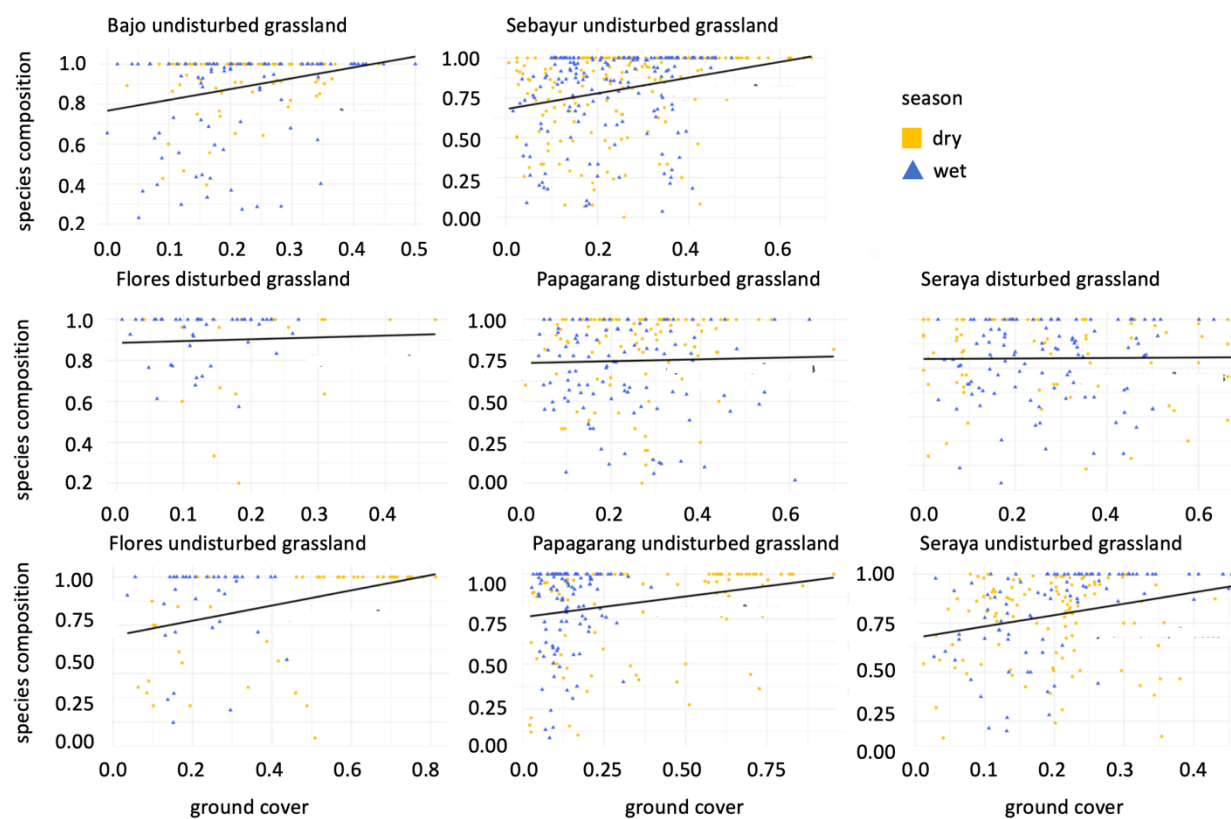


Fig. 1.7. Linear regression of Bray-Curtis vegetative dissimilarity and ant community composition dissimilarity between all pairs of samples within land use type on islands surveyed in both the dry and wet seasons.

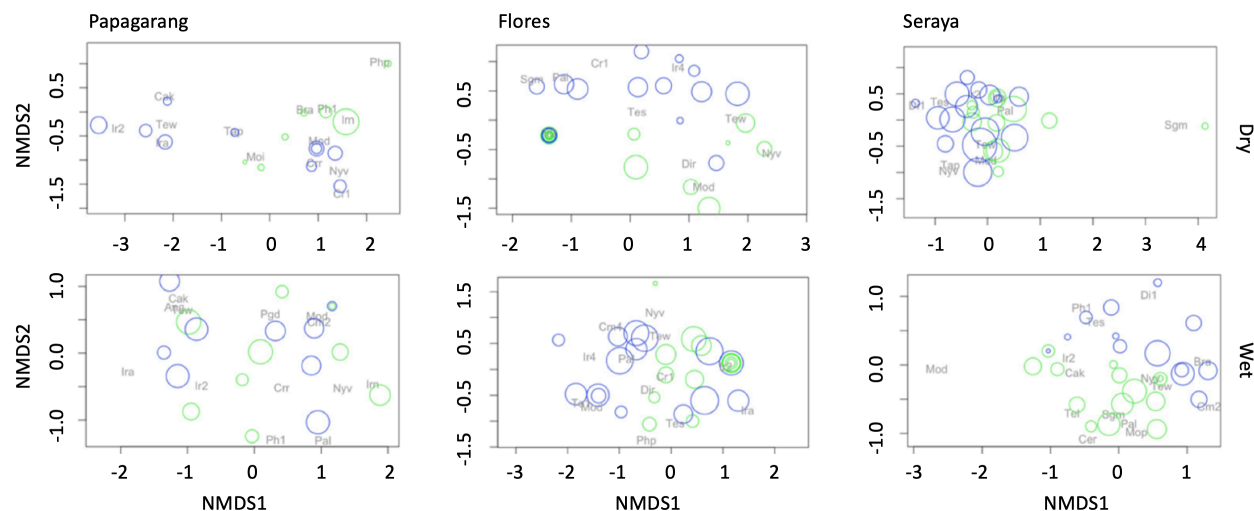
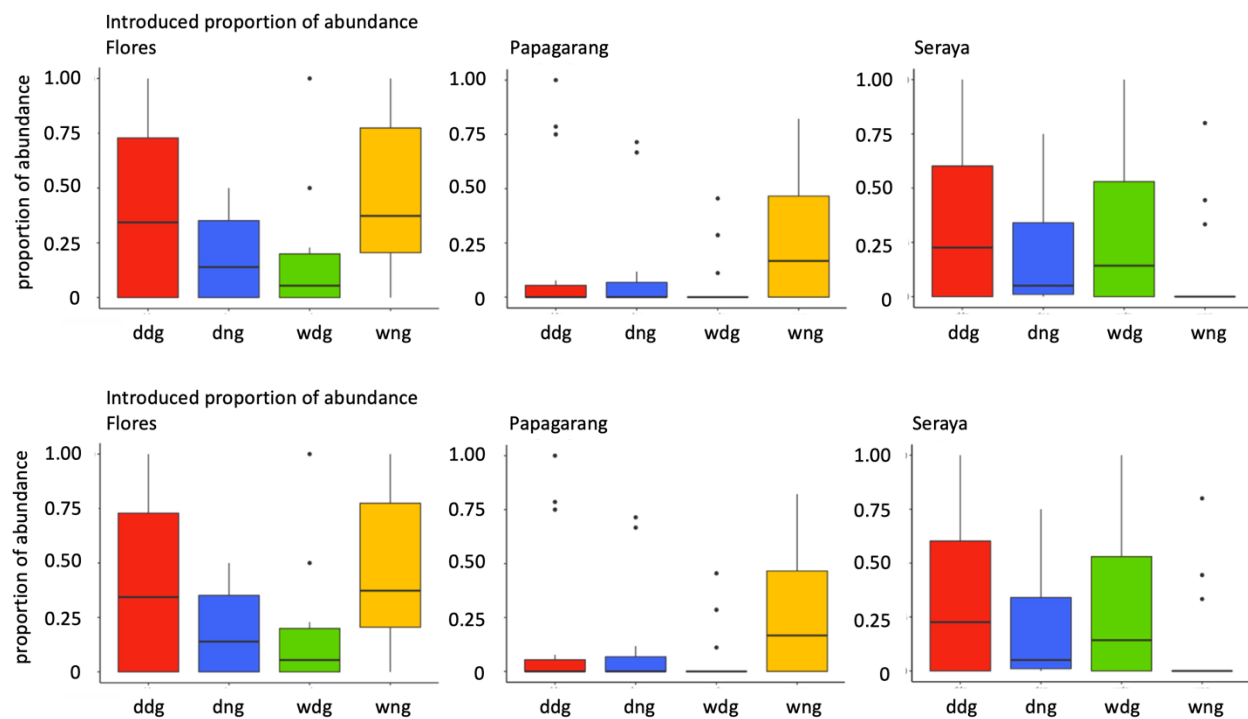


Fig. 1.8. Non-metric multidimensional scaling (NMDS) plots of ant communities on three islands. Undisturbed grassland samples are marked as blue open circles and disturbed grassland samples are marked as green open circles. Circle size is proportional to the total abundance of ants collected in that sample. Species are denoted by three-letter codes.



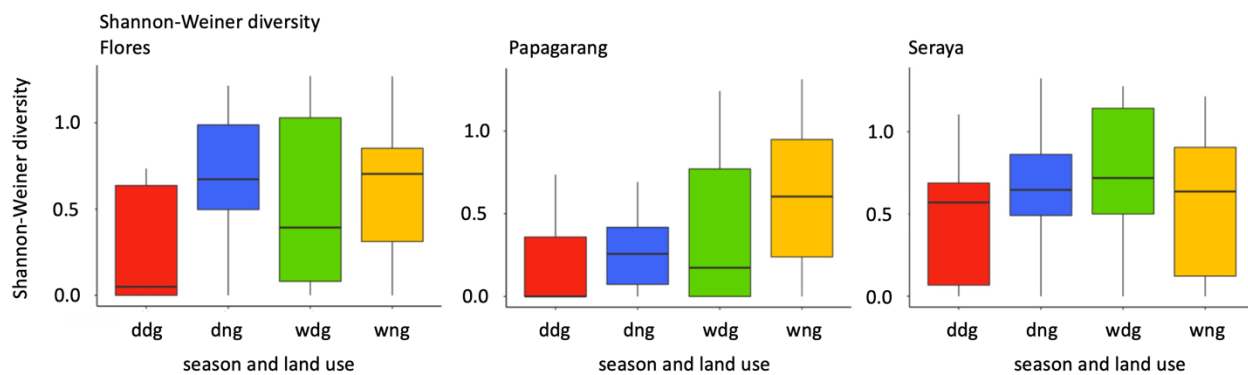
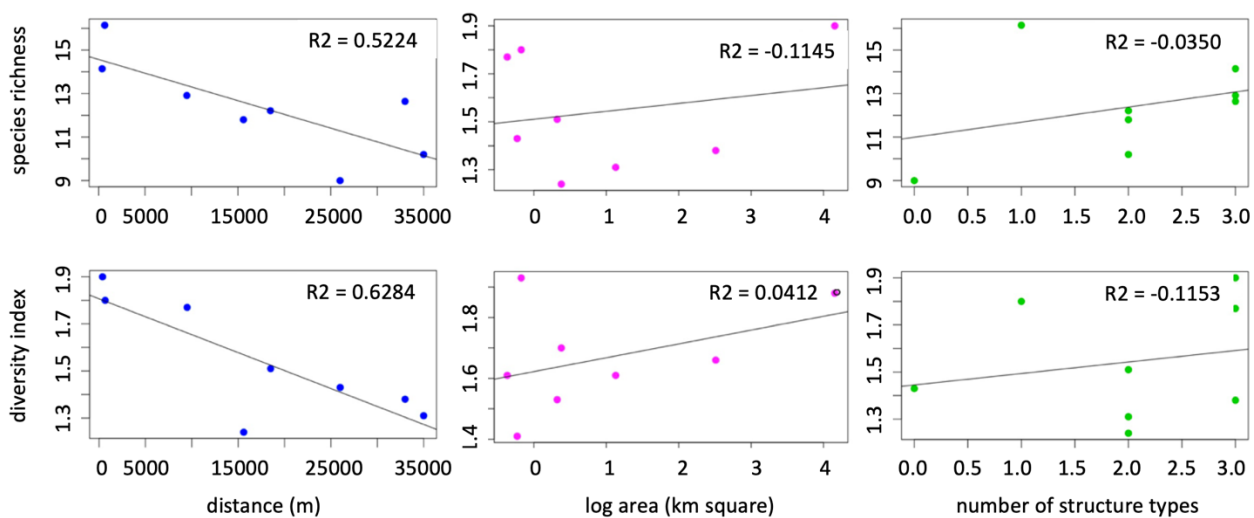


Fig 1.9. Total abundance of ants, proportion of abundance that are introduced species, and Shannon-Weiner diversity in open grasslands. Flores $n = 40$; Papagarang $n = 60$; Seraya Kecil $n = 60$. Significance level after Bonferroni correction, $\alpha < 0.025$. ddg = dry, disturbed; dng = dry, undisturbed/native; wdg = wet, disturbed; wng = wet, undisturbed/native.

A. Wet season, open grassland rarefied to 20 samples per island.



B. Wet season open grassland and trees, rarefied to 40 samples per island.

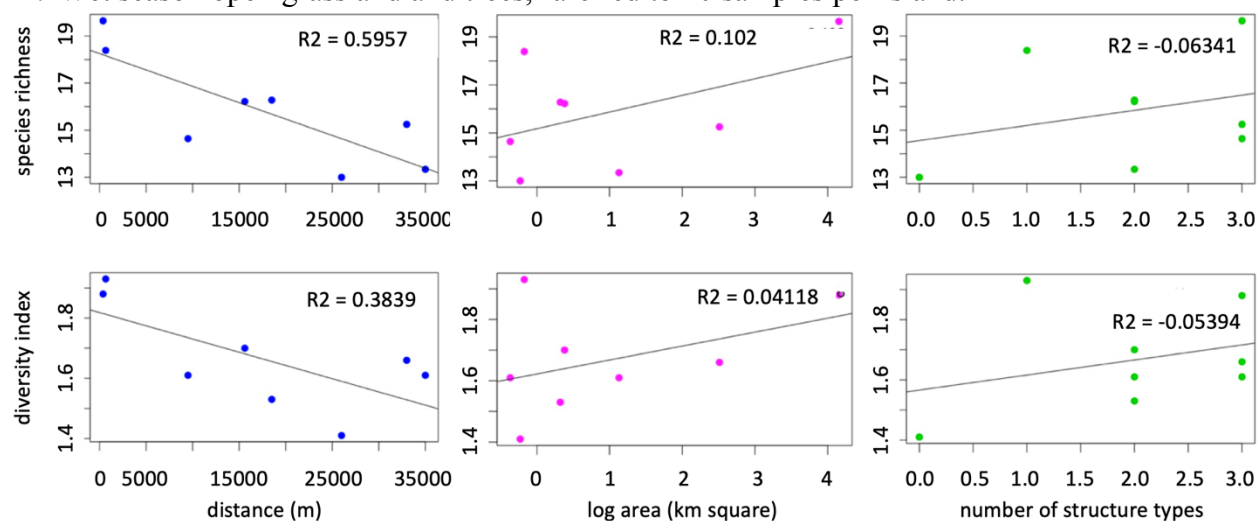


Fig. 1.10. Linear regression scatter plots for analysis of wet season samples collected in A. open grassland samples only and B. open grassland and beneath tree canopy samples. Points represent rarefied results from each of eight islands sampled. Distance(m) is distance between the port of Labuan Bajo and each island. Log-area (km square) is island size with log transformation. Number of structure types is the presence of docks, village residences, and hotels.

1.7 Tables

Island Name	Size (km ²)	Port (km)	Human Pop	Development	Structures	Disturbed	Undisturbed	native spp : intro spp
Seraya Kecil	< 1	9.5	400	village and hotel	3	heavy	yes	16 : 6
Bajo	< 1	0.66	20	few small houses	1	light	yes	14 : 4
Tatawa	< 1	18.6	0	none	0	no	yes	9 : 4
Sebayur Besar	2.4	11	10-50	hotel	2	no	yes	15 : 5
Papagarang	2.1	7.5	>1500	village	2	heavy	yes	14 : 4
Padar	13.5	24	0	none	2	no	yes	12 : 5
Komodo	325	25	>1500	village	3	heavy	yes	12 : 5
Flores	14,300	0	many	cities	3	heavy	yes	20 : 6

Table 1.1. Islands used in diversity survey and conditions at sites. Size = island size; Port = distance to Labuan Bajo; Structures = docks, hotels, villages. Disturbed = disturbed grassland; Undisturbed = undisturbed grassland; native spp : intro spp = native species richness and introduced species richness.

Island	ACE%	ICE%	n	Individuals	Richness	max	SD
Bajo	0.7915	0.9412	40	2022.86	18.41	22.05	1.86
Flores	0.7155	0.8279	40	1903.5	19.82	24.87	2.58
Komodo	0.6869	0.7501	40	1217.54	15.25	18.61	1.72
Padar	0.8026	0.7713	40	1390.32	13.42	18.04	2.36
Papagarang	0.9487	0.7845	40	3181.88	16.27	18.41	1.09
Sebayur Besar	0.5647	0.6464	40	718.22	16.2	21.17	2.54
Seraya Kecil	0.8974	0.7546	40	747.25	16.79	22.49	2.91
Tetawa Besar	0.9441	0.6796	40	1118	13	16.39	1.73

Table 1.2. Rarefied wet season collection data (40 samples) with area-based coverage estimator (ACE) and incidence-based coverage estimator (ICE). Richness is equal to the number of unique species collected on each island.

Subfamily/Species	(Native)(Distributed)	Status	Islands	Habitat	Season	Abundance	Frequency
Dolichoderinae (7)							
<i>Dolichoderus thoracicus</i>	(I)(T,I)	N	1	T	W	1	1
<i>Iridomyrmex anceps</i>	(A,I,O)(A,I,O,P)	N	1	G	*	236	9
<i>Iridomyrmex angusticeps</i>	(A,I)	N	4	*	*	227	68
<i>Iridomyrmex sp. 1</i>		N	8	*	*	1100	59
<i>Iridomyrmex sp. 2</i>		N	8	*	*	5267	317
<i>Philidris cordata protensa</i> _nr	(A,I)	N	1	T	W	5	2
<i>Tapinoma sp.</i>		U	3	G	D	10	6
Dorylinae (1)							
<i>Cerapachys rufithorax</i> _nr	(I)(T,A,I,N,O,P)	N	1	G	W	2	1
Formicinae (13)							
<i>Anoplolepis gracilipes</i>	(I)(A,I,M,N,O,P)	I (Tr)	3	*	*	908	48
<i>Camponotus sp.1</i>		N	1	T	W	1	1
<i>Camponotus sp.2</i>		N	6	*	*	38	12
<i>Camponotus sp.3</i>		N	6	*	*	16	10
<i>Camponotus sp.4</i>		N	4	*	W	18	14
<i>Nylanderia vaga</i> _cf	(I,A)(A,I,N,O)	N (Tr)	8	*	*	1124	191
<i>Oecophylla smaragdina</i>	(A,I,P)	N	1	T	*	5	2
<i>Paratrechina longicornis</i>	(T)(T,A,M,C,N,O,P)	I (Tr)	8	*	*	4267	167
<i>Polyrhachis sp.1</i>		N	3	*	W	3	3
<i>Polyrhachis arcuata</i> _cf	(A,I)	N	1	T	W	1	1
<i>Polyrhachis dives</i>	(A,I,P)	N	2	T	*	3	2
<i>Polyrhachis inconspicua</i> _nr	(A,I)	N	4	G	W	13	10
<i>Polyrhachis zopyra</i>	(I)	N	1	G	W	1	1
Myrmicinae (20)							
<i>Cardiocondyla kagutsuchi</i>	(I)(A,I,M,O)	N	5	*	*	69	22
<i>Carebara diversa</i>	(A,I)(I,P)	N	1	*	W	1592	14
<i>Crematogaster rothneyi</i> _nr	(I,P)	N	5	*	*	317	70
<i>Crematogaster simoni</i> _nr	(I)	N	2	T	W	5	3
<i>Crematogaster sp. 1</i>		N	5	*	*	59	27
<i>Meranoplus bicolor</i>	(I,P)	N	1	*	*	94	15
<i>Monomorium sp.1</i>		U	1	T	W	8	2
<i>Monomorium floricola</i>	(A,I)(T,A,I,M,C,N,O,P)	N (Tr)	2	*	*	13	3
<i>Monomorium intrudens</i>	(I,P)(A,I,O,P)	N	5	*	*	14	12
<i>Monomorium pharoanis</i>	(T)(T,A,I,M,C,N,O,P)	I	1	*	*	10	6
<i>Pheidole sp.1</i>		U	4	*	*	283	35
<i>Pheidole parva</i>	(I)(I,M,O,P)	N	5	*	*	545	26
<i>Solenopsis geminata</i>	(C,N)(T,A,I,M,C,N,O,P)	I	4	*	*	173	16
<i>Tetramorium sp.1</i>		N	4	G	*	21	14

<i>Tetramorium bicarinatum</i>	(I)(T,A,I,M,C,N,O,P)	N	1	T	W	1	1
<i>Tetramorium insolens</i>	(A,I)(A,I,M,C,O,P)	N	1	T	W	1	1
<i>Tetramorium lanuginosum</i>	(A,I)(A,I,M,C,N,O,P)	N (Tr)	4	*	*	22	8
<i>Tetramorium simillimum</i>	(T)(T,A,I,M,C,N,O,P)	I (Tr)	8	*	*	780	153
<i>Tetramorium walshi</i>	(I,P)	N	5	*	*	2419	127
<i>Trichomyrmex destructor</i>	(T)(T,A,I,M,C,N,O,P)	I (Tr)	8	*	*	5121	200
Ponerinae (4)							
<i>Brachyponera sp.</i>		N	3	*	*	437	45
<i>Diacamma sp. 1</i>	(A,I)	N	1	*	*	43	24
<i>Diacamma rugosum</i>	(A,I)(A,I)	N	4	*	*	254	81
<i>Odontomachus floresensis_cf (I)</i>		N	2	*	*	17	7
Pseudomyrmecinae (1)							
<i>Tetraoponera sp.</i>		N	1	T	*	1	1

Table 1.3. List of recorded species, native and recorded ranges, local status, number of islands with records and the habitats they were found in. T = Afrotropical, A = Australasian, I = Indomalayaa, M = Malagasy, C = Nearctic, N = Neotropical, O = Oceania, P = Palearctic. Recorded distribution regional codes are italicized. I = introduced, N = native, Tr = tramp, U = unknown. For habitat occurrences, T = under tree only, G = in open grassland only, * = found in both habitats. For seasonal data, W = wet season only, D = dry season only, * indicates species was recorded in both seasons.

Species	Season		Land Use		Habitat	
	(wet)	(dry)	(dist.)	(und.)	(grass)	(tree)
Dolichoderinae						
<i>Iridomyrmex sp. 1</i>			(0)	(5.4)	(7.2)	(0.1)
<i>Iridomyrmex sp. 2</i>	(24.1)	(19.1)	0.516	(13.3)	(33.4)	0.05955
<i>Iridomyrmex angusticeps</i>	(2.3)	(0.2)	0.5071	(0.1)	(2.5)	0.01131
Formicinae						
<i>Anoplolepis gracilipes *</i>	(15.6)	(0.8)	0.07474	(0.3)	(2.8)	0.05149
<i>Camponotus sp.4</i>					(0.05)	(0.1)
<i>Paratrechina longicornis *</i>	(41.2)	(30.6)	0.4778	(20.2)	(49.7)	0.2527
<i>Nylanderia vaga_cf</i>	(6.4)	(5.3)	0.3634	(1.9)	(4.7)	0.1642
Myrmicinae						
<i>Cardiocondyla kagutsuchi</i>	(0.5)	(0.4)	0.7781	(0.5)	(0.7)	0.7532
<i>Crematogaster sp. 1</i>	(0.3)	(0.6)	0.0458			
<i>Crematogaster rothneyi</i>	(1.5)	(2.2)	1			
<i>Pheidole sp. 1</i>	(3.8)	(0.3)	0.004855	(4.9)	(0.8)	0.1958
<i>Pheidole parva</i>	(6.5)	(3.8)	1	(8.1)	(1.1)	0.4002
<i>Pheidologeton diversus</i>					(0.6)	(22.5)
<i>Solenopsis geminata *</i>				(3.8)	(0)	0.0464
<i>Tetramorium simillimum *</i>	(5)	(3)	0.0769	(2.7)	(4.7)	0.1053
<i>Tetramorium walshi</i>	(16.2)	(22.8)	0.3647	(16)	(40.6)	0.1004
<i>Trichomyrmex destructor *</i>	(55.6)	(15.7)	0.4489	(24.6)	(7.9)	0.3244
Ponerinae						
<i>Brachyponera sp.</i>	(1.9)	(0.2)	0.0854	(0.1)	(2.5)	0.04776
<i>Diacamma rugosum</i>	(0.6)	(1.7)	0.4959	(2.5)	(0.4)	0.1601
					(0.66)	(0.58)
					(0.9)	(0.7)

Table 1.4. Wilcoxon signed-rank test of median values of abundances between: wet and dry seasons, disturbed and undisturbed grasslands, and open grass or beneath tree habitats. Species with abundances too low to achieve a 95% confidence interval in seasonal comparison tests are excluded. * indicates an introduced species.

Island	land use	Bray p	Jaccard p
Flores	U	*0.001113	*0.001707
Flores	D	0.7023	0.9557
Seraya Kecil	U	*0.0002858	*1.201e-06
Seraya Kecil	D	0.8806	0.7409
Papagarang	U	*0.001244	*0.003513
Papagarang	D	0.6986	0.05743
Sebayur Besar	U	*7.617e-07	*2.951e-09
Bajo	U	*0.0002449	*0.001514

Table 1.5. Linear regression results of Bray-Curtis and Jaccard vegetative dissimilarity and ant community composition dissimilarity. With Bonferroni correction for 8 tests, level of significance is $\alpha = 0.00625$. U = undisturbed grassland, D = disturbed grassland.

Season	Land Use	n	Measure	p	Grass Average	Tree Average	Season	Land Use	n	Measure	p	Grass Average	Tree Average
dry	disturbed	6	total I	0.2255	14.50	105.83	wet	disturbed	12	total I	0.3636	30.67	63.58
			total N	0.1846	16.00	82.83				total N	*0.0464	73.00	22.75
			prop. I	0.9367	0.57	0.55				prop. I	*0.0053	0.26	0.64
			prop. I nP	0.933	0.47	0.44				prop. I nP	0.1671	0.25	0.46
			Shannon	0.9356	0.68	0.70				Shannon	0.7685	0.93	0.89
			(absolute value) richness I		5	5				(absolute value) richness I		6	6
			(absolute value) richness N		3	7				(absolute value) richness N		10	12
dry	undisturbed	13	total I	0.1129	12.92	86.54	wet	undisturbed	32	total I	*0.0082	34.41	161.34
			total N	0.2164	95.62	27.46				total N	0.9994	73.47	73.50
			prop. I	*0.0001	0.12	0.62				prop. I	*0.0000	0.23	0.64
			prop. I nP	0.0251	0.09	0.43				prop. I nP	*0.0001	0.22	0.56
			Shannon	0.9860	0.83	0.83				Shannon	0.0353	0.71	0.90
			(absolute value) richness I		5	5				(absolute value) richness I		6	5
			(absolute value) richness N		12	18				(absolute value) richness N		20	25

Table 1.6. Differences (paired *t*-test) in diversity between open grassland sites and paired, below tree canopy samples by season and land use. n = number of below tree/open grassland transect pairs. Critical p-value $\alpha = 0.0125$.

Chapter 2 Isotopic and behavioral analysis of *Solenopsis geminata* diets

2.1 Introduction

Invasion biology emerged as a field of study in the 1950's to address the relationship between the uniqueness of plant and animal communities by location and increased globalization as a driver of the deteriorating barriers on exotic species establishment (Hayden and White, 2003). Dietary requirements of species are a critical determinant in their ability to move into novel habitats. Theories about dietary specialization and generalism often posit contradictory views of the benefits of certain diets and the evolution of diet as it relates to resource competition. Existing tradeoffs between generalism and specialization become particularly relevant in the broad framework of invasion biology as both offer mechanisms to avoid competition and successfully establish within a preexisting community of organisms. Co-invasion of multiple invasive species has led to the '*invasion meltdown*' concept made famous by a study conducted on Christmas Island revealing a mutualistic relationship between invading land snails and invading, predatory Yellow Crazy Ants (O'dowd et al., 2003). The Tropical Fire Ant (TFA), a ubiquitous and invasive species, possesses characteristics of both a dietary generalist and a dietary specialist. The TFA can consume tremendous amounts of grass seeds in addition to a wide range of other foods. The combined impact of TFA invasion and invasive grass species is not well studied despite a global prevalence of both. Focused study of dietary shifts in the TFA during range expansion into new habitat types may provide insight into how diet and co-invasion are related within the field of invasion biology.

Dietary flexibility and dietary specialization have evolved countless times in organisms as a mechanism for increasing competitive ability or altogether avoiding competition for food resources. Dietary specialization may co-occur with morphological adaptations that enhance consumption of the focal food (Brown and Wilson, 1956; Svanbäck and Bolnick, 2007). Specialization is linked to increased competitive ability (Ehinger et al., 2014; Marvier, 2004) and, in ants, food resource competition is a driver of worker caste polymorphism (Wills et al., 2018; Traniello, 1989). Diet is not just an external force driving phenotypic heterogeneity seen in ants. Manipulation of larval diet, along with genetic and hormonal components, actually determines adult worker caste (Amor et al., 2016; Wills et al. 2018). Species with access to a wide range of resources are provided increased opportunity for specialization which has been shown to occur at higher rates in these diverse, resource-rich systems (Araújo et al., 2011; Roughgarden, 1974). It seems, however, that generalism rather than specialization is promoted when a species is mobile between habitats with major differences in the resources it must utilize (Marklund, 2018). Dietary flexibility, or dietary generalism, is often considered a defining characteristic of invasive species and a critical trait in determining the ease by which a species can establish itself beyond its native range (Marvier, 2004; McGlynn, 1999). Omnivorous species that feed on a wide range of foods are considered '*dietary generalists*' and include most invasive organisms. Species that are able to occupy a wide range of habitat types and tolerate variable environmental conditions are considered '*habitat generalists*'. Highly invasive ants are often both habitat and dietary generalists, allowing them to utilize a wide range of resources in novel environments, particularly in disturbed habitats (Marvier, 2004; McGlynn, 1999;

Romanuk, 2009). Dietary generalism provides opportunities to attain nutritionally balanced diets that are minimally impacted by environmental changes and variability in food resources (Funk and Bernays, 2001; Nurkse et al., 2009). Similarly, omnivores are more likely to show dietary shifts in response to environmental changes than relatively inflexible specialist species (Gibb et al., 2003).

The Tropical Fire Ant, *Solenopsis geminata*, is an omnivorous fire ant with a specialized, seed-milling major worker caste. The TFA is found in tropical regions around the world and considered an invasive pest (McGlynn, 1999; Wetterer, 2011) native to Central America, parts of South America, and Florida in the United States. Major workers possess large, muscular mandibles and large heads, which are adaptations for milling grass seeds that are collected by minor workers. The behavioral repertoire of major workers in *S. geminata* is reduced in comparison to smaller worker castes and major workers of closely related species, with *S. geminata* majors performing only two tasks, self-grooming and seed milling (Wilson, 1978). In related species of *Solenopsis*, seeds are consumed by the colony, however, the major worker caste performs additional duties as foragers and soldiers. The well-documented correlation between worker size and size of seeds they are able to collect (Davidson, 1978; Kaspari, 1996, Shutner and Mullie, 1991) would logically suggest that foraging by *S. geminata* majors would increase dietary breadth. These additional tasks performed by the major worker caste in other species are sacrificed in *S. geminata*, but their specialized adaptations for granivory may offer a competitive advantage that outweighs the costs.

Competition manifests in three main forms within ant communities: interference, exploitation, and apparent (Parr and Gibb, ch. 5 Ant Ecology). The effects of interference and exploitation competition are decreased when food resources are not overlapping (Davidson, 1978; May and MacArthur, 1972), potentially bringing about competitive release for the TFA in grasslands. Furthermore, despite the advantages afforded by dietary generalism, studies have found inefficiencies in cognitive processes involved in decision-making around food resources (Egan and Funk, 2006) and superior nutrition afforded by host specificity (Bernays and Minkenberg, 1997).

Stable isotope techniques are useful in conducting dietary analyses for individual species and constructing community trophic webs (Peterson and Fry, 1987; Post, 2002). The most commonly used isotopes in constructing terrestrial community food-webs are ^{13}C and ^{15}N . Dietary carbon sources, specifically utilization of C3 versus C4 plants, can be inferred by analyzing the difference between collected samples and a standard with known isotopic values, indicated as the difference between measured ^{13}C of the standard used and the ^{13}C value of the sample (Peterson and Fry, 1987). Values are measured in parts per thousand (‰) and differences are expressed using the “ δ ” symbol, for example $\delta^{13}\text{C} = -14\text{‰}$. Accumulation of the ^{15}N isotope increases with higher trophic position and is expressed as a shift from the ^{15}N value of the standard used, or $\delta^{15}\text{N}$. The trophic value range within a system is generally defined at the lower bound by plants and the upper bound by top predators. Analyzing and comparing $\delta^{15}\text{N}$ values of focal species with co-occurring species across the trophic range will situate focal species on the spectrum from herbivory to top predator in the sampled area (Perkins et al., 2014; Peterson and Fry, 1987). If vegetation and/or soils are collected across sites to provide a lower bound for local isotopic input, inferences can be made about the environmental contributions to community-wide isotopic patterns found amongst organisms at higher trophic levels (Post, 2002). Without this baseline, only relative positions of species experiencing the same conditions can be inferred but not their positions relative to the base of the food-chain, i.e. their trophic level compared to the

trophic level of organisms collected in separate conditions. Stable isotope techniques have been used to study trophic ecology and diet in prominent invasive species such as the Argentine ant, *Linepithema humile* (Tillberg et al., 2007), the red imported fire ant, *Solenopsis invicta* (Wilder et al., 2011), and the Asian needle ant, *Brachyponera chinensis* (Suehiro et al., 2017).

The topics of invasion biology and habitat susceptibility are becoming increasingly important as the impacts of human populations on the environment increase in rapidity and area affected. Global changes in climate and increasing demand for foods such as agricultural products that are shipped great distances (Aklesso et al., 2015) facilitate the spread of invasive ants, in particular (Wetterer, 2011). Many ant (Bertelsmeier et al., 2015) and grass species are among the most invasive and widespread pest groups. Ants reside in all but the frozen, polar regions (Guénard et al., 2011). Grasslands cover approximately 40% of the Earth's land surface area (White and Rohweder, 2000). The competitive abilities of resident species are important in determining the invasibility of a site. In the grasslands of southeastern Indonesia, *S. geminata* has established populations across village borders into disturbed grasslands but is not found in intact, native grasslands. The TFA is of concern in southeastern Indonesia where grasslands potentially provide unlimited food resources for the ant in a region where ground-nesting, vertebrate species are common. Nest destruction through direct predation is a conservation concern for protected species (Erickson and Baccaro 2016; Wetterer et al., 2016) such as *Komodo veranus*, the Komodo dragon.

Our study addresses a lack of knowledge regarding the behavior and dietary attributes of a widespread invasive ant, *Solenopsis geminata*, at an invasion front in native tropical grasslands. Resource use and relationships between the TFA and grasses, their primary food source, were investigated via manipulative field assays and stable isotope analysis of the ant community. We address three main aims in this study: (i) describing TFA dietary characteristics and seed utilization, (ii) seed species preference and foraging behavior, and (iii) the relationship between foraging behavior and species distribution with special focus on the apparent resistance to TFA invasion in native grasslands. We consider the limitations of specializing on seeds as a food resource in the context of optimal foraging theory (MacArthur and Pianka, 1966), which would explain seed selection as being influenced by nutritional value of the resource, availability of a resource, and handling time during foraging (Araújo et al., 2011; Sinervo, 1997). Our primary focus is on the relationship between handling time and grass seed preference in explaining habitat selection based on availability of preferred species. Here, the importance of seed handling time is suggested as a barrier to habitat invasion; a conclusion that is buttressed by the higher availability of seeds that were not preferentially collected.

Study area

Field studies were conducted in southeastern Indonesia in the province of Nusa Tenggara Timur. Savanna grasslands are the dominant vegetation type in the region. Development of villages and hotels has introduced goats into grassland systems and, where goats are present, exotic grasses coexist with native grass species. Study sites were located in the village and in adjacent disturbed and undisturbed grasslands on the island of Seraya Kecil at altitudes ranging from 0m to 15m above sea level. Rainfall follows a monsoonal pattern with the driest conditions from May through November and wettest from December through April. These islands receive approximately 800mm of rainfall each year. Seraya Kecil Village is located approximately 9 km from Labuan Bajo, Flores, where a local port serves the large island of Flores and nearby small islands. Multiple trips are made by residents each day between the port at Labuan Bajo and

Seraya Kecil Village, on the very small island of Seraya Kecil, causing great potential for the transportation of exotic species and providing an ideal location for isotopic study of a community with high native and exotic plant and ant diversity.

Open, grassland savannas cover 70% of the area inside Komodo National Park. Grassland coverage is similar throughout the study area outside of the park. Undisturbed grasslands are dominated by two grasses, *Heteropogon contortis* and *Chrysopogon subtilis* and their presence characterizes native grasslands in the region. In disturbed areas, native grasses and exotic grasses occur in mixed stands. In the disturbed areas, *C. subtilis* and *H. contortus* coexists with exotic species including *Dactyloctenium aegyptium* and *Panicum delicatulum* along with native grasses common to disturbed habitat. Several tree species are found in open grasslands and in gallery forests. In addition to large expanses of grassland habitat, islands usually have forested patches and areas of thick riparian vegetation dominated by mangrove species.

An in-depth analysis of seed foraging behaviors and dietary comparisons with five species was conducted on one island that contained all habitat types in close proximity. In order to achieve the depth of the study, incorporating foraging assays and isotopic analysis of six ant species, the study was not replicated across islands. This is not uncommon in trophic studies of a site or habitat type. The site on Seraya Kecil was the only site with such a diverse grass community in the disturbed grassland, having all of the most common native and introduced species seen in the broader Komodo region. Furthermore, transporting seeds of exotic grasses between islands to conduct foraging assays carried the potential for accidental introductions. Seraya Kecil also supported an especially diverse ant community, enabling the collection of enough material from several species to make between-species comparisons within habitat types. Few *S. geminata* colonies were found beyond village borders on Papagarang and Komodo and these grass communities were not as diverse. Searches did not reveal sufficient colony numbers to conduct similar experiments. With these conditions in mind, I focused on going in depth at one site, collecting all species with sufficient abundances for isotopic analysis.

2.2 Methods

Sample collection and field assays

The vegetation and plant community data used in this study to describe grasslands were collected in a separate study. Vegetation cover and species composition were assessed by placing a one-meter square quadrat and calculating total coverage and presence/absence of the six selected grasses. Samples were collected along randomly placed transects consisting of five quadrat samples, spaced 10m apart in a line. Vegetation transects were not spatially associated with seed-preference trial locations but were distributed to assess the overall vegetative community characteristics of each habitat on the island.

Dietary incorporation of C4 grass material and relative trophic position of ant communities was measured using stable isotope methods to determine $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in dried samples. Workers were collected from colonies found within three habitat types: (i) villages and (ii) disturbed (goat-grazed) grasslands adjacent to villages and (iii) undisturbed grasslands. Workers were collected from 5 sites in each habitat in which they occur. *Trichomyrmex destructor*, previously *Monomorium destructor*, exists in disturbed savanna but only two sites were found in the study area. Sites were at least 30 m away from one another and assumed to be separate colonies. Village samples were collected from within a two square meter area on the ground and from one support beam of a house with the beam at the center of the

ground quadrat. Grassland samples were collected from within a two square meter area on the ground and a single tree trunk that marked the center of the quadrat.

Six abundant and widespread ant species were used in isotope analysis. Two species, *Diacamma sp.* and *Tetramorium walshi*, are considered native to the region. *Brachyponera sp.* is considered native, as it is native to Southeast Asia, but may be locally invasive. *Paratrechina longicornis*, *Solenopsis geminata*, and *Trichomyrmex destructor* are widespread invasive, tramp species, common throughout Indonesia. Species identification was based on available literature, AntWeb information, and confirmation by Dr. Alan Andersen of CSRIO, Darwin, Australia and by Dr. Eli Sarnat at the California Academy of Sciences, San Francisco, California. Current knowledge of native versus introduced ranges is lacking for many species. Native or introduced status was assigned based on information available in literature and on AntWeb (Ant Web, 2013).

Samples were collected by aspirating ants or hand collecting and ants were collected in a 50ml conical tube. Samples were dried in the field by placing 50ml sample tubes partially submerged in hot sand and left in the sun for approximately 6 hours. Tubes had a large hole cut in the top that was covered by mesh to allow moisture to escape. After 6 hours, Delta Adsorbents blue-indicating, 3-5mm silica beads were added to each sample tube, an airtight cap was placed on each tube, and samples were stored overnight. The following day, samples were placed in hot sand and exposed to sun for the duration of daylight. Fresh silica was put into tubes and airtight caps were placed on each tube before transporting samples. Dried samples and silica beads were transferred to small vials or into whirl packs for long-term storage and placed in a freezer. Isotopic analysis was conducted at the Center for Stable Isotope Biochemistry at the University of California, Berkeley. Samples were analyzed using a CHNOS Elemental Analyzer in combination with an IsoPrime100 mass spectrometer. Pee Dee Belemnite (PDB) was used as a standard for comparison. Simultaneous analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were performed by continuous flow (CF) dual isotope analysis. Precision for C isotope measures was $\pm 0.10\text{‰}$ and for N isotope measures, $\pm 0.20\text{‰}$.

Seed preference experiment

The six most abundant grass species were selected for behavioral assays of *S. geminata* foraging in the field. Grasses were divided into three groups, disturbed-exotic (DE), disturbed-native (DN), and undisturbed native (UN). Disturbed-exotic grasses and disturbed-native grasses were only found in disturbed grasslands. Undisturbed-native grasses were found in both disturbed and undisturbed grassland, dominating both, and comprising the large majority of vegetation in the former. Each group contained two species of grasses. After determining that seeds belonging to undisturbed-native grasses, *C. subtilis* and *H. contortus*, were larger than seeds of grasses adapted to disturbed habitat and we sought to explore seed size as an underlying reason for the absence of *S. geminata* in undisturbed grasslands. Seed preference studies were conducted over a three-week period at the end of the wet season in April and May of 2013. Grass samples were collected fresh while flowering. Seeds were collected fresh for seed preference studies. Intact grasses were packed in herbarium collection presses for identification. Identification was conducted by botanists at Lembaga Ilmu Pengetahuan, Cibinong, Indonesia.

I first performed seed preference experiments using whole, intact grass seeds. *Solenopsis geminata* workers were offered five seeds of each grass species (30 seeds total) which were placed on a 5cm² plastic card. Six cards, each with 30 seeds, were placed 20cm from a nest

entrance. Foraging was observed for one hour and the number of seeds taken for each grass species was recorded during four, consecutive 15-minute periods.

Later, treatment assays with cut seeds were performed as in whole-seed trials, but with individual large seeds of *Chrysopogon subtilis* and *Heteropogon contortis* cut in halves and thirds, respectively. One cut piece of seed was then treated as a single seed.

To provide a measure of interest versus difficulty or ease in collecting seeds, foraging activity by individual ants was recorded as three separate behaviors. ‘Antennating’ was defined by an ant approaching a seed, contacting the seed with their antennae, and leaving the seed unmoved. ‘Carrying’ behavior was defined by an ant approaching a seed, attempting to carry the seed off the depot card, and then dropping the seed and abandoning it before leaving the card area. ‘Collecting’ was defined by an ant successfully removing a seed from the card. “Carrying” and “Collecting” behaviors were typically preceded by antennation, but antennation in these contexts was not included in the “Antennating” score. Thus, “Antennating” includes only instances in which ants antennated a seed, but did not move or remove the seed. Behaviors were recorded for each ant-seed interaction over the one-hour observation period.

Data analysis

The first part of our study aimed to determine if *S. geminata* utilizes seeds as a food resource in Indonesian grasslands and if this differentiates *S. geminata* diets from that of other ant species. Comparison of $\delta^{13}\text{C}$ determinations was used to assess the relative importance of C3 and C4 plants in ant species diets within habitat types. Non-parametric, Wilcoxon signed-rank tests were used to make statistical comparisons between samples pooled by species and general community-level comparisons between habitats. Comparison of $\delta^{15}\text{N}$ determinations were used to described relative differences in trophic positions of ant species within habitats and general community-level comparisons between habitats. Statistical tests were run in the base package ‘stats’ in R version 3.4.1 ‘Single Candle’. Samples sizes for each species in each habitat were $n = 5$, representing five separate colonies within the designated habitat. Samples size for *T. destructor* in disturbed grassland was $n = 2$ and these data were excluded from group comparisons. Results were supported by post-hoc Tukey’s honest significant difference (Tukey’s HSD) tests. Multiple tests were Bonferroni corrected.

The second part of this study focused on explaining the absence of *S. geminata* in undisturbed grassland. Differences in average seed size were based on the average length of 20 seeds of each of the six, selected species. The lengths of dried seeds were measured to the nearest 100th of a millimeter under a dissecting microscope fitted with a micrometer in one eyepiece.

Seed depots with zero ant-seed interactions were considered to be undiscovered and were removed before analysis. To test for normality, Shapiro-Wilks tests were applied to seed collection data grouped by habitat and treatment. In most cases, data were not normally distributed and Wilcoxon signed-rank tests were used to compare seed collection between habitat and treatment groups. Foraging assays, as described previously, produced sample sizes sufficient for non-parametric tests, despite non-normality, however the more conservative test was chosen. Statistical tests focused on determining the influence of seed size on collection rates. Pairwise Wilcoxon signed-rank comparisons were made between seed groups within habitat and treatment, specifically noting the change in collection of UN seeds after size-standardizing treatments. Where multiple tests were implemented, Bonferroni corrections were applied to resulting p -values to reduce the likelihood of a type I error.

Finally, the collection of seeds relative to the abandonment of carried seeds was calculated as (difference = collected – carried) for each grass species within the control and treatment groups. Mean values for the differences between treatment and control groups were compared for each habitat using one-tailed, Welch’s independent two sample *t*-tests with no assumption of equal variance (Welch, 1947) and analyses were conducted the R base package ‘*stats*’. The Welch’s *t*-test was chosen over a non-parametric test in order to apply a one-tailed test in which the alternative hypothesis was that the difference between collected and carried seeds was not only different, but *greater* for the treatment group. Data did not fit a normal distribution; however, sample sizes were similar for groups, sufficiently large ($n > 15$) for each group, and variances were somewhat similar. When these conditions are met, parametric tests perform better than non-parametric tests (Pearson, 1931; Bartlett, 1935; Geary, 1947). A Bonferroni correction applied to *t*-test results for 12 tests resulting in a critical alpha value of $p < 0.004167$.

2.3 Results

Seed utilization and habitat

Isotopic analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Solenopsis geminata, the focal species, were found in village and disturbed habitat but not undisturbed grassland, following the overarching distribution pattern across islands (Sandidge, Chapter 1). It was the second most abundant species collected on Seraya Kecil during the wet season, comprising 30.4% of total ant abundance. Dry season abundance was much lower, making up only 1.6% of total abundance (Sandidge, unpublished). *Trichomyrmex destructor*, previously *Monomorium destructor*, is a competitor species found in disturbed savanna and villages, however only two locations in disturbed grassland were found in the study area for this study. *Paratrechina longicornis* was the only species found in undisturbed grassland, disturbed grassland, and village habitat. Native species, *Diacamma sp.* and *Brachyponera sp.*, were not found in the village habitat but were common in both grassland types.

In disturbed savannas, seeds from six grass species, labeled as “SED” (Fig. 2.2), predictably fell within $\delta^{13}\text{C}$ values for C4 plants with values being between -14‰ and -10‰. As expected, $\delta^{13}\text{C}$ in *S. geminata* was closer to the range of C4 plants and significantly differed from other ant $\delta^{13}\text{C}$ values, with the exception of *Brachyponera sp.* (Fig. 2.2). After applying a Bonferroni correction to Wilcoxon signed-rank tests, statistical results were as follows: *Brachyponera sp.* ($W = 24$, p -value = 0.0159), *Diacamma sp.* ($W = 25$, p -value = 0.0079), *P. longicornis* ($W = 25$, p -value = 0.0079), seeds ($W = 0$, p -value = 0.0043), *T. walshi* ($W = 25$, p -value = 0.0079) (Fig. 2.2). Post-hoc, Tukeys HSD comparisons confirmed these differences with p -value = 0.0018 for *Brachyponera sp.* and $p < 0.0001$ for remaining ant species and seeds. All four species collected in villages had similar isotopic profiles ranging from approximately -20‰ to -22‰. In the village habitat, where grasses are not readily available, $\delta^{13}\text{C}$ values for *S. geminata* were not distinguishable from *T. destructor*, *P. longicornis*, or *T. walshi*, nor were differences found between any other species pairs.

Ants within each habitat occupied similar trophic positions, as measured by differences in $\delta^{15}\text{N}$ determinations, with maximum differences being approximately 2.5‰ between *P. longicornis* and *Brachyponera sp.* in undisturbed grassland. The difference between *P. longicornis* and *Brachyponera sp.* was not significant in pairwise Wilcoxon signed-rank tests

after a Bonferroni correction was applied making the critical p value = 0.0167 ($W = 23$, p -value = 0.0318). Post-hoc Tukey's HSD tests were applied and *P. longicornis* and *Brachyponera sp.* were then found to have significantly different means (adjusted p -value = 0.018). Measures of $\delta^{15}\text{N}$ in C4 grass seeds were compared to that of ant species in disturbed grassland and all seed/ant pairs did not differ significantly after Bonferroni corrections were applied; p -value = 0.065 for seeds and each ant species and $p > 0.119$ for paired ant species comparisons. In disturbed grassland the average $\delta^{15}\text{N}$ value for ants was 8.65‰. The average $\delta^{15}\text{N}$ value for seeds was 4.48‰ less, indicating that ants are one to two trophic levels above the seed food resource.

When ant species were pooled within habitats, the $\delta^{13}\text{C}$ values in undisturbed habitat were higher than both disturbed savanna and village habitats (p -value = 0.0001, p -value = 0.0000) (Fig. 2.2). Average community-level isotopic nitrogen values for pooled ant species declined across habitats, from village (12.87‰), to disturbed grassland (8.65‰), to native grassland (4.74‰). Without analysis of abiotic factors, the isotopic separation of communities by habitat cannot be attributed to dietary differences and is described in greater detail in the discussion.

Seed availability and preference

Disturbed grasslands averaged 59.6% vegetation cover and native grasslands averaged 75.7% vegetation cover near the end of the wet season when preference assays were conducted (Sandidge, unpublished). In surveys, the six selected grass species were all found in disturbed grassland. Two of the six selected species were found in undisturbed grassland. *Chrysopogon subtilis* was the most common grass found in both disturbed (72% of samples) and undisturbed grasslands (88% of samples). *Chrysopogon subtilis* and *Heteropogon contortus* were the only grasses present at undisturbed sites. In disturbed areas, *C. subtilis* and *H. contortus* were found in mixed stands with exotic species and produced the largest seeds. Seed size was smallest in exotic species *Dactyloctenium aegyptium* and *Panicum delicatulum*, which were found in 20% and 16%, respectively, of disturbed grassland samples and did not occur in undisturbed grassland (Table 1). *Brachiaria reptans* and *Agrostis infirma* were two native grasses found only in disturbed areas and produced larger seeds than the exotic species, *D. aegyptium* and *P. delicatulum*, but smaller seeds than *C. subtilis* and *H. contortus*.

Anecdotal observations suggest that major workers of *S. geminata* rarely forage for seeds. *Paratrechina longicornis*, *Diacamma sp.*, and *T. destructor* were occasionally observed approaching seeds, particularly in the village trials, however, they never carried a seed away from the seed depot. Seeds were intentionally placed nearby to *S. geminata* nest entrances, as this was the focal species, results most likely do not reflect the potential interest in seeds by other species.

Seeds of two small-seeded, exotic grasses (group DE), *D. aegyptium* and *P. delicatulum* (Table 2.1), were the preferred food seeds of *S. geminata* in both savanna and village trials when seed sizes were unaltered. When seed sizes were standardized, the seeds of two large-seeded, native species, *C. subtilis* and *H. contortus* were as attractive as the smaller-seeded species. In whole seed trials, *S. geminata* colonies in disturbed grassland collected small-seeded group DE at higher rates than groups DN and UN (S-DE/S-DN, p -value = 0.0026; DE/UN, p -value = 0.0077; S-DN/S-UN, p -value = 0.6029) (Fig. 2.3). Colonies in the village habitat were similar with DE collection being higher than collection of the two other seed groups (S-DE/S-DN, p -value = 0.0002; DE/UN, p -value = 0.0014; S-DN/S-UN, p -value = 0.5901). After standardization of seed size (cut seed trials), disturbed grassland colonies collected the three seed groups at

similar rates (S-DE/S-DN, p -value = 0.0418; DE/UN, p -value = 0.4834; S-DN/S-UN, p -value = 0.1659). Seed standardization in the village habitat resulted in a significant increase in the collection of seed group UN indicating a preference for those seeds when available at a smaller size (S-DE/S-DN, p -value = 0.1864; DE/UN, p -value = 0.0839; S-DN/S-UN, p -value = 0.0025). Bonferroni adjustment for multiple tests reduced the critical alpha value to 0.017 for each set of three tests.

In village seed preference assays, the difference between seeds collected and seeds carried increased for seeds *Brachiaria reptans* (ND1: $t = 3.5977$, $df = 46.305$, p -value = 0.000389), *Chrysopogon subtilis* (NU1: $t = 3.5323$, $df = 56.979$, p -value = 0.000412), and *Heteropogon contortus* (NU2: $t = 2.8217$, $df = 41.324$, p -value = 0.003656), meaning fewer size-standardized seeds were abandoned before being removed from the seed depot. After applying a Bonferroni correction for 12 tests, differences between seeds collected and seeds carried were not higher for the treatment (seed-standardized) group for any seed species in disturbed grassland assays. *Heteropogon contortus* (NU2) just missed the cutoff p -value of 0.004167 for $\alpha=0.05$ with the Bonferroni correction ($t = 2.699$, $df = 49.406$, p -value = 0.004747).

2.4 Discussion

We found that *S. geminata* commonly collects grass seeds, and that foragers display a marked preference for smaller seeds over larger seeds. Worker size was fairly consistent as foraging behavior was restricted to the minor worker caste. As result, our behavioral assays showed that removing large seeds for consumption was difficult and seeds were often abandoned. Major workers did not forage for seeds and this is most likely limiting the dietary niche width of the TFA. In this case, specialization was beneficial for moving into grasslands but detrimental in moving beyond disturbed areas.

Nitrogen isotope enrichment distinguished ant communities, with village-living ants having the highest $\delta^{15}\text{N}$ ratios and undisturbed savanna ants having the lowest (Fig. 2.2). Households primarily consume animal-based foods, which then become available to insects and other species via open waste piles under each home. Additionally, the absence of weeds and grasses in villages appears to limit access to C4 carbohydrates. Comparisons cannot be made across habitat types, meaning that regardless of observed potential food resources, we cannot conclude that village diets contain more animal protein than grassland diets. Though ant communities were separated between habitat types, all sampled species occupied the same trophic level within habitats. We concluded from this result that the major difference between the TFA diet and that of other species of ant is not variation in the animal-based food consumed but rather in the plant-based foods at the base of their diets.

Solenopsis geminata was the only ant species to have a delta $\delta^{13}\text{C}$ measure consistent with consumption of C4 plants which, in our study, were tropical grasses. The ability to take advantage of seeds as a food resource allows *S. geminata* to avoid direct competition for at least a major component of its diet. Ant species within each habitat had similar enough $\delta^{15}\text{N}$ to suggest all ants were at the same trophic level. Greater variation was seen in $\delta^{13}\text{C}$ isotopic shifts. The variation in $\delta^{13}\text{C}$ between species within a habitat suggests that food resource partitioning may be defined, to some extent, by the plant community that ants feed in and the plants their prey feed upon. Spatial partitioning of foraging areas is exemplified by a preference for arboreal feeding commonly seen in *P. longicornis*, and this behavior would lead to a diet with trees and shrubs, C3 plants, at the base of the food-chain. Indeed, in undisturbed grasslands, *P. longicornis*

showed greater utilization of C3 plants than *Diacamma sp.* and *Brachyponera sp.*, both known to be epigeic and, in this context, inhabiting C4 grass-dominated niches. Resource partitioning can also arise from specialization leading to consumption of a food that is not preferred by competitors. While it is known that other species do consume seeds, only *S. geminata* has specific adaptations for seed consumption, and was the only species in our study to show evidence of a significantly greater C4 grass dietary component.

Trichomyrmex destructor is known to consume seeds and was viewed as a potential competitor for seed resources. During trials, *T. destructor* was rarely seen approaching seeds and never attempted to carry a seed away. Results indicate that *T. destructor* is not relying on seeds and C4 plants in the study area. In other assays conducted at the same site using tuna baits, *T. destructor* was the main competitor of *S. geminata* (Sandidge, Chapter 3). Its virtual absence from seed depots was interpreted as a genuine lack of interest or inability to utilize local seeds as a significant food resource, though proximity to *S. geminata* nest entrances could be a deterrent in addition to being a greater distance from *T. destructor* nests.

Diacamma sp. and *Brachyponera sp.* are considered predatory scavengers, often specializing on a group of prey such as termites (Wheeler, 1936; Bednar and Silverman, 2011). Two species are known to consume seeds however those species display a level of caste polymorphism not found in *Brachyponera sp.* sampled here. Our findings indicate that both *Diacamma sp.* and *Brachyponera sp.* have similar diets to that of other ant species in the area, most likely feeding on prey feeding on a mix of C3 and C4 plants.

Paratrechina longicornis and *Tetramorium walshi* are species with generalized diets. Both species will feed on dead insects, plant material, honey dew, and other sugary or protein-rich substances. *Paratrechina longicornis* is a prominent honey dew consumer, utilizing aphids and other honey dew producing insects as a source of food. We found that *P. longicornis* and *T. walshi* are most likely feeding on a mixture of C3 and C4 plant consumers and perhaps the nectar of these plants. Their diets and the diets of other species fell within one trophic level, suggesting they are not more or less predatory than co-occurring species.

The aim of this study was to compare *S. geminata* diets to the diets of other ant species, particularly seed consumption, within the immediate area and habitat, i.e. their competitors. These data were used to highlight the $\delta^{13}\text{C}$ split from other ant species in the direction of C4 plant consumption within disturbed grassland conditions, where seeds are readily available. The $\delta^{13}\text{C}$ separation between *S. geminata* and co-occurring species was not seen in the village where very few grasses reach maturity. This Measured differences between habitat types can only be attributed to dietary differences when an abiotic baseline is used to adjust for the effect of environmental conditions. Soil moisture can shift $\delta^{13}\text{C}$ values (Palta and Gregory, 1997). Nitrogen inputs in soil may shift the baseline to show greater nitrogen enrichment throughout the system (Szpak, 2014) rather than the enriched community being more predatory. Goats are common in villages and are less common with greater distance from the village. Nutrients in goat feces may impact soil nutrient values. Additionally, the village may have greater soil moisture due to lower elevation and reduced plant cover. These abiotic differences would impact entire communities as they lie at the base of the food chain. Within habitat types, abiotic factors are assumed to be similar, allowing for dietary interpretation of differences between species.

Our results suggest that seed consumption plays an important role in *S. geminata*'s ability to live in open grasslands by providing a food resource that does not overlap with that of competing ant species. Reliance on granivory would be expected of a species with physical traits that have evolved as adaptations for dietary specification, particularly in a group that otherwise

has a generalized, omnivorous diet characteristic of invasive species. The cost of producing a major worker caste with a severely limited behavioral repertoire is assumed to be high, and other studies have shown that increases in worker size occur as colony size increases, and concomitant increases in foraging (Porter and Tschinkel, 1985; Tschinkel, 1999). Given the high cost of major worker production, it follows that competitive advantages gained through granivory must be significant. The ability to consume such large quantities of seeds might allow the TFA to occupy any habitat with plentiful production of acceptable grass seeds. Yet, *S. geminata* is not found in undisturbed grasslands even when the habitat abuts invaded, disturbed areas. The notable absence of *S. geminata* in undisturbed, native grasslands likely is related to seed size of the available grasses and the added difficulty of transporting large seeds of the dominant grasses. Preference for small-seeded grasses was likely driven by the ability of small ants to carry seeds, rather than their attractiveness as a food source (Fig. 2.4, Fig. 2.5). Native grass species that undisturbed grasslands have large seeds that were difficult for *S. geminata* workers to transport, though size-standardized seeds were collected at similar or higher rates than the smaller seeds. Because seeds are a significant portion of *S. geminata* diets in grasslands (Fig. 2.2), access to preferred species most likely determines the potential range of the invasive ant, limiting it to disturbed habitats where small-seeded, exotic grasses are abundant.

This study poses interesting questions about the benefits and drawbacks of specialization. Seed resources are strictly seasonal and, although *S. geminata* is apparently able to survive in between seed production events, total absence of seed access may be a limiting factor in their spread within natural grasslands. The TFA is prolific in villages where grasses are completely absent but human food waste is abundant, disturbance is high, and ant diversity is lower. Access to small-seeded grasses may be a critical factor that enables the TFA to move into disturbed grasslands. However, undisturbed grasslands are afforded protection from invasion when dominant grasses possess large seeds. Furthermore, our results suggest that grassland-living TFA learn to accept the smaller-seeded grasses and ignore the larger seeded grasses even when seed size is reduced (Fig. 2.3) unlike village-living TFA, which were presumably naïve to seed resources prior to our assays. Dietary specialization is fairly well-studied in other groups, particularly birds and fish. Our understanding of diet in invasive ant species is still superficial despite the economic and environmental consequences of these invasions (Gutrich, 2007; Holway, 2002). Clearly, diet plays an important role in colony maintenance and survival. Larval diets are important in determining caste (Amor et al., 2016; Wills et al., 2018). Access to palatable foods determines the potential range of a species. At least in the Komodo region, simply leaving large areas of grassland undisturbed may be sufficient to prevent the TFA from moving into habitats used by the charismatic ground-nesting fauna that, in many ways, define the region.

2.5 Acknowledgements

Funding for this project was provided, in part, by Fulbright. We would like to acknowledge Todd Dawson and the Stable Isotope Center at the University of California Berkeley for their assistance and advice. We would also like to acknowledge the hard work of our field technicians, Servas and Incen whose knowledge of Labuan Bajo, Indonesia and the outlying islands was invaluable.

2.6 Figures

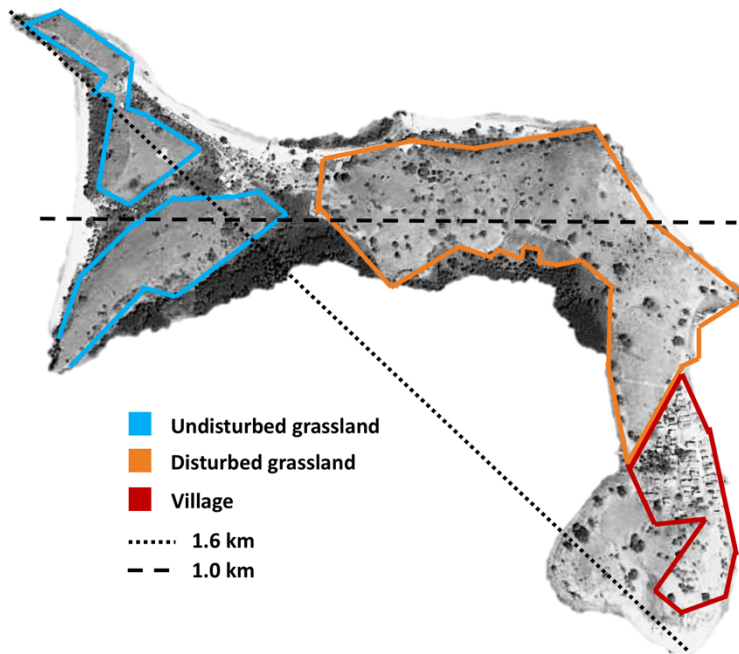


Fig. 2.1. Map of Seraya Kecil with major study habitat types delineated. Source: Google Earth.

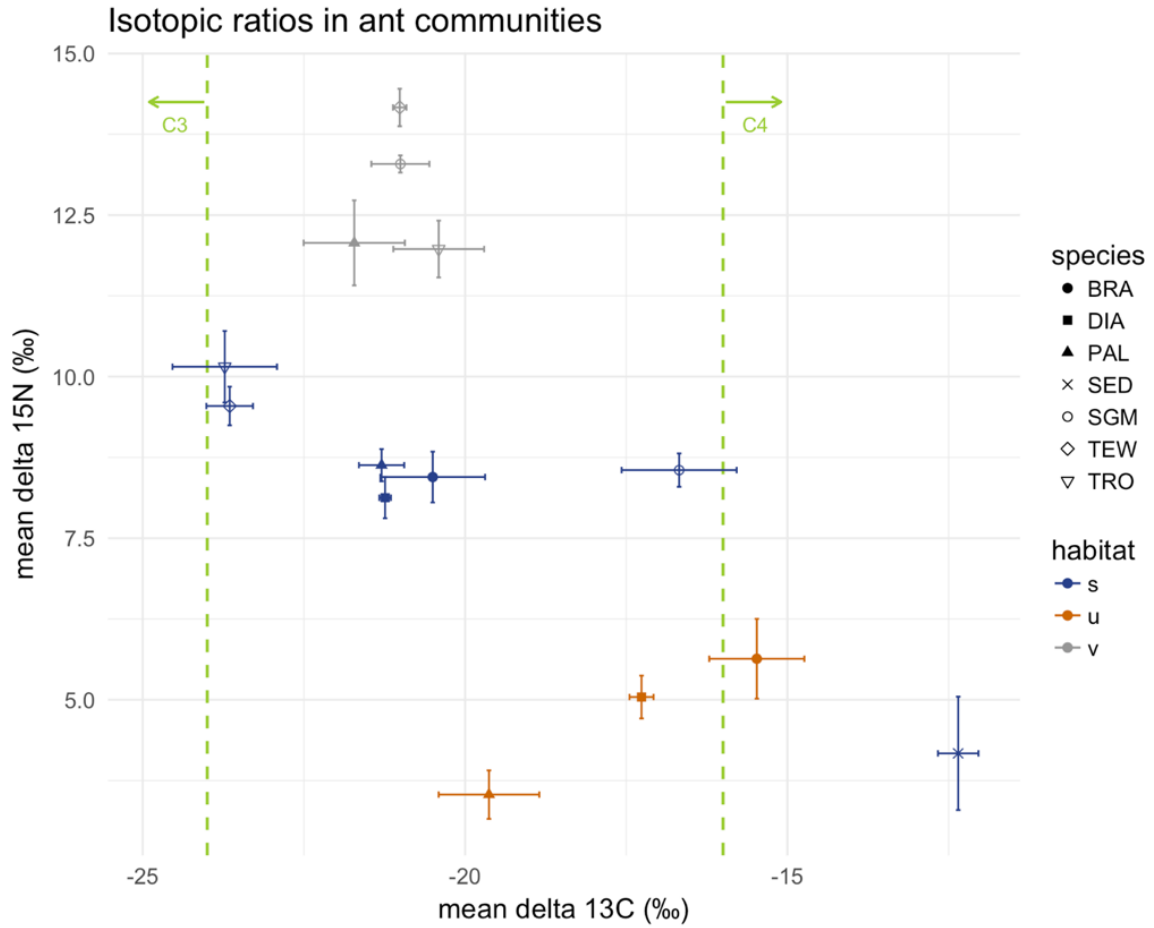


Fig. 2.2. Biplot of mean delta 15N and mean delta 13C across habitats and species. BRA = *Brachyponera sp.*, DIA = *Diacamma sp.*, PAL = *Paratrechina longicornis*, SED = grass seeds, SGM = *Solenopsis geminata*, TEW = *Tetramorium walshi*, TRO = *Trichomyrmex destructor*; s = disturbed savanna, u = undisturbed savanna, v = village.

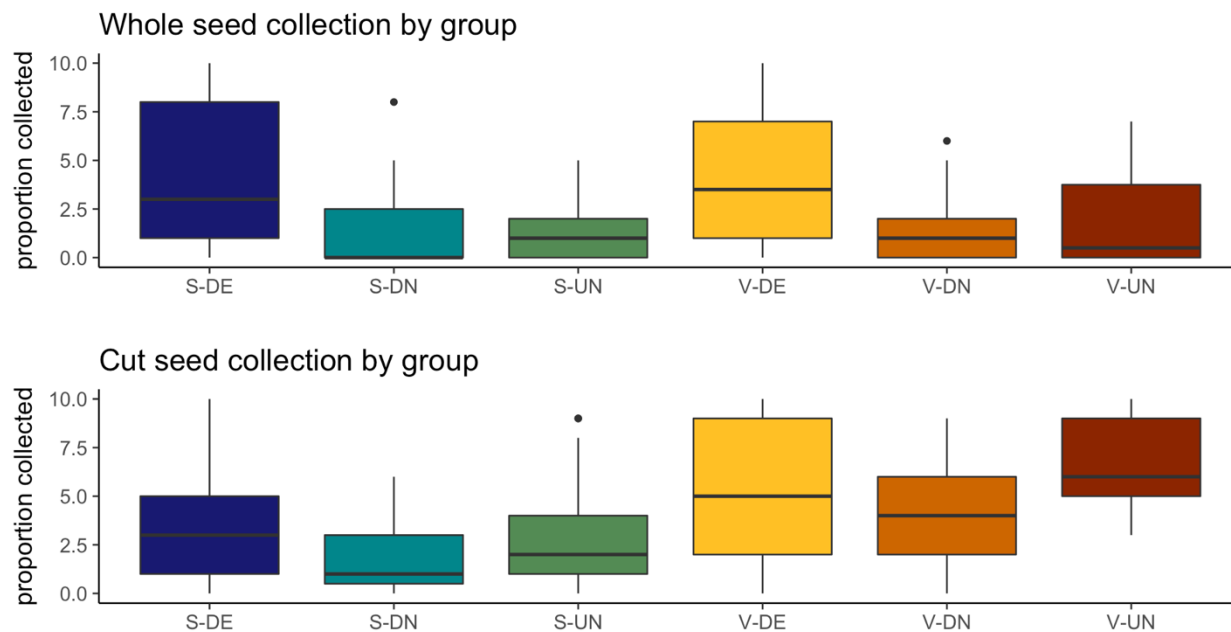


Fig 2.3. Boxplot of seed collection by species in treatment and control groups. S = disturbed grassland; V = village; DE = disturbed grassland, exotic species; DN = disturbed grassland, native species; UN = undisturbed grassland, native species.

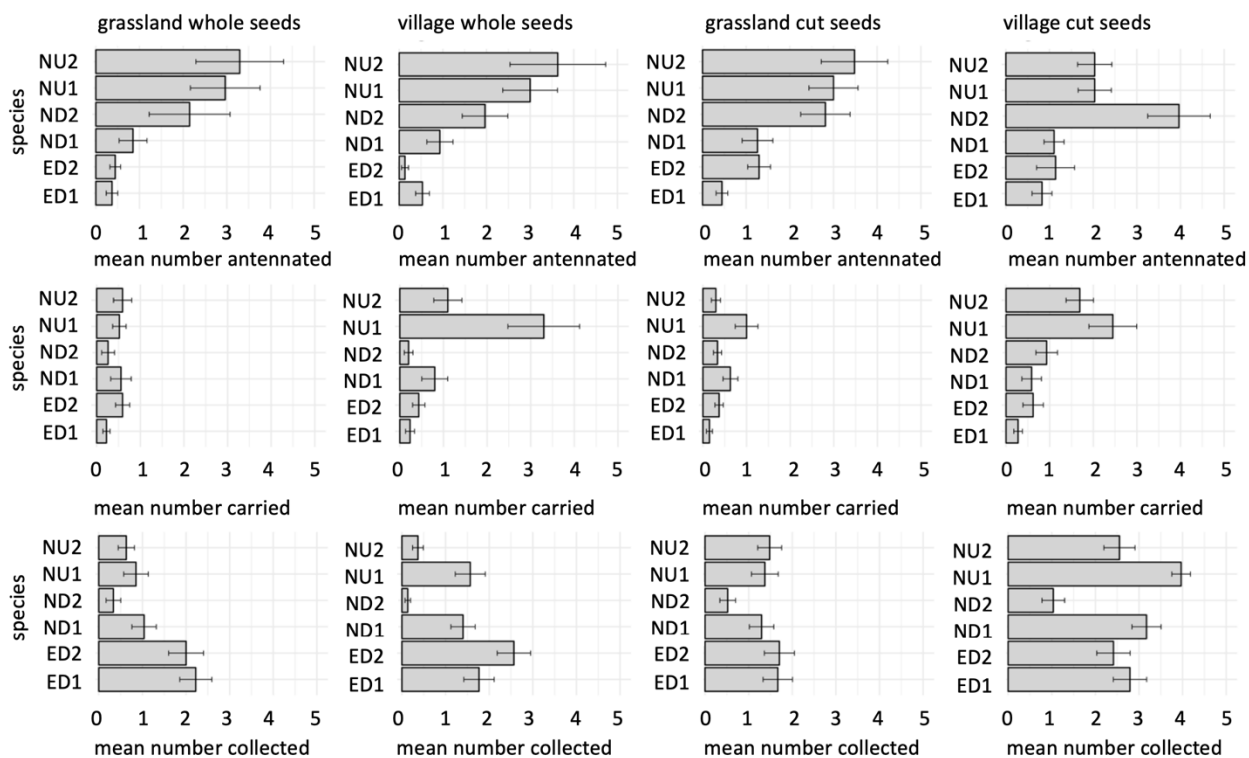


Fig. 2.4. Bar-plot showing number of ant-seed interactions by seed species in village and disturbed grassland (savanna) habitats. NU2 = *Heteropogon contortus*, NU1 = *Chrysopogon*

subtilis, ND2 = *Agrostis infirma*, ND1 = *Brachiaria reptans*, ED2 = *Dactyloctenium aegyptium*, ED1 = *Panicum delicatulum*.

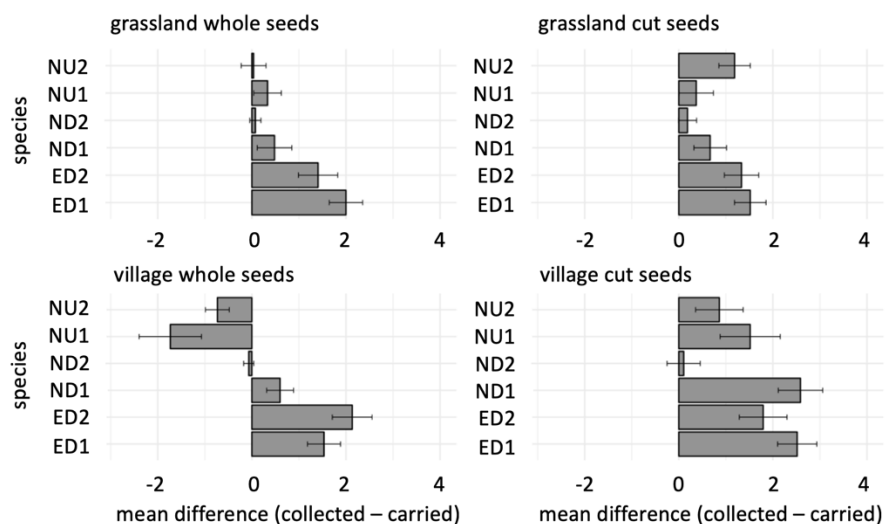


Fig. 2.5. Bar-plot of differences in collection relative to carrying behaviors in whole seed and seed-standardized (cut) treatments. Differences were calculated for each sample as difference = collected-carried and means are plotted with 95% confidence interval, error bars.

2.7 Tables

Code	Species	Status	Whole (mm)	Cut (mm)	% of samples	
					U	D
DE1	<i>Dactyloctenium aegyptium</i>	Exotic	0.8	NA	0	20
DE2	<i>Panicum delicatulum</i>	Exotic	1.39	NA	0	16
DN1	<i>Brachiaria reptans</i>	Native	1.56	NA	0	8
DN2	<i>Agrostis infirma</i>	Native	2.95	NA	0	8
UN1	<i>Chrysopogon subtilis</i>	Native	5.63	2.32	88	72
UN2	<i>Heteropogon contortus</i>	Native	7.3	2.43	36	20

Table 2.1. Whole (control) and cut (treatment) seed size in each selected grass species. DE = disturbed grassland, exotic grass; DN = disturbed grassland, native grass; UN = undisturbed grassland, native grass.

Chapter 3 The foraging behavior and competitive interactions of Indonesian grassland ants

3.1 Introduction

Ants are found in every ecosystem on Earth outside of frozen polar regions. An estimated 25,000 species are thought to currently exist with approximately 14,000 described in literature. They provide a wide range of ecological functions and can have profound influence on both floral and faunal communities (Walsh et al., 2016). Ants may be seed dispersers (Carney et al., 2003; Escobar-ramirez et al., 2011), seed predators (Retana et al., 2004), predators of other arthropods (Hölldobler and Wilson, 1990), predators or partners of plant pests (Way and Heong, 2009), and ecosystem engineers, moving massive amounts of soil (Hölldobler and Wilson, 1990) and altering vegetation (Carlson and Whitford, 1991; Holbrook et al., 2015). Ants are well-represented among the world's 100 most invasive species (GISD, 2018). While native ants play critical roles in maintaining ecosystem health, invasive ants cause significant ecological damage by reducing populations of native species (Holway et al., 2002) and preying upon nesting species (Crossland, 2003; Plentovich et al., 2009). Habitat destruction and species invasion are the leading causes of declining ecological health (Vitousek, 1997). Shifting land uses toward increasingly intensive human activity cause disturbances to the physical environment which favor invasive species (Holway et al., 2002; MacDougall and Turkington, 2005). Much of the success of invasive ant species can be attributed to human-mediated dispersal (Holway et al., 2001; McGlynn, 1999b; Wetterer, 2013) linked to development. Large colony sizes, omnivorous diets, and polygyny (Holway et al., 2002; Palmer, 2004; Tsutsui and Suarez, 2003) are defining characteristics of invasive ants species differentiating them from less abundant ants with more specific dietary and habitat needs. Parts of colonies, 'buds', can be moved great distances during the distribution of agricultural and construction materials (Holway et al., 2002; McGlynn, 1999b). Mitigating the impacts of ant invasion generally involves implementing invasive species eradication programs which have low success rates and can cost billions of dollars (Hoffman et al., 2011; Lee et al., 2015; USDA-ARS 2010). Preventing invasion requires an accurate understanding of local ecosystems, the likely response by native communities faced with invasion, and knowledge of the biology of the invader.

Indonesia lies at the center of a major trade route and centuries of long-distance shipping have brought introduced ant species to many of the 17,000 islands in the archipelago. Island clusters with exposure to trade and development, such as those found across Indonesia, provide opportunities for researchers to look at the behavior of invasive ants in communities with differing species compositions and land use practices. Several species of invasive ants have been introduced to grasslands in southeastern Indonesia. Among them are *Solenopsis geminata*, *Trichomyrmex destructor*, *Paratrechina longicornis*, and *Anoplolepis gracilipes*. These species have widespread distributions and cause significant damage where they are able to proliferate. *Solenopsis geminata*, the tropical fire ant, is known to alter arthropod communities (Porter and Savignano, 1990) and harm or kill the young of ground nesting animals (Crossland, 2003; Plentovich et al., 2009), which are common in the Komodo region and include the endangered Komodo dragon, *Veranus komodoensis*. *Trichomyrmex destructor*, the destroyer ant, damages infrastructure, food products, and other goods while attacking humans (Wetterer 2009). *Paratrechina longicornis* feeds extensively on honeydew producing insects that are often crop

and plant pests (Wetterer et al., 2008). It is capable of high population densities and may reduce or eliminate other arthropod species (Wetterer et al., 1999). *Anoplolepis gracilipes* can have devastating impacts on local communities through aggression, high population densities, and interference competition with other species (Drescher et al., 2010; Lester and Tavite, 2004; O'Dowd et al., 2003; Sarty et al., 2007). Robust native ant populations may impose barriers to establishment of exotic species (Kennedy et al., 2002; Walters and Mackay, 2005). In cases where propagule pressure from invasive ants is low and native species are aggressively competitive, invasion may at least be suppressed (Levine et al., 2004). Dominant and abundant native species present in grasslands may provide resistance to invasive ant proliferation (Henriksson, 2016). Four native ants in the genus *Iridomyrmex* and one native species of *Nylanderia* are common in Indonesian grassland (Sandidge, Chapter 1). *Iridomyrmex* ants are notoriously strong competitors (Walters and Mackay, 2005), dominating ecosystems in their native ranges (Andersen, 1997; Andersen, 2000). Ant in the genus *Nylanderia*, including *N. vaga*, can reach high abundances and cover large areas (Wilson and Taylor, 1967). In some cases, *Nylanderia* may even be a formidable opponent of *Solenopsis* (Horn et al., 2013). Behavior and biotic resistance exhibited by native species most likely influences the impact invasive species can have on an ecosystem. This may, in part, explain the varied results found across studies that look at invasive impacts of a particular species.

Despite detailed studies of ecological collapse (O'Dowd, 2003) and numerous examples of native species decline following invasion (Drescher, 2011; Human and Gordon, 1996; Porter and Sauvignano, 1990; Walker, 2006), the large-scale impacts of invasive ant species is poorly understood. Declining species diversity is a common measure linked to declining ecosystem health but diversity measures may be misleading when associated with invasion. Ant species diversity can be quite high in invaded communities (Forys and Allen, 2005; Sax and Gaines, 2003) with co-dominance by multiple invasive species being common (Lee, 2002; MacDougall and Turkington, 2005; Perfecto and Vandermeer, 2011). Though native ants can survive in invaded habitats (Arnan et al., 2011; Gotelli and Arnett, 2000; Sarty and Lester, 2007), invasive ants can drastically reduce their populations through competitive exclusion (Drescher, 2011; Human and Gordon, 1996; Porter and Sauvignano, 1990; Walker, 2006) shaping the communities in which they occur (Gotelli and Arnett, 2000). A more insightful approach to understanding negative consequences of invasion may be to examine the interactions within invaded communities and to describe the compositional changes and resource allocation. Great importance has been placed on describing competitive interactions as a driving force behind changes in community composition (see review by Tilman, 1982) along with the negative, trickle-down ecological effects resulting from removal of species with important ecological functions (O'Dowd, 2003; Carney et al., 2003; Beggs and Wardle, 2006). Competition includes territorial disputes over nesting space, aggressive contact related to resource acquisition, and superior foraging abilities (Rowles and O'Dowd, 2007). In simplified competition theory, a dominant species should eventually cause the extirpation of the poorer competitor where a limiting resource is shared (Bengtsson, 1989; Capitán et al. 2016). Ecosystems are often complex with multiple resources available and flexibility in invasive reduces the likelihood of resource exhaustion.

Efficiency in acquisition of quality resources from outside the nest is critical to colony growth (Kay et al., 2010; McGlynn, 2006). Asymmetries in foraging behavior allow species to partition resources both spatially and temporally (Lessard et al., 2009) and are likely influenced by a number of factors beyond superiority in physical interactions. Colony size will influence a

competitor's ability to establish a population (Kaspari and Vargo, 1995) and recruit large numbers of individuals (Holway and Case, 2001). Dietary flexibility or specialization offer additional ways to partition available resources (Ehinger et al., 2014; Funk and Bernays, 2001; Marvier, 2004; Nurkse et al., 2009). Environmental factors, such as temperature, cause physiological responses that can alter movement, and thereby affect interaction rates among individuals (Dell et al., 2014) as well as influence the time of day foraging activity will peak (Lee, 2002). Chemical defense compounds can be released into the air and may produce different results depending on interspecific pairings (Chen et al., 2013; Sorrells et al., 2011). Physical traits of each species play an additional role in determining how fast ants can run, how much they can carry, and how well they perform in combat. The 'dominance-discovery tradeoff' is a concept that explains coexistence through asymmetries in species rates of discovering resources and ability to defend them (Bertelsmeier et al., 2015; Perfecto and Vandermeer, 2011). A less-dominant species would still have access to a resource if it could arrive or 'discover' the resource sooner than dominant species. Likewise, slower species could access resources if they are able to displace other species and 'dominate' that resource. Researchers have challenged the simplicity of this concept, arguing that many other factors, as described, determine the success of a species (Parr and Gibb, 2012; Riccardi et al., 2013; Stuble et al., 2017; Tilman, 2004; Yitbarek et al., 2017).

This study is a first effort to describe competition between ant species in Indonesian grasslands. The study area lies within and around Komodo National Park, a World Heritage Site and conservation area. To date, no studies have been conducted to determine the extent of invertebrate invasions, the causes of invasion, or the impacts they may have. Local studies, such as this one, provide detailed information on the behavior and distribution of invasive species in the area. We specifically documented the prevalence of invasive ants in competitive interactions and identified dominant native ants that might resist and suppress invasive competitors. We look for relationships between abundance, distribution, and dominance in ant communities at five sites. We test for temporal differences in foraging behavior over the period of a day and seasonally at three sites. Lastly, we look at arrival, recruitment, and departure to determine if a discovery-dominance tradeoff exists between competitors. Disturbance is taken into consideration as a factor that might influence the presence and abundance of invasive ants. Undisturbed grassland, disturbed grassland, and human-dominated environments (villages and hotels) are represented in our analysis as habitats with low, medium, and high levels of disturbance. Emphasis was placed on competitive inequalities between invasive versus native species. We identify species that may offer biotic resistance as well as identifying the most prevalent and behaviorally dominant invasive species that may pose the greatest threat to conservation efforts.

3.2 Methods

Study sites

The study region encompassed small islands inside or nearby to Komodo National Park, Nusa Tenggara Timur, Indonesia. This group of approximately 100 small islands lies between the larger islands of Sumbawa to the west and Flores to the east. Islands range in size from 325 square kilometers to less than 1 square kilometer. Most islands in the study region are uninhabited and a small number have evidence of settlements and development projects that were abandoned. The region experiences highly seasonal rainfall patterns with a wet season

starting in November and ending around April, and a distinct dry season starting in May and lasting through October. The dominant habitat types are forest and tropical grassland. Our work focused on grassland ant communities. Grasslands consist of a mixture of grasses, less abundant forbs, and sporadically dispersed trees. *Heteropogon contortus* and *Chrysopogon subtilis* are the most common native grass species, representing the majority of vegetation in undisturbed areas. Disturbed grasslands are defined by the presence of introduced grass species. *Brachiaria reptans*, *Dactyloctenium aegyptium*, and *Panicum delicatulum* are common introduced grass species found where habitat has been disturbed through development and grazing.

At the time of this study, permanent villages were located on five islands throughout the entire study region: Komodo, Mesa, Papagarang, Seraya Kecil and Seraya Besar. Resorts were located on the islands of Kenawa, Pungu, Seraya Kecil and Sebayur Besar. Five sites were selected across four islands based on the availability of grassland habitat adjacent to an area of development. Forested areas and development adjacent to forested areas were not included. Villages with adjacent disturbed grassland ($n = 3$) were located at three sites: Komodo, Papagarang, and Seraya Kecil. Disturbed grassland adjacent to undisturbed grassland ($n = 1$) was located at one site on Seraya Kecil. A resort adjacent to undisturbed grassland ($n = 1$) was located on Sebayur Besar. Observations were conducted in October and November 2011, at the end the dry season, and in March and April 2011, at the end of the following wet season.

Sampling methods

At each site, we placed three parallel, 70-meter transects centered on a habitat edge. Transects were laid 20 meters apart (Fig. 3.1). We placed a 1cm³ tuna bait (canned, in water) in the center of a 5cm x 5cm plastic card every 10 meters along each transect. We observed the baits four times during 2 hours sampling periods, at three separate times of day: morning (7am-9am), midday (11am – 1pm), and afternoon (3pm-5pm). Each observation lasted 2 minutes and observations were made at 30-minute intervals. The approximate abundance of ants of each species was recorded during each observation. At the end of each sampling period, we collected the remaining ants for identification. Less common species were collected when possible, but we did not collect ants during the observation period to avoid disrupting recruitment. Morning and evening observations were conducted on the same day and midday observations were conducted either the day before or the day after morning and evening sampling to avoid observing lingering workers from the previous observation period. Species were identified in the entomology laboratory at Ilmu Lembaga Pengetahuan (LIPI), in Cibinong, Indonesia. Dry season data from two sites on Seraya Kecil were excluded from the analysis due to insufficient ant collection which made it impossible to associate positive species identifications with observations. Analyses that include five sites only include wet season data from Seraya Kecil along with data from both seasons at the remaining three sites.

Species abundance and distribution

We predicted that invasive species would be more abundant and widespread than native species. Two analyses were conducted to describe community-wide distribution and abundance patterns and a third tested for differences between native and invasive ant species. First, we calculated relative abundances for each species recorded. We included notably seasonal differences and reported on the distribution of each species across the five sites and three habitat types (Table 3.1). Next, we modeled the relationship between spatial distribution and absolute abundance using linear regression. We identified outliers that may represent numerically and

spatially dominant species and obscure differences based on native or invasive status. A follow-up regression excluded the outlying abundant species to confirm any disproportionate influence on the model fit (Fig. 3.2). Finally, we looked at relative abundances of native and invasive ants across pooled data and within habitat type. Abundance was calculated as the maximum abundance achieved by each species over the four time points (observations) throughout the 2-hour observation period. Maximum abundances were summed for ‘native species’ and for ‘invasive species’ recorded at each bait for each period of day. Maximum values recorded for ‘native’ and ‘invasive’ groups were compared with paired *t*-tests. This analysis was conducted for pooled data and then separately by habitat types (Table 3.2) representing high disturbance (villages and hotels), medium disturbance (grazed grasslands near developments), and low disturbance (undisturbed grasslands dominated by native grass species).

Interaction coding

Competitive interactions were recorded when a bait was occupation of a bait changed, with one or more other species having been recorded during or within one observation point (30 minutes) previous to the arrival of another species. A case where species 1 arrives and departs, leaving an empty bait in the next observation, is not a competitor of a species subsequently arriving to the empty bait. ‘Winning’ a bait was defined by sole occupation of a bait following the presence of an interspecific competitor. Aggression was not measured, nor was chemical attack and the species still occupying the bait was assumed to have caused the departed ‘loser(s)’ to leave. Simultaneous occupations were only recorded as competition when one species departed before the other. Multiple competitions per bait were possible when more than one species departed before the end of the observation period with one or more species remaining after abandonment by multiple ‘losers’. Dummy variables were assigned to each competition outcome as 0 = ‘lost’ and 1 = ‘won’. The number of wins and losses for each genus in a pair provided a numerical measure of success used in statistical analysis and modeling.

Species occupying a bait with no other species present were not considered to be in competitive interactions but were recorded as the species being ‘occupational winners’ in dominance measures (Fig 3.3). ‘Competitive winners’ were winners of competitive interactions as described above. Both of these conditions are considered ‘dominance’ in analyses using measures of frequency of occurrence at baits (Fig. 3.3).

Duration of contests (Fig. 3.6) were recorded as the time two competing species were both present plus 0.5 hours (the time in which the new species would have arrived prior to detection and/or the losing species left before no longer being observed). Duration of stay (DUR) was recorded as sum of 0.5 hours per observation for each species. For example, if a species was seen at 0.5 and 1 hours but not at 1.5 hours, the duration was coded as 1 hour. Estimated time of arrival (ETA) in the previous example, where a species was present during the first observation, would be less than 0.5 hours and entered as ‘0’. Time of departure would be recorded as 1.5 hours, representing departure before the third observation.

Dominance and interspecific competition

Analyses conducted under the niche partitioning hypothesis and dominance-discovery hypothesis required that dominant species were identified prior to hypothesis testing. Individual species were pooled by genus for analyses of dominance in three parts: overall spatial distribution, in frequency of competitive interactions, and in competition outcome. Competitive outcomes between species were then statistically analyzed to acquire a fourth measure of

dominance. For some species, interspecific competition observation numbers were too low to conduct statistical analysis. Species were pooled by genus which enabled us to obtain more meaningful results. Where only one species represented a genus, we used the full species name though we refer to each as ‘genus’ regardless of the number of species included.

‘Dominance’ was described with three measures. ‘Spatial dominance’ was defined as simply the number of baits the species was present at within the entire study area. This measure captured the overall distribution of the species. Not all species were found across all sites. ‘Occupational dominance’ reflected spatial dominance within the realized range of the species which is defined as all the sites that the species was found in. ‘Competitive dominance’ measured the proportion of all competitions that a species was involved in and the proportion of those contests that it won (Fig. 3.3).

Coded competitive outcomes for genus pairs were used to describe competitive relationships between genera and assess the hierarchical complexity of these competition networks. Multiple regression analysis was used to assess the influence of competitor genera on the competition outcome of the focal genus, treated as the response. Multiple regression was selected over logistic regression because it offers associated R-squared values and both test types produced identical results. Analyses were run in the ‘stats’ package in R. Multiple aggression analysis was attempted for all genera that competed at 10 or more baits. Less common genera are represented as competitors for the genera that could be further analyzed. Regression coefficients for competitor genera were interpreted as a likeliness to win (positive) or likeliness to lose (negative) against the focal genus.

When we conducted field work for this study, *Trichomyrmex destructor* was included in the genus *Monomorium* (*Monomorium destructor*). In several instances, a fairly uncommon species, *Monomorium salomonis*, was collected at baits with *T. destructor* and the two could not be distinguished in written observations. Considering this difficulty due to phenotypic similarity and their previous taxonomic relatedness, we combined observations of these two species and call this the ‘TM complex’ which is treated as a genus.

Temporal niche partitioning

We hypothesized that common and widespread species would forage at different times of day, as a strategy for avoiding direct competition. Separate analyses were conducted for wet season and dry season data to describe seasonal differences along with daily differences in foraging activity. We selected three invasive species and two native species with wide distribution and high abundance for analysis. *Iridomyrmex sp. 2*, *P. longicornis*, and *T. destructor* were found at all sites and *S. geminata* and *T. walshi* were very abundant and fairly widespread. Data were pooled from 3 sites, Komodo, Papagarang, and Sebayur. Seraya was excluded from analysis because only wet season data were available for the two sites on the island and seasonality was a component of the analysis.

‘Absolute abundance’ (AA) was calculated for each species across seasons (wet and dry) and the three time periods (morning, midday, and evening). AA was calculated as the sum of recorded abundances from individual baits within a season and a time period for a species. The measure was used to highlight fluctuations or stability in the number of individuals present between seasons and throughout the day and to compare one aspect of foraging behavior between species. ‘Proportional abundance’ (PA) was used to report the number of ants of each species within each season and time period relative to the number of ants of all species. The sum of all ants of all species, including those less common and not included in statistical analyses,

was calculated for each season and time period. The number of individuals of each species at every bait was divided by the total number of ants at all baits in that season and time period. This measure allowed us to look at fluctuating abundances of species relative to ant abundance in the entire community. Pairwise Wilcoxon tests were conducted for each species and season in the R package ‘*stats*’ using a Bonferroni correction for multiple tests between morning, midday, and evening.

Dominance-discovery tradeoffs

We assessed the relative influence of variables other than competitor identity on winning or losing a bait. Logistic regression was conducted using the ‘*glm*’ function in the ‘*stats*’ package within the program R. The full model included the variables: island, habitat type, season, period of day, estimated time of arrival, abundance during competition, maximum abundance over the observation period, duration of occupancy, and place in the order of arrival of species along with interaction terms for all variables. The model was reduced by removing insignificant variables one by one, starting with interaction terms, until all remaining variables made significant contributions to the model fit. The final model included abundance during competition, maximum abundance over the observation period, estimated time of arrival, and duration of occupancy. ANOVA was used in combination with a chi-squared test to analyze final model fit and identify variables that contributed most to model improvement.

The impact of recruitment rate on winning baits was determined by building a second logistic regression model (Table 3.4) run with a reduced data set. First, generalized linear models were fit for each bait to obtain slope and intercept values for abundance increase and decrease of each species at each bait observed ($n = 388$). All data for species with positive slopes (recruiting) were retained. Data was pooled across all sites sampled ($n = 221$) and included competitive interactions as well as dominance without competition, ‘occupational dominance’. Slope data were then added to the list of variables and run in full generalized linear model, reduced as previously described, and followed with chi-squared ANOVA. Recruitment rate (slope) was assessed for any relationship to winning/losing a bait over the entire observation period based on p -value, interactions with other variables, and contribution to model improvement. In a final analysis, recruitment rates were compared between species. Slope calculations for each observation for a species were compiled and compared between each species pair using pairwise Wilcoxon sum-rank tests in the program R.

3.3 Results

Species abundance and distribution

Nineteen species were observed across five wet season sites and three dry season sites. Six introduced species, including five invasive ants of global concern, represented 73% of the 82,188 ants recorded throughout the study. The high percentage of introduced species was driven by two particularly abundant species. *Trichomyrmex destructor* made up 35.4 % and *Solenopsis geminata*, 32.4 %, of the total number of ants. *Iridomyrmex sp. 2* was the third most abundant ant species and made up 14.2 % of total abundance. Cosmopolitan species, those found on every island and in every habitat type, included *Iridomyrmex sp. 2*, *Tapinoma sp. 1*, *Paratrechina longicornis*, and *Trichomyrmex destructor* (Table 3.1).

A total of 216 baits was analyzed in seasonal comparisons: 108 in each season. In total, 27,951 ants of 10 species were recorded in dry season observations, with 73.6% of bait locations

being occupied in at least one observation period. *Trichomyrmex destructor* was the dominant species, found at 41.3% of all occupied baits. *Trichomyrmex destructor* accounted for 52.6% of total dry season abundance. *Iridomyrmex sp. 2* was the second most abundant and spatially common species, accounting for 25% of all individuals collected and present at 28.4% of occupied baits. *Solenopsis geminata*, was present at two of three sites sampled in both seasons (Table 3.1), comprised 5.2% of total dry season abundance, and was found at 11.1% of occupied baits.

Total wet season abundance was similar to dry season abundance, with 29,736 ants collected and 75% of baits being occupied. *Trichomyrmex destructor* dominated baits during the wet season, comprising 35.8% of total abundance, and was found at 25.9% of occupied baits. *Solenopsis geminata* was the second most abundant and common wet season species with numbers similar to *T. destructor*. *Solenopsis geminata* accounted for 29.6% of abundance and was present at 24.1% of occupied baits, but was present at fewer sites. *Iridomyrmex sp. 2* comprised 11.8% of wet season abundance and occurred at 17.3% of occupied baits.

The three most dominant species had a strong influence on the relationship between abundance and distribution of species across sites. There was a strong positive correlation between the number of baits a species was observed at (frequency) and the number of individuals observed overall (abundance) (adj. R-squared = 0.728, F = 54.53, DF = 1 and 19, p -value = 5.387e-07) (Fig. 3.2B). This relationship was driven primarily by three high-abundance, high-frequency species, *Iridomyrmex sp. 2*, *S. geminata*, and *T. destructor*. When these species were excluded, the relationship between abundance and distribution was no longer significant (adj. R-squared = 0.132, F = 3.586, DF = 1 and 16, p -value = 0.07649) (Fig. 3.2A).

Six introduced species were recorded across the study. Four introduced species were not more abundant than native species of ants. *Anoplolepis gracilipes* occurred at a single site and made up less than one percent of total abundance. *Paratrechina longicornis* made up less than one percent of total abundance. *Monomorium salomonis* and *Tetramorium simillimum* occurred at two sites and made up 2.7% and less than one percent of total abundance, respectively.

Invasive ant abundance was higher than native ant abundance at baits for all habitats combined, in village environments, and in disturbed grasslands. No difference in invasive versus native ant abundance was found in undisturbed grasslands. Data were Bonferroni corrected and the critical p -value was $p < 0.0125$ with $\alpha = 0.05$ (Table 3.2).

Dominance and Interspecific competition

Across sites, the TM complex was both numerically and spatially dominant (Fig. 3.2, Fig. 3.3A). *Solenopsis geminata* was co-dominant, being most frequent competitor for TM. Within the realized range of each genus, dominance was represented by two measures: ‘occupied baits won’ included baits at which a species was present but had no competitor (Fig. 3.3B) and ‘contested baits won’ included only baits at which a competitor was present and displaced (Fig. 3.3C). TM were the most common ants at occupied baits. Their recorded distribution (realized-range) included all sites. This group was successful in competition, winning 24.3% of all recorded competitions across sites (Fig 3.3B, yellow bar) and 69.4% of competitions it entered (Fig 3.3B, yellow bar divided by green bar). *Solenopsis geminata* were present at 4 of 5 study sites, winning 24.1% of all competitions recorded within its realized-range and 60.6% of those it entered.

Ant genera were often common within their realized ranges, where they may have been fairly successful competitors, but not common across sites and, in these cases, had low regional

dominance (Fig. 3.3A). *Anoplolepis* (represented by the invasive *Anoplolepis gracilipes*) was locally common at two sites, both on the island of Seraya Kecil. *Anoplolepis gracilipes* was an aggressive competitor, entering 66.7% realized-range competitions. The competition win rate for *A. gracilipes* was 20.8% revealing a realized-range success rate (14% of competition baits) similar to the most dominant species, however, this invasive ant was not widespread.

Brachyponera (*Brachyponera sp. 1*) was locally common at one site and present at 35.5% of occupied baits within its realized range. It dominated 25.8% of all occupied baits where it was observed. Despite a relatively high success rate in dominating baits, *Brachyponera sp. 1* rarely had a direct competitor and had a low measured competition win rate being present for 14.8% of realized-range competitions and winning 0% of observed competitions.

Solenopsis geminata, the TM complex, and *Iridomyrmex spp.* (*Iridomyrmex sp. 1* and *Iridomyrmex sp. 2*) were frequent enough competitors to provide statistically significant results when placing them as the focal genera of their respective interspecific competition models (Fig. 3.4). *Solenopsis geminata* was significantly less likely to win in competition with ants in the genus *Iridomyrmex* (Estimate = -1.000e+00, T = -2.195, *p*-value = 0.0395), however the model fit was low (F = 1.406, DF = 6 and 21, *p*-value = 0.2588, adj. R-squared = 0.0827). Ants in the TM complex were significantly worse at competing with *S. geminata* than other species (Estimate = -0.5833, T = -3.397, *p*-value = 0.00164) and the model fit was good (F = 7.905, DF = 8 and 37, *p*-value = 3.871e-06, adj. R-squared = 0.5511). *Paratrechina longicornis* showed evidence of a negative relationship with the TM complex (Estimate = -0.6667, T = -2.812, *p*-value = 0.0157) however model fit was low (F = 1.835, DF = 5 and 12, *p*-value = 0.1803, adj. R-squared = 0.1972). *Anoplolepis gracilipes* (n = 23), *Crematogaster sp. 1* (n = 11), and *Nylanderia vaga* (n = 14) had no significant positive or negative competition outcome relationships with focal genera and models were not a good predictive fit for outcomes.

Temporal niche partitioning

Although fluctuations by period of day and season were found within species, there was no evidence of niche partitioning between invasive species or between any of the most abundant and common species (Fig. 3.5). When fluctuations were found, absolute abundance (AA) tended to be lowest at midday for all species. *Solenopsis geminata* was less abundant at midday than in the evening (*p*-value = 0.0112) or the morning (*p*-value = 0.0253), during the wet season (Fig. 3.3). *Trichomyrmex destructor* had a higher AA in the evening compared to midday (*p* = 0.0048) in the dry season. *Iridomyrmex sp.2* had higher AA in the evening than in the morning (*p* = 0.0139) and at midday (*p* = 0.0033) during the dry season. *Tetramorium walshi* was more abundant in the morning than at midday during the dry season (*p*-value = 0.0367). *Paratrechina longicornis* AA did not differ between periods of day.

When comparing proportional abundances (PA), the proportion of total seasonal abundance of all species by period, *S. geminata* had a lower PA at midday than in the morning (*p*-value = 0.0220) during the wet season. No PA differences between morning, midday, and evening were found for any other species.

Dominance-discovery tradeoffs

Later estimated time of arrival (ETA) and longer duration of stay (DUR) were associated with higher rates of winning in competition for a bait, with DUR being the best predictor of outcome. Abundance at time of competition, and maximum abundance achieved were not

statistically significant, but substantially improved overall model fit. Island, season, period of day, and order of arrival had little impact on model fit.

Duration of stay (DUR) for each species produced the highest number of significant differences between species pairs (Fig. 3.6). Mean DUR for *P. longicornis* was lowest (0.95 hours) and was significantly lower than DUR for *Crematogaster sp. 1* (p -value = 0.0089), *Iridomyrmex sp. 2* (p -value = 0.0084), *T. destructor* (p -value = 0.0012), and *S. geminata* (p = 0.0001). Mean DUR for *Tapinoma sp.* and *T. walshi* were lower than DUR for *S. geminata* (p -value = 0.0463, p -value = 0.0139).

While DUR was indicative of dominance over extended periods of time, arrival and departure times were more useful in highlighting species that may occupy baits earlier and leave when more competitive species arrive. Mean estimated time of arrival (ETA) was lowest for *Nylanderia vaga* (0.61 hours) and highest for *T. destructor* (0.87 hours). *Nylanderia vaga* mean ETA was significantly lower than that of *P. longicornis* (p -value = 0.0271) and *Tapinoma sp.* (p -value = 0.0374). *Solenopsis geminata* ETA was significantly higher than that of *P. longicornis* (p -value = 0.0290). Mean estimated time of departure (ETD) was lowest for *N. vaga* (1.47 hours) and highest for *T. destructor* (1.83 hours). *Paratrechina longicornis* departed significantly earlier than *T. destructor* (p -value = 0.0007) and *S. geminata* (p -value = 0.0215). *Tetramorium walshi* also departed significantly sooner than both *T. destructor* (p -value = 0.0002) and *S. geminata* (p -value = 0.1399), the two co-dominant species (Fig. 3.5).

A generalized linear model using only baits for which slope of recruitment rate could be measured showed no significance for slope (recruitment rate) in influencing the likelihood of winning a competition (Table 3.4). Otherwise, the slope-calculated model, with reduced data points, was very similar to models run using all baits where competition occurred. Pairwise, Wilcoxon rank-sum tests comparing recruitment, measured as slope of abundance increase, were performed for species pairs (Table 3). *Tetramorium walshi* (TEW) was slower to recruit individuals (p -value < 0.0643) than *Anoplolepis gracilipes* (ANG), *Iridomyrmex sp. 2* (IR2), *Monomorium salomonis* (MOS), *N. vaga* (NYV), *S. geminata* (SGM), and *Tapinoma sp.* (TAP). *T. destructor* and *S. geminata* recruited at faster rates than *P. longicornis* with a cutoff of p -value < 0.1 for determining significance.

3.4 Discussion

Grassland ant communities on several small islands in Indonesia were found to have high abundances of two invasive ant species that were able to spatially and behaviorally dominate food resources at baits. *Solenopsis geminata* and *Trichomyrmex destructor* were dominant spatially, distributed widely across sites, numerically (Fig. 3.3B), comprising 67% of total ant abundance, and behaviorally, effectively taking control of baits when other species were present (Fig. 3.3C). *Solenopsis geminata* and *T. destructor*, were co-dominant with one native ant species, *Iridomyrmex sp. 2*. As in other studies (Andersen, 1997; Andersen, 2000; McGlynn, 1999b; Perfecto, 1994; Perfecto and Vandermeer, 2011), dominant species came from the subfamilies Myrmicinae and Dolichoderinae. Populations of four additional invasive species have been established throughout grassland habitats but were present at relatively low abundances. High abundances of the three dominant ant species was related to their representation at a large number of baits (Fig 3.2B), linking dominance to abundance. When dominant ants were removed from the data set, no relationship was found between abundance and distribution. This suggests that non-dominant species not only have smaller colony sizes but

vary in the way they are distributed through space. Dominant invasive ants may diminish populations of native ant species and less common invasive ants, exaggerating the disparity in abundances (Drescher, 2011; Human and Gordon, 1996; Porter and Sauvignano, 1990; Walker, 2006). However, native ant species may also decline when habitat is altered by human activity as a response to habitat destruction rather than pressure from introduced ants (King and Tschinkel, 2006). Mean abundances of invasive species did not fluctuate greatly between undisturbed grassland, disturbed grassland, and villages while native ant abundances were significantly reduced in disturbed habitat types (Table 3.2). Maintenance of abundant native ant populations in undisturbed, but invaded, demonstrate that in the absence of disturbance, native ant species can be as abundant as invasive species. Though some sites had fewer invasive ant species present, all sites were invaded. Eradication of invasive ant species but not native ant species was not possible, however sites located further from development may have lower rates of invasion allowing for a better comparison of native ant species abundance in highly invaded versus mildly invaded grassland.

Our work focused on describing interactions between ants at food resources and behavioral mechanisms that facilitate the coexistence of native and invasive ant species. We hypothesized that dominant ants would forage at different times of the day to avoid competing with one another, a strategy known as ‘temporal niche partitioning’. After determining which ants were dominant in the system we looked for evidence of temporal niche partitioning. An example of temporal partitioning would be a species with high heat tolerance, such as ants in the TM complex, foraging during the hottest parts of the day while competitor species remain in their nests. Ant foraging fluctuated throughout the day but no pattern was evident that would support our hypothesis (Fig. 3.5). Calculations of species abundances and frequency at baits suggested that *S. geminata* was more prevalent in the wet season and that *Iridomyrmex sp. 2* was more prevalent in the dry season. This seasonal shift was not apparent in temporal niche partitioning analyses (Fig. 3.5).

Dominance-discovery tradeoffs were hypothesized to exist with non-dominant species arriving at baits sooner than dominant species that were able to take control of baits. The dominance-discovery tradeoff concept has been popular in describing how foraging asymmetries can lead to species coexistence (Bertelsmeier et al., 2015; Perfecto and Vandermeer, 2011). Quickly discovering a food resource would enable non-dominant ants to access food resources when faced with ubiquitous, aggressive species. Duration of stay and estimated time of arrival were related to likelihood of winning a bait. This is probably, at least in part, an artifact of our study design which defined the winner as a species remaining at the bait after the departure of another species. But interestingly, abundance at time of competition and maximum abundance reached improved the model fit, further supporting the idea that high abundances are related to dominance and that colony structure of species plays an important part in determining how that species acquires food. Still, some evidence supported the dominance-discovery tradeoff hypothesis. *Nylanderia vaga* arrived sooner than some other species and both *S. geminata* and *T. destructor* arrived later than some other species. *Paratrechina longicornis* and *Tetramorium walshi*, two non-dominant species, departed sooner than dominant invasive species but not *Iridomyrmex sp. 2*, the dominant native species. It is notable that these differences did not separate invasive species from native species and non-dominant invasive species, such as *P. longicornis*, behaved similarly to non-dominant native ant species. Though invasive ant species share large colony sizes as a defining trait and high abundance was linked to competitive success, not all invasive species achieved numerical dominance. High abundance

was not related to a higher recruitment rate, leading us to further conclude that the biological trait of large colony sizes is more important in dominating resources than behavioral attributes such as speed or an elevated recruitment rate.

No one species was apparently superior in competing directly at food resources, with the success of each dominant ant being diminished by another (Fig. 3.4). *Iridomyrmex* sp. 2 is a cosmopolitan, native species capable of defending baits against *S. geminata* and occurring at relatively high abundances across the study region. *Trichomyrmex destructor* was able to win control of baits when competing with *S. geminata*. *Paratrechina longicornis* had some success in taking control of baits occupied by *T. destructor*. In addition to biotic resistance, where native species eliminate or suppress invasive species, invasive ants seemed to have some limiting effects on one another. High species diversity is generally thought to deter invasion (Kennedy et al., 2002) and this concept may apply even when diversity is among invasive species.

Invasive ants are of concern for the small island ecosystems in and around Komodo National Park. Many birds and reptiles living in the region are ground nesters, including the endangered Komodo dragon. These species are particularly vulnerable to predation by invasive ants such as *Solenopsis geminata*. Native ant populations appear to be fairly resilient to total exclusion but it is difficult to predict long-term changes in composition and ecosystem function. Explanations for species coexistence have struggled to prove broadly applicable (Chesson, 2000; Schoener, 1976; Tilman, 2004; Yitbarek et al., 2017). We believe that localized studies would be better for assessing threats to areas of conservation concern. Broadly, invasive ant species have serious negative consequences for native habitats. However, some ecosystems are more resilient than others and managing invasions may be enough to protect diversity and ecosystem function avoiding costly eradication programs. By conducting local research, preventative measures can be taken to avoid the expansion of invasive ant populations. Solutions can be developed in ways that prioritize the specific threats presented by invasive ants, identifying which are potentially the most problematic. Native species that offer resistance can be identified and management could focus on maintaining these species.

3.5 Acknowledgements

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3.6 Figures

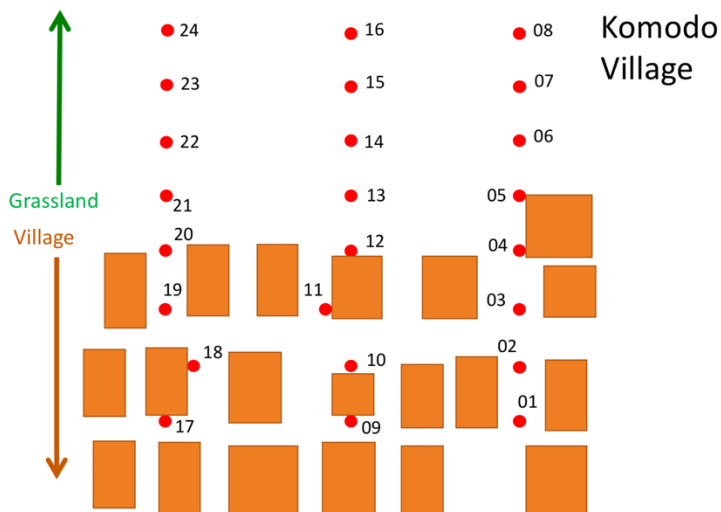


Fig. 3.1. Example bait transect layout across village-grassland boundary. Each site was sampled across a habitat gradient.

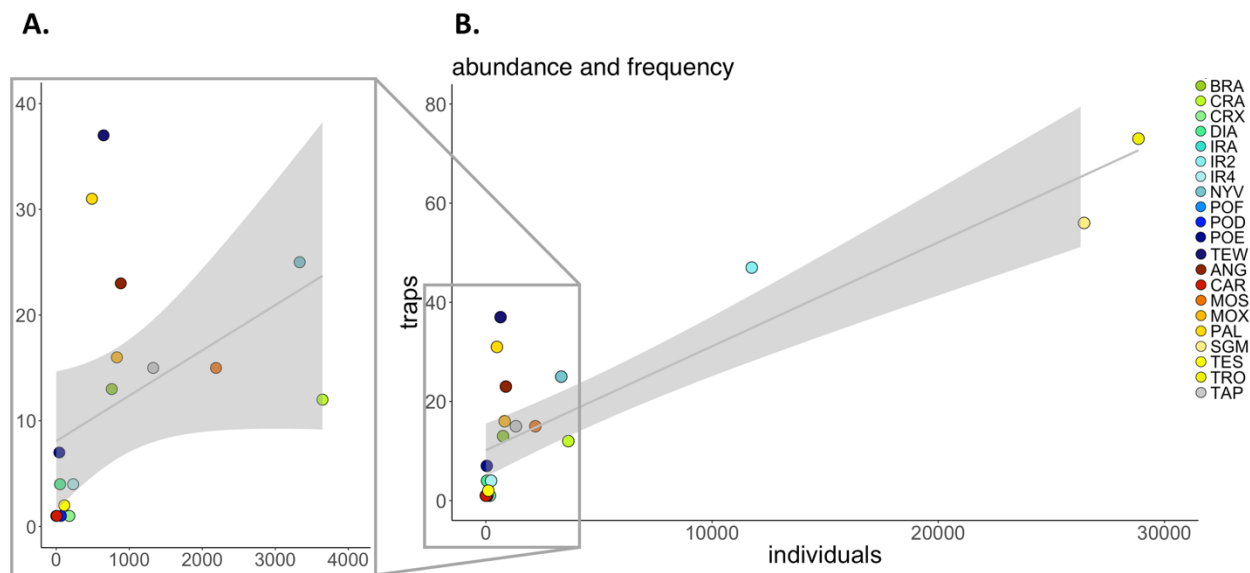


Fig. 3.2. A. Linear regression of abundance (individuals) and frequency (baits) across 5 sites excluding three most abundant species. B. Linear regression for all species recorded across 5 sites. Native species are in shades of green and blue. Introduced species are in shades of red, orange, and yellow. The unknown origin of TAP is represented by gray.

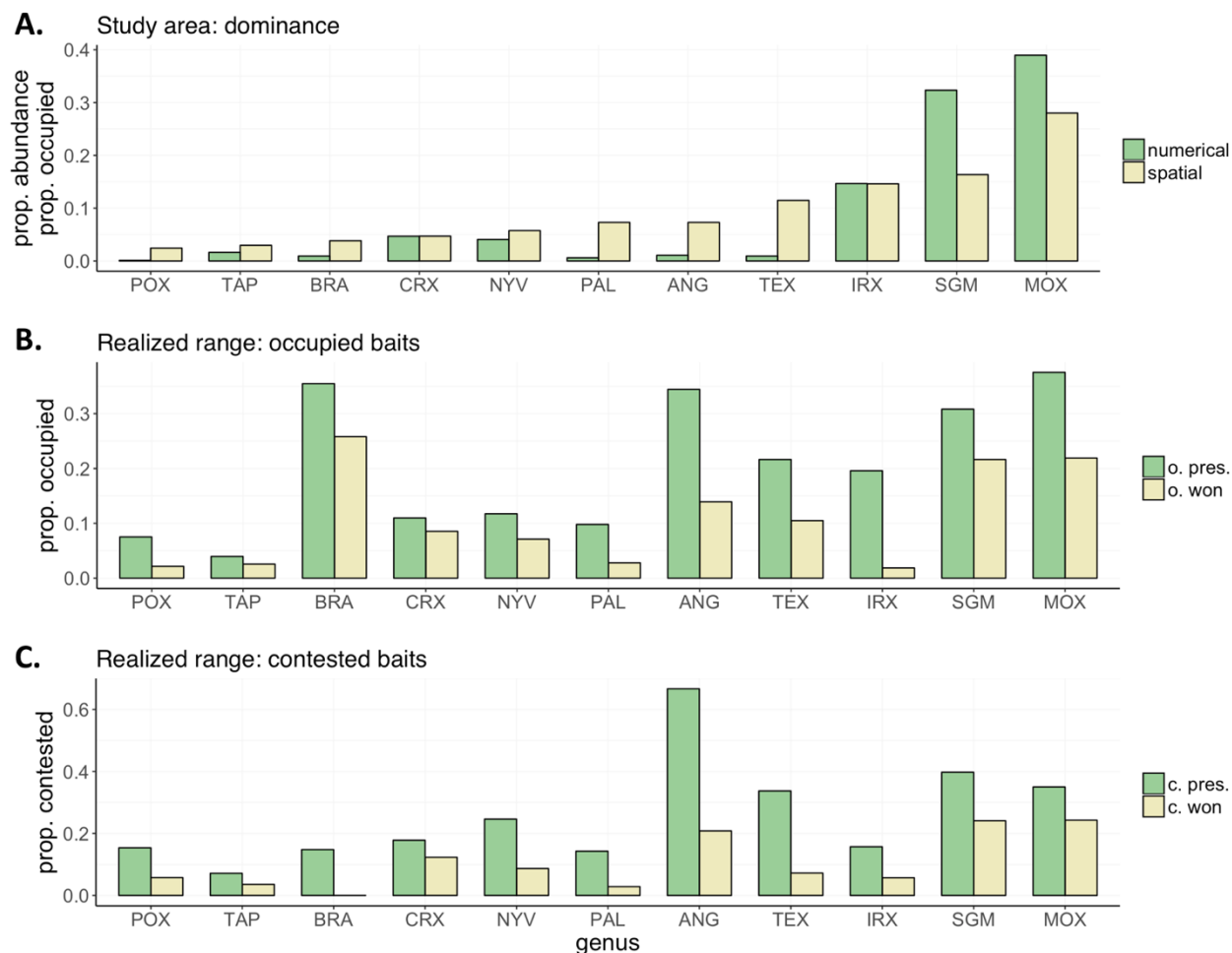


Fig. 3.3. Bar-plots of dominance and bait occupation measures by ant species. A. Numerical dominance = proportional abundance across all sites surveyed, spatial dominance = proportion of baits occupied across all sites surveyed; B. “o. pres.” = proportion of occupied baits at which species was present within the sites at which it was observed, “o. won” = proportion of occupied baits a species occupied last and alone within its realized-range; C. “c. pres.” = proportion of contested baits at which species was present within its realized-range, “c. won” = proportion of contested baits a species occupied last and alone within the sites at which it was observed.

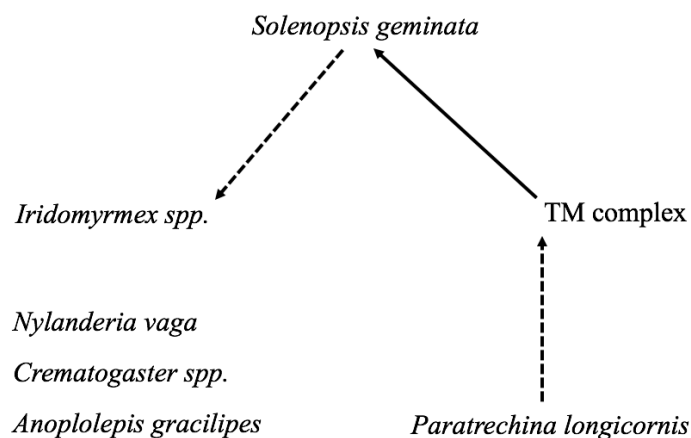


Fig 3.4. Diagram showing competitive success between species. Arrows point to better competitor. Dashed arrows indicate significant coefficient values but poor model fit. Species/genera with no associated arrows did not influence competitive outcomes.

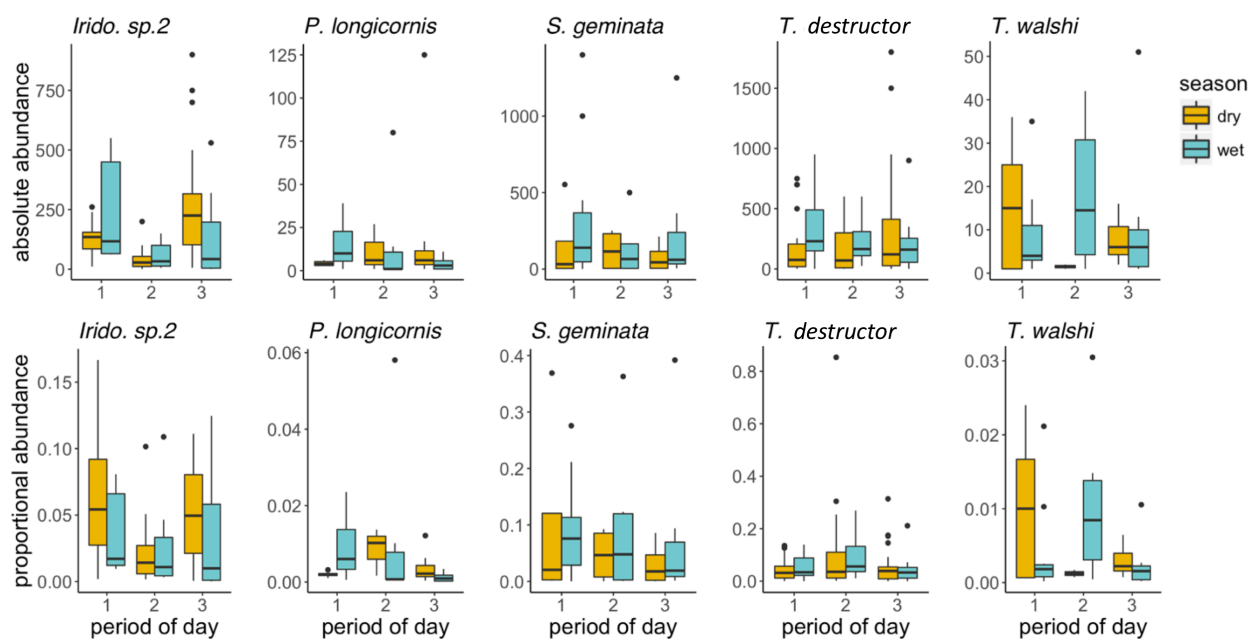


Fig. 3.5. Boxplots representing abundance measures of common ant species found across sites during different period of day. Data is from sites used in seasonal and time period comparisons.

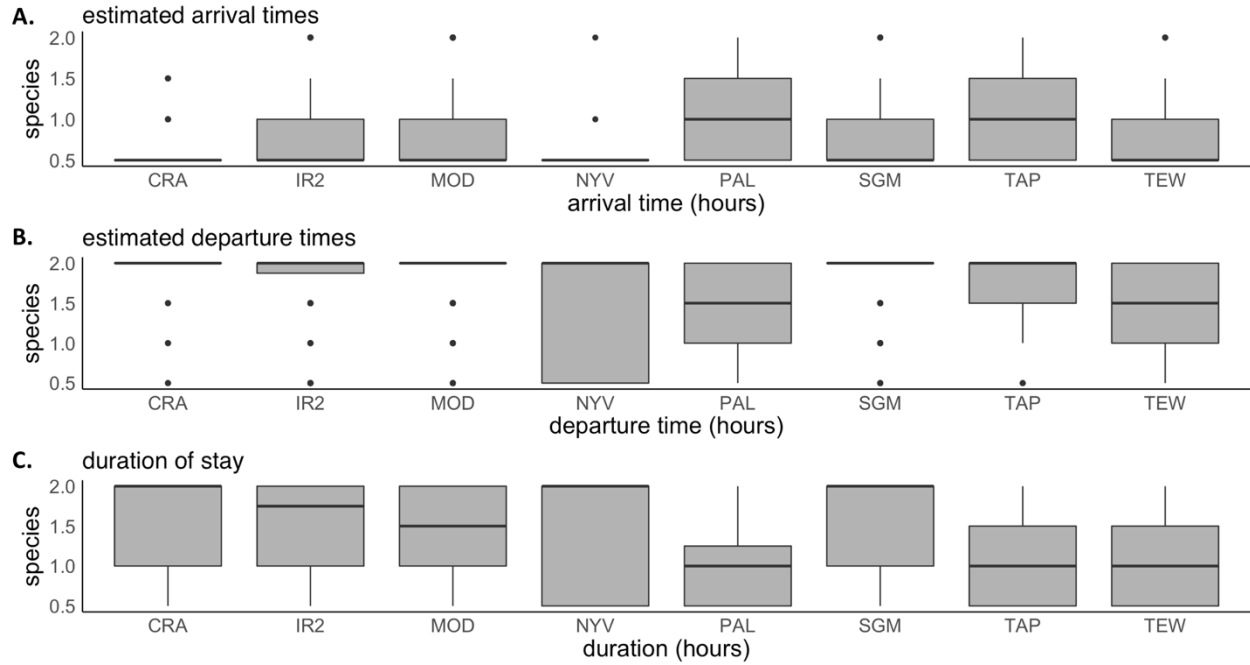


Fig. 3.6. Boxplots of estimated time of arrival, estimated time of departure, and duration of stay for species present at more than 10 baits. Data includes all sites, seasons, and periods of day.

3.7 Tables

Subfamily	Species	St	%	K	P	B	Sh	Sv	Season	U	D	H	V
Dolichoderinae	<i>Iridomyrmex angusticeps</i>	N	< 1				●		W		●		
	<i>Iridomyrmex sp. 1</i>	N	< 1					●	D - W	●			
	<i>Iridomyrmex sp. 2</i>	N	14.2	●	●	●	●	●	W	●	●	●	●
	<i>Tapinoma sp. 1</i>	U	1.6	●	●	●	●	●	D - W	●	●	●	●
Formicinae	<i>Anoplolepis gracilipes</i> *	I	< 1				●	●	W	●	●		●
	<i>Nylanderia vaga</i>	I	4.2	●		●	●		D - W	●	●	●	●
	<i>Paratrechina longicornis</i> *	I	< 1	●	●	●	●		D - W	●	●	●	●
	<i>Polyrhachis dives</i>	N	< 1				●		W	●			
	<i>Polyrhachis sp. 1</i>	N	< 1			●			D - W	●		●	
	<i>Polyrhachis sp. 2</i>	N	< 1			●			D	●			
Myrmicinae	<i>Cardiocondyla kagutsuchi</i>	N	< 1				●		W	●			
	<i>Crematogaster sp. 1</i>	N	4.7			●			D - W	●		●	
	<i>Monomorium salomonis</i> *	I	2.7	●				●	D - W		●		●
	<i>Solenopsis geminata</i> *	I	32.4	●	●		●	●	D - W	●	●		●
	<i>Tetramorium simillimum</i> *	I	< 1	●				●	W				●
	<i>Tetramorium walshi</i>	N	< 1	●	●		●		D - W	●	●		●
	<i>Trichomyrmex destructor</i> *	I	35.4	●	●	●		●	D - W	●	●	●	●
Ponerinae	<i>Brachyponera sp. 1</i>	N	1.1				●		W	●	●		
	<i>Diacamma sp.</i>	N	< 1				●		W	●	●		

Table 3.1. Table of abundance and presence or absence of all species collected on each island and habitat type. St = status as native, introduced, or unknown. % = percent of total abundance. Islands: K = Komodo, P = Papagarang, B = Sebayur, Sh = Seraya Kecil Hotel, Sv = Seraya Kecil Village. Habitat types: U = undisturbed grassland, D = disturbed grassland, H = hotel, V = village. * indicates an introduced and/or invasive species.

habitat type	mean native	mean invasive	p-value
all	112.44	341.7142857	0.00000287
undisturbed	247.7714286	332.7428571	0.25735633
disturbed	69.27868852	455.6721311	0.00002930
village	85.81012658	257.6962025	0.00237858

Table 3.2. Results of paired *t*-tests comparing pooled abundances of native ants versus invasive ants in habitats with differing levels of development and disturbance. Undisturbed grassland, n = 35; disturbed grassland, n = 61; human settlements, n = 79.

Genus	Species	Code
<i>Anoplolepis</i>	<i>Anoplolepis gracilipes</i>	ANG
<i>Brachyponera</i>	<i>Brachyponera sp. 1</i>	BRA
<i>Crematogaster</i>	<i>Crematogaster sp. 1</i>	CRX
<i>Iridomyrmex</i>	<i>Iridomyrmex sp. 1</i>	IRX
	<i>Iridomyrmex sp. 2</i>	IRX
<i>Monomorium</i>	<i>Monomorium salomonis</i>	MOX / TM
<i>Nylanderia</i>	<i>Nylanderia vaga</i>	NYV
<i>Paratrechina</i>	<i>Paratrechina longicornis</i>	PAL
<i>Polyrhachis</i>	<i>Polyrhachis sp. 1</i>	POX
	<i>Polyrhachis sp. 2</i>	POX
<i>Solenopsis</i>	<i>Solenopsis geminata</i>	SGM
<i>Tapinoma</i>	<i>Tapinoma sp. 1</i>	TAP
<i>Tetramorium</i>	<i>Tetramorium simillimum</i>	TEX
	<i>Tetramorium walshi</i>	TEX
<i>Trichomyrmex</i>	<i>Trichomyrmex destructor</i>	MOX / TM

Table 3.3. List of genus and species codes used in figures.

	mean	n=8	n=12		n=9		n=31		n=11		n=6		n=40		n=5		n=14		n=69	
	slope	ANG	BRA	CRA	IR2	MOS	NYV	PAL	SGM	TAP	TEW	TRO								
ANG	9.4																			
BRA	2.8	0.3121																		
CRA	26.6	1.0000	0.7628																	
IR2	19.4	1.0000	0.1053	1.0000																
MOS	19.0	1.0000	0.3675	1.0000	1.0000															
NYV	13.0	1.0000	1.0000	1.0000	1.0000	1.0000														
PAL	3.0	1.0000	1.0000	0.8373	0.5176	0.7676	0.8159													
SGM	25.3	1.0000	0.0058	1.0000	1.0000	1.0000	1.0000	0.0730												
TAP	30.2	1.0000	0.2484	1.0000	1.0000	1.0000	1.0000	0.5176	1.0000											
TEW	1.27	0.0184	1.0000	0.2134	0.0049	0.0127	0.0392	1.0000	1.8e-05	0.0643										
TRO	31.2	1.0000	0.0012	1.0000	1.0000	1.0000	1.0000	0.0700	1.0000	1.0000	1.0000									

Table 3.4. Pairwise Wilcoxon rank-sum tests of mean slope representing recruitment rates to baits. Values are p -values. Bold values are $p < 0.05$, black values are $p < 0.1$, and gray values are insignificant. A Holm correction was applied to all tests.

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