The association of *Lantana camara* with elephant (*Elephas maximus*), their food, habitat use and feeding behaviour in southern India

By

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ABSTRACT

Invasive exotic species pose an enormous threat to the world's biological diversity. Invasions can alter native communities, replacing local biotas with non-indigenous species introduced by humans. Exotic plant invasions can have negative effects on native flora, which can be in turn detrimental to the herbivores that depend on the vegetation. In this dissertation, I examined the association of an exotic invasive weed, *Lantana camara* L., with the Asian elephant (*Elephas maximus*), its food resources (grass and browse), habitat use and feeding behaviour in Mudumalai Tiger Reserve, southern India.

Exotic plant invasions are often associated with alterations or declines in native floral species. I first examined the association of *L. camara* and measured environmental covariates with floral species assemblage and richness, elephant browse plants, percentage grass cover and percentage grass occupancy. A multivariate analysis revealed a significant association of *L. camara* with floral species assemblage and richness, some elephant browse plants and grass cover within the moist deciduous forest (MDF) and dry deciduous forest (DDF), but not in the thorn forest (TF) of Mudumalai. My results suggest that *L. camara* appears to be capable of altering the floral community in some habitats. These results also suggest that changes in the floral community and a reduction in grass cover due to *L. camara* invasion could be detrimental to elephant and other herbivores that depend on grass in this reserve.

I then examined the association of *L. camara* with habitat use by elephant. Elephant dung density was used to assess elephant habitat use from 62 line transects, each 1-km in length. I found no evidence that *L. camara* was associated with elephant habitat use across habitats, although the interaction term between one habitat (DDF) and *L. camara* was significantly associated with elephant dung density suggesting that the effect of *L. camara* was different in different habitats. This indicates that *L. camara* is associated with elephant habitat use within certain habitats. Habitat and impact of human settlements were significantly associated with elephant habitat use across habitats within Mudumalai. In the DDF, however, only *L. camara* was associated with elephant habitat use. I conclude that while no significant effects of *L. camara* were seen across habitats, in specific habitats, negative associations of this invasive plant with

elephant habitat use, possibly through the reduction of grass cover, are possible. These results indicate that *L. camara* appears detrimental to elephant in certain habitats and removal of *L. camara* in these habitats should be prioritised so as to facilitate growth of grass and native browse species, especially if elephant populations continue to expand.

Lastly, I examined the association of elephant behaviour, assessed from feeding and stepping rates, with variation in *L. camara* invasion. Fifty-seven elephants were observed for a total of 64.3 hours using the focal-animal sampling method. Elephant were never observed to feed on *L. camara*, but rather fed on grass and browse that were present within and around *L. camara* patches. Feeding rates (number of trunksful·min^{-1}) were negatively associated with *L. camara* invasion. A path analysis, which assesses both direct and indirect effects of independent variables, indicated that the total effect of *L. camara* on feeding rates was 11% less than the direct negative association owing to a positive indirect relationship between *L. camara* and feeding rates through grass cover and browse density. *Lantana camara* was not significantly associated with variation in stepping rates (number of steps·min^{-1}). Rather, stepping rates were negatively associated with grass cover and positively associated with browse density. My results indicate that *L. camara* is potentially capable of changing elephant feeding rates, likely through a loss of grass areas due to *L. camara* invasion.

Wild elephants do not eat *L. camara*, and this invasive plant appears to take the place of an important food source. My results indicate that managers should prioritize their focus on certain habitats to control the impact of *L. camara* on elephants and vegetation. However, this study was of a correlational nature based on observational data. Experimental work is therefore needed to test for causal relationships among the variables I measured, over multiple seasons and in different habitats. Experimental evidence will enhance our understanding of how invasive weeds modify floral communities, elephant habitat use and behaviour and help determine whether *L. camara* is a ‘passenger’ or ‘driver’ of these changes in this ecosystem.

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Statement of authorship

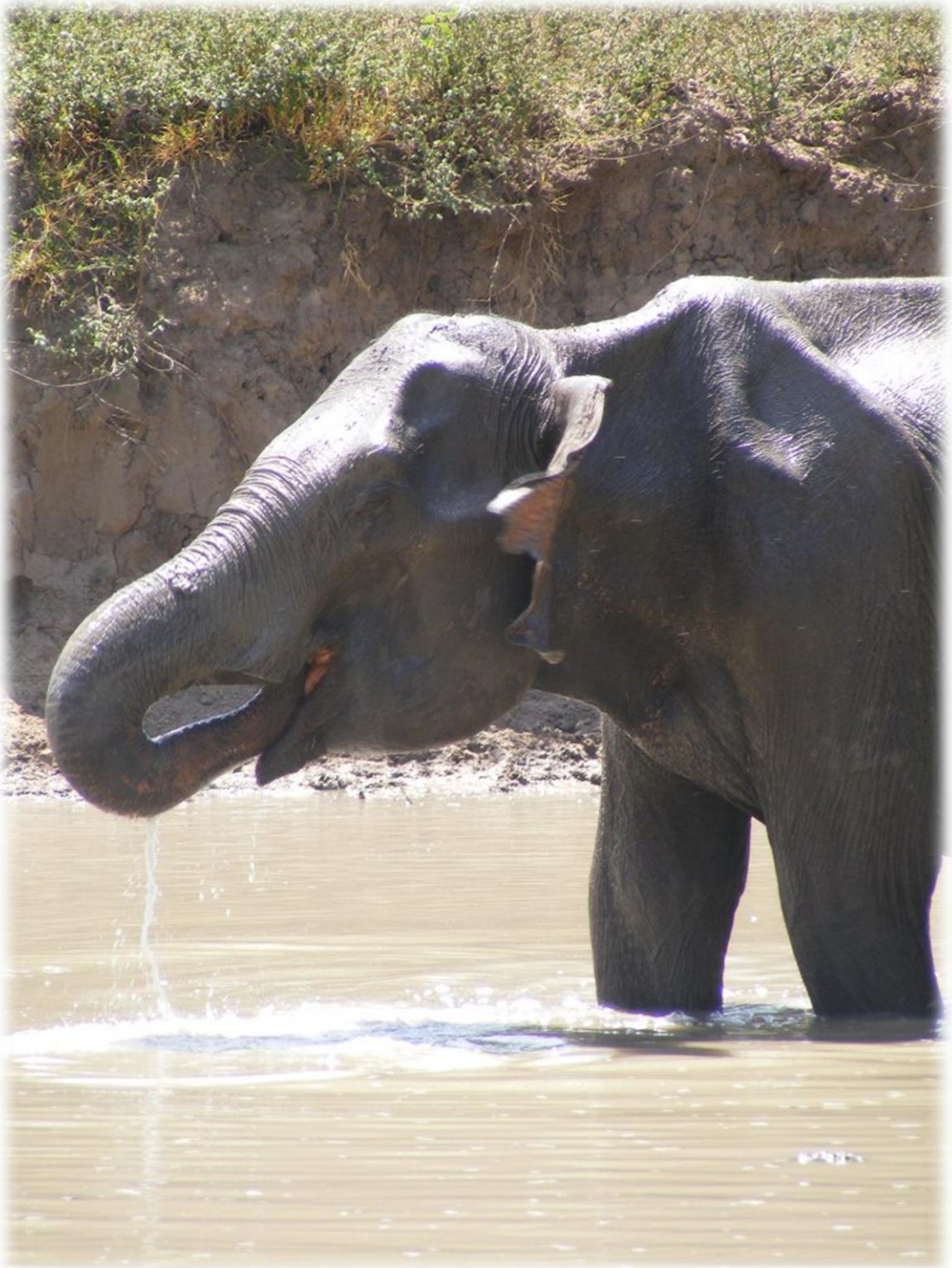
This study was originally designed by me, Gaius Wilson (GW), under the guidance of, and in consultation with Ajay A. Desai (AAD). The study design was then modified by me in consultation with Wayne L. Linklater (WLL) to meet the requirements of a Victoria University of Wellington Ph.D. thesis. Chapters Two, Three and Four presented in this thesis were written with the intention of being published in peer reviewed journals. All manuscripts were written by GW. Initial advice on field work and data collection was provided by AAD. Phil J. Lester (PJL) provided advice on the statistics and writing the manuscripts. Dalice A. Sim (DAS) was the statistician consultant. Contributions of collaborators who are co-authors on the manuscripts are outlined below.

Chapter Two was designed by GW who also formulated the research question, in consultation with PJL and AAD. Data were collected by GW. Statistical advice was provided by PJL and AAD. Statistical analyses were conducted by GW and DAS. GW interpreted the results. PJL, AAD and Monica Gruber (MG) provided comments on the manuscript. The manuscript was written with the intention of submitting it to 'Plant Ecology'.

Chapter Three was designed by GW who also formulated the research question, in consultation with AAD and WLL. Data were collected by GW. Statistical advice was provided by PJL, AAD, MG and R. Nagaraj (RN); a part of the statistical analyses were run by GW and part by DAS. GW interpreted the results. PJL and AAD provided comments on the manuscript. DAS provided initial comments on the statistical methods and results. The manuscript was accepted for publication by the 'Journal of Tropical Ecology' on the 13th of March 2013 and published online on 11th of April 2013. The editor of the journal and two anonymous reviewers also provided feedback on the manuscript.

Chapter Four was designed by GW who also formulated the research question, in consultation with AAD. Data were collected by GW. AAD, PJL and RN provided statistical advice. Statistical analyses were run by GW. GW interpreted the results. PJL, AAD, MG and N. Sivaganesan provided comments on the manuscript. The manuscript was written with the intention of being submitted to 'Biotropica' for publication.

CHAPTER ONE



GENERAL INTRODUCTION

Biological invasions can occur when humans, both deliberately and inadvertently, introduce organisms to new habitats, with detrimental consequences to the biota where they invade (Mack 1996, Vitousek *et al.* 1997). The world's biological diversity faces an enormous threat posed by invasive species, second only to land-use change (Chapin *et al.* 2000). Such invasions can alter native species assemblage and richness and increase biotic homogenization, with replacement of local biotas by non-indigenous species (McKinney & Lockwood 1999). Alterations to a community either through replacement or displacement of local biotas with non-indigenous species can have significant consequences on entire communities (Mgobozi *et al.* 2008, Olson 1999).

The present study was undertaken in order to help understand the relationship between the Asian elephant (*Elephas maximus* Linnaeus) and an alien invasive weed, *Lantana camara* L. (family: Verbenaceae). *Lantana camara* was hypothesized to bring about changes to the floral and faunal community of a forest in southern India through alterations and reduction of forage (grass and browse) and in turn on herbivores that depend on the vegetation (Subramanian *et al.* 2001). I was therefore interested in assessing the association of *L. camara* with food resources of elephant, their use of habitat and feeding behavior. It is critical that we understand how invasive weeds may be associated with elephants, especially in ecosystems where elephants play an important role (Campos-Arceiz & Blake 2011, Fernando & Leimgruber 2011).

1.1 Weed invasion

Weed invasions have been recognized as a serious threat to biodiversity (Greene & Blossey 2012, Higgins *et al.* 1999, Poulette & Arthur 2012). The World Conservation Union described the impacts of alien invasive weeds on biodiversity as "immense, insidious and usually irreversible" (IUCN 2000). Invasive weeds not only compete with native species for water and nutrients, but can also alter ecosystem processes such as decomposition, hydrology and nutrient cycling (Bhatt *et al.* 1994, Ehrenfeld *et al.* 2001, Mack *et al.* 2001, Standish *et al.* 2004). Further, invasive exotic plants can affect the

structure (type and abundance of organisms), function (various processes that occur) and organization (relative abundance of species) of ecological systems (Olson 1999).

The role of disturbances in facilitating the spread of invasive weeds has long been known (Gentle & Duggin 1997b, Masters & Sheley 2001, Myers 1983, Rejmanek 1989). Invasive exotic weeds have an efficient dispersal mechanism and are capable of rapidly establishing themselves (Sharma *et al.* 2005). Disturbances such as herbivory and trampling of native plants by mammals also enhance invasions by exotic plants, many of which are not palatable or are of low palatability to herbivores, and frequently favours the survival of weeds over native plants (Parker *et al.* 2006, Vavra *et al.* 2007). Episodic disturbances like fire also facilitate the establishment and spread of invasive weeds that are likely to change the vegetation composition and structure (Gentle & Duggin 1997b, Hiremath & Sundaram 2005, Morrison *et al.* 1995). Such changes often result in replacement of indigenous species with invasive weeds leading to biotic homogenization (McKinney & Lockwood 1999).

Mammals and birds that feed on invasive weeds may also contribute to the spread of invasive weeds (Parker *et al.* 2006, Swarbrick *et al.* 1995, Vavra *et al.* 2007). For example, seeds that pass through the digestive canal of herbivores may exhibit improved germination and be spread far and wide (Blackshaw & Rode 1991, Campos-Arceiz & Blake 2011, Davis *et al.* 2010, Gill & Beardall 2001, Hogan & Phillips 2011, Jordaan *et al.* 2011, Jothish 2013, Nishida *et al.* 1998, Vavra *et al.* 2007). However, the probability of seeds surviving mouth and gut treatment also varies with seed characters such as seed size, hardness, and protection offered by pulp (Campos-Arceiz & Blake 2011).

Selective grazing and browsing by herbivores on preferred plant species can result in altered floral species composition, dominated by unpalatable and browse-resilient species and reduced species richness and diversity (Augustine & McNaughton 1998). Browsing by herbivores on preferred species of regenerating saplings also reduces the chance of these saplings reaching adulthood (Sivaganesan & Sathyanarayana 1995, Sukumar *et al.* 2004). Thus, herbivores can also contribute to weed invasion, further reducing native food species, thereby increasing pressure on the habitat, particularly when the weed is not eaten or is of low nutritional value (Davis *et al.* 2010, Reinhart *et al.* 2001, Vavra *et al.* 2007).

Some invasive weeds may be palatable or a source of nutrition to some animals (Day *et al.* 2003, Kerley *et al.* 2010, Reinhart *et al.* 2001). Other invasive weeds such as leafy spurge (*Euphorbia esula* L.) have been known to deter cattle from weed-infested sites in Montana and North Dakota (Hein & Miller 1992, Lym & Kirby 1987). Furthermore, Reinhart *et al.* (2001) concluded that the carrying capacity and fecundity of Yellowstone's grizzly bear (*Ursus arctos horribilis*) population could decline because of the presence of exotic species, which could also reduce an overall resilience to long term stressors. Thus, understanding how invasive weeds may impact the fauna is vital for managing ecosystems where both invasive weeds and animals are found.

1.2 Biology and impact of *Lantana camara*

The International Union for Conservation of Nature lists *Lantana camara* L. (Figure 1.1), belonging to the Verbenaceae family, in a list of 100 of the world's worst invasive species (Lowe *et al.* 2000). *Lantana camara* was introduced to India from South America at the Indian Botanic Garden, Calcutta as an ornamental plant in 1809 (Thakur *et al.* 1992). It has since spread from the sub-montane Himalayas to Southern India (Aravind *et al.* 2010). *Lantana camara* grows particularly well in unshaded, disturbed habitat and in human created gaps like forest trails in conserved habitat (Sharma *et al.* 2005, Totland *et al.* 2005). Anthropogenic disturbances such as cultivation, road construction, changes in fire regimes and domestic animal activities appear to promote the spread of *L. camara* (Sharma *et al.* 2005).

This widely invasive species can reach heights of up to 5 m and stem girths of up to 40 cm (pers. obs.). In southern India, heavily infested sites have attained densities of up to 91 stems /100 m^2 (Ramaswami & Sukumar 2011), and above-ground biomass of up to 5.46 kg m^{-2} and a mean biomass of 2.09 ± 0.2 kg m^{-2} (Prasad 2012). The stems of *L. camara* are initially four-angled, becoming cylindrical with age, up to 15 cm thick, and can be arching, scrambling or prostrate (Swarbrick *et al.* 1995). The main stem and lateral branches have growing points located from the lowest to the uppermost node (Babu *et al.* 2009).The stems have small, soft, but sharp, recurved prickles (Stock 2005). Profuse coppicing is known to occur at the meristematic zone, found at the transition between the stem and root, when the plant is cut or burnt (Babu *et al.* 2009).

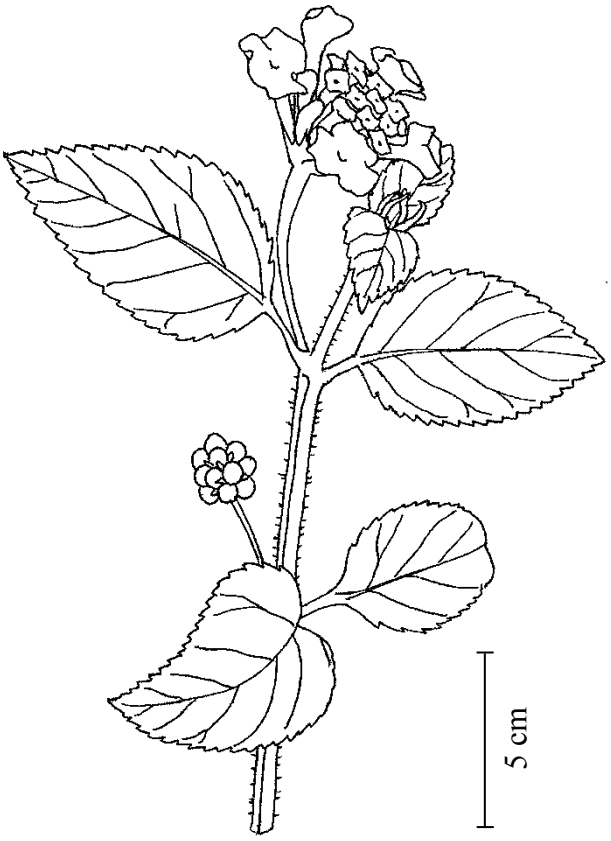


Figure 1.1: Botanical drawing of *Lantana camara* showing the four-angled stem, leaves, fruits and inflorescence (drawing by Louise Askin).

The shallow root system of *L. camara* has a short stout taproot, that tapers gradually, penetrating to 0.2 m (Babu *et al.* 2009). The taproot has many lateral branches that spread horizontally in the top soil and can form a dense root mat (Babu *et al.* 2009, Stock 2005). The taproots of *L. camara* penetrate to 1 m and lateral roots spread up to 5 m in the top 6 cm soil horizon (Love *et al.* 2009), so is comparatively efficient at nutrient uptake and use, and appears highly competitive even in impoverished soils (Bhatt *et al.* 1994).

Lantana camara grows rapidly through vegetative reproduction forming impenetrable thickets (Stock 2005) and flowers all year round producing an enormous number of fruits (10,000 to 12,000 per plant annually) and seeds, primarily dispersed by frugivorus birds and mammals (Day *et al.* 2003, Kohli *et al.* 2006, Swarbrick *et al.* 1995). *Lantana camara* can also spread via a process called layering, where stems take

root at nodes when they come in contact with moist soil, or when covered by fallen leaves or other debris (Day *et al.* 2003, Swarbrick *et al.* 1998).

Inflorescence contains 20-40 sessile flowers, each of which are subtended by a stiff deciduous bract and develop in the axils of young leaves (Swarbrick *et al.* 1995). The leaves are 3-10 cm long and 2-6 cm wide, with finely toothed margins, rough and finely hairy on both surfaces (Swarbrick *et al.* 1995). The leaves of *L. camara* are rich in volatile essential oils, phenolic compounds and triterpenoids such as lantadenes and a number of other phenolic compounds like aesulin, quercetin, isorhamnetin, fisetin, gossypetin, tricin, aesculetin and dicaffeoyl tartaric acid which provide allelopathic properties to further their invasive ability and discourage herbivory (Kohli *et al.* 2006). In addition, *L. camara* can cause fodder scarcity by replacing native grasses (Kohli *et al.* 2006), and has been known to affect livestock when eaten, causing toxicosis in cattle and red Kangaroo (*Megaleia rufus*) including photosensitization, hepatotoxicity and changes to behaviour (Heemstra *et al.* 1999, Sharma *et al.* 1988, Sharma *et al.* 1981, Tokarnia *et al.* 1999).

Lantana camara has invaded India's tropical dry forests and appears to be associated with a reduction in native vegetation, which is food species for herbivores (Fensham *et al.* 1994, Sharma & Raghubanshi 2006, Sharma & Raghubanshi 2007). *Lantana camara*-invaded sites generally have lower species richness and diversity, and the plant is thought to impede the growth of grass and native seedlings in India and elsewhere (Fensham *et al.* 1994, Gooden *et al.* 2009a, Sharma & Raghubanshi 2007, Stocker & Mott 1981). Changes to the vegetation community may affect herbivores such as elephant that are dependent on native grass and browse (Baskaran *et al.* 2011a, Prasad 2012).

1.3 Asian elephant ecology

The Asian elephant (*Elephas maximus*) is listed as endangered in the International Union for Conservation of Nature (IUCN) 'Red List' (IUCN 2012) and 'Appendix I' under the Convention on International Trade in Endangered Species of wild flora and fauna (CITES; UNEP-WCMC 2013). The Indian Wildlife Protection Act (1972) categorizes it as a 'Schedule I' species. This categorization prohibits it from being

traded internationally for commercial purposes. Elephants are large, charismatic species that are recognised as *ecosystem engineers* (Jones *et al.* 1994) exerting great impact on the ecosystem (Sivaganesan 1991, Sivasubramaniyan & Sivaganesan 1996). They can also be considered an *umbrella species* requiring large tracts of habitat such that saving them will invariably save many other species (Simberloff 1998). India is home to approximately 26,000 to 28,000 Asian elephant which accounts for nearly 60% of the entire Asian elephant population (Baskaran *et al.* 2011c).

Elephants are social animals living in well-structured herds with a mother-offspring forming the basic unit, while two or three such units led by the oldest female known as the matriarch form a family of related individuals (Baskaran *et al.* 1995, Desai & Johnsingh 1995b, Vidya & Sukumar 2005). A herd generally consists of about 6 to 10 individuals whose numbers vary according to the availability of resources (Daniel *et al.* 2008, Sukumar 2003). Cows can produce their first calf between 9 and 10 years of age (Owen-Smith 1988). Female siblings tend to stay with their natal group for life while males leave when they reach puberty at between 13 to 15 years, and only join herds to mate with oestrous females (Sukumar 2003). Musth in bulls commences around 15 years with an increase in the testosterone levels in their blood, accompanied by a continuous dribbling of urine (Desai 1995a, Jainudeen *et al.* 1972a, McKay 1973). During musth, elephants feed less and become extremely aggressive, actively seeking receptive females (Desai 1995a, Jainudeen *et al.* 1972b). The temporal region of the head begins to swell up just before musth and musth fluid is continuously secreted from the temporal opening (Desai 1995a, Jainudeen *et al.* 1972a, Jainudeen *et al.* 1972b).

Elephants are relatively unspecialized in their ecology spending between 60-85% of their day time foraging (Baskaran *et al.* 2010a, Sivaganesan & Johnsingh 1995, Vanculenberg 1977). Elephants feed on grass and browse depending on availability and season (Baskaran *et al.* 2010a, Sivaganesan 1991, Steinheim *et al.* 2005, Sukumar 1989a). In some areas elephant are largely grazers (for example, see Baskaran *et al.* 2010a, Sivaganesan & Johnsingh 1995), while in other areas, elephants depend less on grass and more on browse (Campos-Arceiz *et al.* 2008, Chen *et al.* 2006, Himmelsbach *et al.* 2006), leading to different proportions of grass and browse in an elephant's diet. Several studies have documented a shift in diet from grass to more browse in the dry seasons (Steinheim *et al.* 2005, Sukumar 1990). This strategy has appeared to allow

them to become extreme habitat generalists and has allowed them to occupy various habitat types available within their range.

Depending on the habitat and plant availability, an elephant can consume over one hundred species of plants (Chen *et al.* 2006, McKay 1973, Sukumar 1990). Despite the wide variety of food species eaten, elephants consume larger quantities of certain food species (Sukumar 1990). For example, one estimate of the percentage of grass in elephant diet in Southern India was 85%, of which one species of grass, *Themeda triandra*, formed nearly 40% of the overall grass consumed (Baskaran *et al.* 2010a). Seasonal changes in nutrient status of various grass species (Sivaganesan 1991) and also between plant parts resulted in elephant selecting species and parts optimally (Baskaran 1998, Sivaganesan 1991). The shift between grass and browse has also been attributed to an increase in silica and fibre content as grass matures, making grass less palatable as it grows (Sukumar 1989a). Sukumar (1990) determined that browse leaves had relatively high crude protein and ether extract or fat content even in the dry season in south India, thus elephant altered their food habit to correspond with nutrient availability to supplement their protein intake. Furthermore, browse leaves had less silica when compared to grass and were rich in other minerals that may have added to the palatability (Field 1971, Sukumar 1990). While fresh grass has 8-10% protein dry weight in the wet season this falls to below 2.5% protein in the dry season which cause elephant to switch their diets to browse to maintain over 8 % protein in the dry season (Sukumar 1989a).

The very large body size of the elephant designates it as a megaherbivore (>1000kg) (Owen-Smith 1988). The adult Asian bull elephant weighs between 3500-6000 kg and stands at a shoulder height of about 2.75 metres, while adult females weigh between 2000-3500 kg (Sukumar 2006). Elephants have fast ingesta passage rates, and mean retention times are positively correlated with body weight (Clauss *et al.* 2003). Elephants use hind gut fermentation which is not as efficient as fore gut fermentation (i.e. only 40-50% digestive efficiency) and require large quantities of food to be processed to meet their energy needs (Clauss *et al.* 2003, Dumonceaux 2006). Poor digestive efficiency means large quantities of food are needed and this imposes certain limitations also. For example, elephants cannot feed on plant parts that are well defended with plant chemicals that act as digestion inhibitors (Sukumar 1989a).

Compared to some browse species, grasses have lower levels of chemical defences against mammals (Bryant *et al.* 1991) and hence may be preferred. So despite, and within the coarse bulk feeding strategy, elephants show selection for better food (Sivaganesan & Johnsingh 1995, Sukumar 1990).

It has been suggested for large mammals such as elephants, where natural regulation of the population through predation is uncommon, that food can be a limiting factor (Owen-Smith 1988, Sinclair 1975, Sukumar 1989a). There are numerous examples of food being a limiting factor to the African elephant (*Loxodonta africana*). For example, the large-scale elephant mortality during the 1970-71 drought in Tsavo National Park in Kenya was thought to have been a result of malnutrition (Corfield 1973). Furthermore, circumstantial evidence suggested that food was the primary proximal factor that governed movements and distribution of elephants in Tsavo (Leuthold & Sale 1973). Recent studies on the Bornean elephant (*Elephas maximus borneensis*) have shown that these elephant moved out of habitats at higher rates where food was limiting or there were no suitable plants for foraging (Alfred *et al.* 2012). In India, a decline in the elephant population at Corbett National Park was also attributed to fodder scarcity, among other factors, brought about by developmental activities (Joshi *et al.* 2009). Ranging studies in Sri Lanka have shown that while elephants exhibit high fidelity to their home ranges, there is an overlap of core areas of home ranges also used by females from other groups (Fernando *et al.* 2008). These overlapping core areas were thought to represent highly productive and important feeding areas. Nevertheless, exploitation of food resources that is dispersed necessitates an investment in time and locomotion and therefore represents a limiting resource for elephants (Fernando *et al.* 2008) that spend up to 17 hours a day feeding on low quality food. Thus, food appears to be a limiting source for elephants that govern their movement and ranging patterns.

Habitat use by elephant is thought to be influenced by several factors including season and home ranges (Baskaran 1998, Sukumar 1989b), forage and water availability (Feng *et al.* 2010, Pradhan *et al.* 2007, Sivaganesan 1991, Steinheim *et al.* 2005) and habitat characters such as slope, availability of shade and salt licks (Baskaran 1998, Baskaran *et al.* 2010a, McKay 1973, Sivaganesan 1991). Anthropogenic disturbance from settlements and roads, cattle grazing, fuel wood collection and fire also influence

habitat use because elephants avoid people and disturbed habitats (Baskaran *et al.* 2011a, Desai & Baskaran 1996, Silori & Mishra 2001).

Further, habitat use and selection may also depend on the size and composition of the group. Males and females do not use habitat and their homes ranges randomly, but exhibit distinct habitat selection (Baskaran 1998). According to the 'predation risk hypothesis', larger males are less susceptible to predation, when compared to females and their offspring, and are more likely to select habitats on the basis of foraging opportunities (Ruckstuhl & Neuhaus 2000). Elephants may tolerate poor quality food and gain nutrition from quantity instead of quality, unlike most other mammals (Dumonceaux 2006, Owen-Smith 1988). However, during the dry season, elephants may largely occupy habitat near permanent water (Alfred *et al.* 2012, Sukumar 1989b) where forage and water are proximal (Baskaran 1998, Santiapillai *et al.* 1984, Sukumar 1989a). Thus, a number of factors govern habitat use by elephant.

1.4 Study area

Mudumalai Tiger Reserve (hereafter Mudumalai) and its surrounding reserves are part of the 5,500-km^2 Nilgiri Biosphere Reserve (NBR) (Figure 1.2) that forms an important part of the Asian elephants' range in Southern India (Srivastava 2009). With an estimated population of about 9000 elephants and over 10,000-km^2 of contiguous habitat, NBR represents the single largest Asian elephant population in the world (Baskaran *et al.* 2011c, Vidya & Sukumar 2005). The NBR is rich in biodiversity and is home to several endemic species of flora and fauna. The NBR hosts a range of mammals including carnivores such as tiger (*Panthera tigris*), leopard (*Panthera pardus*), dhole (*Cuon alpinus*), hyaena (*Hyaena hyaena*), and herbivores such as sambar (*Cervus unicolor*), spotted deer (*Axis axis*), four-horned antelope (*Tetracerus quadricornis*), blackbuck (*Antelope cervicapra*), barking deer (*Muntiacus muntjak*), bonnet macaque (*Macaca radiata*) and common langur (*Semnopithecus entellus*). In addition sloth bear (*Melursus ursinus*), civets (*Viverricula* spp.), mongoose (*Herpestes* spp.) and black-naped hare (*Lepus nigricollis*) are also found here (Srivastava 2009).

Mudumalai is located at the foot hills of the Nilgiri district in the southern Indian state of Tamil Nadu (11°32' and 11°42'N latitude, 76°20'and 76°45'E longitude)

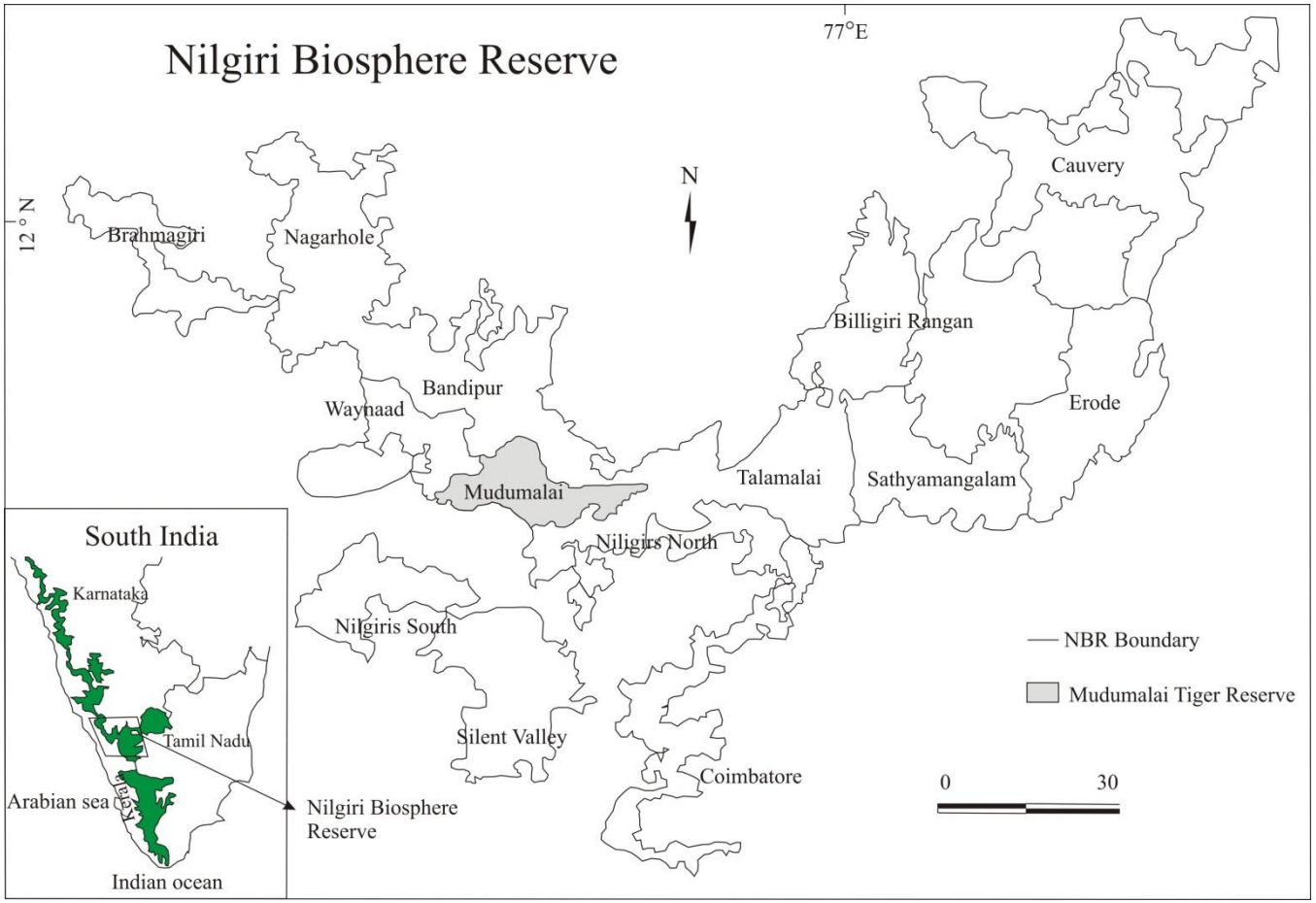


Figure 1.2: Nilgiri Biosphere Reserve and its location in the western ghats (shaded in green in the map of South India with state boundaries) of India and the location of Mudumalai Tiger Reserve (shaded in grey in the map of the Nilgiri Biosphere Reserve). Tiger Reserves include Bandipur and Nagarhole in Karnataka; National Parks/Wildlife Sanctuaries include Silent Valley and Wynaad in Kerala, Brahmagiri, Biligiri Rangan Hill Temple and Cauvery in Karnataka; Reserve Forest Divisions include Nilgiris North and South, Sathyamangalam, Talamalai and Coimbatore in Tamil Nadu.

and covers an area of 321 km^2 and is bounded on the north by Bandipur Tiger Reserve in the state of Karnataka and to the west and northwest by Wynaad Wildlife Sanctuary in the state of Kerala (Srivastava 2009). The general terrain of Mudumalai is gentle and undulating with altitude ranges from 485-m to 1226-m with an average of 900-m asl (Sivaganesan 1991). Minimum and maximum and temperatures vary between 14° – 17° C during December and January and between 29° – 33° C during March to May (Centre for Ecological Sciences, Indian Institute of Science, Bangalore 2010).

The southwest (May-August) and northeast (September-December) monsoons provide most rainfall to the study area. Average yearly rainfall ranges from around 600 to 1800-mm across the eastern to the western regions of the reserve, respectively (Suresh *et al.* 2010). The dry season begins at the end of January with its peak between March and May. The perennial Moyar river flows along the eastern boundary and drains the area. There are several semi-perennial streams that dry up during the dry season. Some of these include Bennehole, Mukkatihole, Doddagattihalla, Doddahalla, Imberhalla, Kekkanhalla, Kalhalla, Hosherihalla, Biderhalla and Avarahalla (Kumar 2011). Permanent water sources in Mudumalai include Game Hutt, Ombatta and Compartment 3 check dam (Baskaran 1998, Daniel *et al.* 2008, Sivaganesan 1991). These are important sources of water during the dry season and large number of elephants and other animals come to these waterholes to drink in the dry season between January and May (Srivastava 2009).

Mudumalai has three major tropical vegetation types: moist deciduous forest (MDF), dry deciduous forest (DDF) and thorn forest (TF) (Champion & Seth 1968). The southern and western regions of the reserve are made up of MDF. In the MDF tall grass species like *Themeda cymbaria*, *Cympopogan flexuous, Apluda mutica* and short grass species like *Themeda triandra, Setaria intermedia* and *Dicanthium carisosum* are present (Kumar *et al.* 2012). The dominant grass species are *Cyrtococcum patens*, *C. oxyphyllum* and *Oryza granulate* (Kumar 2011). The ground layer vegetation includes several species of ground orchids, *Helicteres isora*, *Desmodium* spp. and *Curcuma* spp. (Kumar *et al.* 2012). Tall trees and closed canopy characterise this forest. The common tree species in the MDF include *Tectona grandis, Dalbergia latifolia, Lannea coramandelica, Elaeocarpus tuberculatus* and *Lagerstomia microcarpa***.**

The DDF is the major vegetation of Mudumalai. Trees found in DDF are *Tectona grandis, Grewia tilifolia, Anogeisus latifolia, Terminalia crenulata, T. tomentosa,* and *Kydia calycina* with a semi-open tree canopy (Kumar 2011). *Shorea roxburghii* is seen in the northern part of the reserve. Tall perennial rhizomatous grass species such as *Themeda cymbaria, Cympopogon flexuous* and *Apluda mutica* are dominant in the tall grass areas while *T. triandra* and *Setaria intermedia* are common in the short grass areas of the DDF (Kumar 2011, Sivaganesan 1991).

The TF found on the eastern part of Mudumalai falls in the rain shadow region of Western Ghats. Stunted trees that dominate the region are *Acacia* spp., *Albizia* sp., *Anogeissus latifolia, Ziziphus xylopyrus, Sapindus emarginatus, Phyllanthus emblica, Erythroxylon monogynum, Canthium parviflorum* and *Premna tomentosa*. Grass species include *Aristida adscence, Heteropogon contortus* and *Tragus roxbergii* (Kumar 2011, Sivaganesan 1991).

Mudumalai has a history of selective logging which dates back to the early part of the 19th century. Some patches of *Tectona grandis* plantation still exist. The Tamil Nadu Forest Department has managed captive elephants since 1857, for timber-hauling purposes (Krishnamurthy & Wemmer 1995). However, since 1994 after a ban on timber logging, these captive elephants have been mostly left in the nearby forest for free grazing, except for a few hours in the morning (06:00–08:00) and evening (16:00–18:00), when they provide rides for eco-tourists (Krishnamurthy & Wemmer 1995). At the time of writing the thesis, there were 27 captive elephants (N. Kalaivanan, Forest Veterinary Assistant Surgeon, pers. comm.), some of which are also used by the forest department to drive back into the forest problematic wild elephants which stray into human habitation (pers. obs.). There are two permanent camps in Mudumalai located inside the forested area. The captive elephants are brought to the camps every day (both morning and evening) for bathing, supplementary feed, and veterinarian inspection; they are then left to return to the forest for grazing (Krishnamurthy & Wemmer 1995).

The earliest record of the presence of *L. camara*, in the Nilgiris in southern India was in 1880 (Beddome 1880). However, it was not until 1921 that *L. camara* was recognised as a troublesome weed and eradication of *L. camara* began in 1924 in Benne and Mudumalai blocks of Mudumalai (Troupe 1921). By 1941 *L. camara* was described

as being a problem and spreading rapidly in the DDF and teak plantations of Mudumalai, Benne and Theppakadu (Ranganathan 1941).

Human settlements are concentrated on the southern, eastern and western parts of Mudumalai. A Chettiyar tribal community inhabit the western regions, while mixed communities live in the southern and eastern regions (Silori & Mishra 2001). There are 21 hamlets within Mudumalai that are inhabited by four tribal communities, Kurumbas, Nayakas, Chettys and Paniyas. The Kurumbas and Nakayas are employed by the forest department as elephant-keepers, anti-poaching watchers, fire watchers and forest guards (Sivaganesan 1991). In the past two decades, a large number of holiday resorts have sprung up in the southern and eastern parts of the reserve (Silori & Mishra 2001). A large number of tourists visit the sanctuary each year, with tours for visitors in the mornings and evenings within the designated tourism zone (Srivastava 2009).

1.5 Context of this study

Most of the elephant populations in India are confined to National Parks and protected forest reserves throughout the country. Due to their wide-ranging nature, elephants often come into conflict with humans due to habitat loss and consequent degradation of habitat brought about by human activities (Baskaran *et al.* 2011a, Baskaran *et al.* 1995, Desai & Baskaran 1996). Despite increased protection to threatened and endangered animals in these national parks and forest reserves, limited availability of resources for growing populations of animals is a major concern for forest managers due to habitat loss and degradation (Desai & Baskaran 1996).

Previous studies have indicated an increase in the elephant population in Mudumalai while pressure on the habitat due to anthropogenic activities has also been increasing (Baskaran *et al.* 2010b, Daniel *et al.* 1987). Additionally degradation of habitat through cattle grazing, illegal removal of trees and fuel wood, non-timber forest produce collections and forest fires pose a serious threat to the elephants' habitat (Daniel *et al.* 1987, Silori & Mishra 2001). Fragmentation of habitat due to developmental activities (roads, agriculture, settlements and resorts) is becoming an all too real a threat to the integrity of the existing habitat (Silori & Mishra 1995, 2001). This fragmentation would reduce the existing large tracts of habitat into smaller fragments and also increase

the potential for human-elephant conflict (Sukumar & Easa 2006). With increasing elephant numbers and human impact that promotes weed invasion and affects natural vegetation, there is a reduction of food for elephant and space for regeneration of grass and native vegetation further increasing pressure on the habitat (Baskaran *et al.* 2011a).

Poaching for ivory has been a major threat to the elephants in this area and has led to diminished male numbers resulting in skewed sex ratios heavily in favour of females (Baskaran *et al.* 2010b). In Mudumalai, a male-female ratio of 1:29 was reported (Baskaran & Desai 2000). However even at those highly skewed ratios, reproduction does not appear to have been affected significantly, possibly because elephants are polygamous and females have long inter-calving intervals, ensuring that only a small proportion of the female population is receptive in any given year (Baskaran & Desai 2000). While the male population has been severely depressed by selective poaching, the female population has been increasing as females are not being killed and legal capture of elephants was banned from the early 1970's (Baskaran *et al.* 2010b, Krishnamurthy & Wemmer 1995). Baskaran *et al.* (2010b) point to a significant increase in the female population and the dangers of local overabundance that is likely to result as a consequence of increasing male numbers due to increased protection. Such increases in population size would result in reduced resource availability to elephants as they are likely to exceed the carrying capacity which could also lead to increased competition due to reduced feeding areas.

Invasive weeds such as *L. camara* have become widespread in Mudumalai and now appear to cover significant parts of the reserve (pers. obs.). The most obvious visual impact appears to be the disappearance of large areas of grass (N. Sivaganesan, pers. comm.), which formed the dominant ground cover in this reserve (Daniel *et al.* 1987, Sivaganesan 1991). The disappearance of large areas of grass directly reduces a major food resource for herbivores dependent on grass. While this reduction in grass would affect most herbivores dependent on grass, past studies on the foraging ecology of elephants (Baskaran *et al.* 2010a, Sivaganesan 1991, Sivaganesan & Johnsingh 1995) show that elephants in this reserve depend upon grass for the bulk of their dietary requirements. Weed invasion may also cause the gradual transition of tropical deciduous forests into an exotic-dominated shrubland due to reduced recruitment of tree saplings (Prasad 2012).

Despite the large and physical impact (occupying space) that *L. camara* appears to have on the on the natural system in India, this invasion has previously received only superficial attention by scientists and managers. While there appears to be a general agreement that *L. camara* is detrimental to the floral and faunal community here, there is limited assessment of the actual impact of *L. camara* and the kind of response it requires (for example, Prasad 2010, Prasad 2012, Ramaswami & Sukumar 2011, Ramaswami & Sukumar 2013). Some reserves, however, manage habitats by investing valuable resources in *L. camara* removal by cutting, uprooting and using excavators to mechanically remove this invasive plant (Srivastava 2009).

Given that the elephant population appears to be increasing (Baskaran *et al.* 2010b), we need to assess if there is an association of *L. camara* with elephants and whether elephants have changed their behaviour in response to possible changes brought about by weed invasion. Despite the association that *L. camara* appears to have with biodiversity decline (Prasad 2010, Prasad 2012) and on the ecosystem, to my knowledge there have been no studies on the association that *L. camara* may have with elephant in Mudumalai. Managers of wildlife reserves require information on habitat use and distribution of large mammals such as elephant. It is important to understand what drives habitat use and why large mammals select some parts of the reserve and avoid others. Anecdotal information suggests that invasive weeds such as *L. camara* that have now covered many areas of reserves throughout India, may be driving elephants to select those areas that are not yet invaded. However, there is a lack of information on how invasive weeds such as *L. camara* are associated with habitat use and feeding ecology of elephant. The main focus of this study was to assess the potential impact *L. camara* has on the vegetation community and structure, food resources for elephant, elephant habitat use and feeding.

1.6 Thesis outline

In my thesis, I examine the relationships between *L. camara*, an alien invasive plant and the Asian elephant, a native large mammalian herbivore. My main objective was to determine if there was an association of *L. camara* with native floral species and elephants, and the type of association. Consequently, each of the three data chapters presented in my thesis address different objectives to explore this relationship between

L. camara and the Asian elephant. The term 'browse' used throughout this thesis refers to both shrubs and tree saplings. Note: 'browse' may not always refer to elephant food species. Where browse species are elephant food species, this is specifically mentioned.

In Chapter Two, I examine the relationship between *L. camara* and the native floral species assemblage and richness at the community level, percentage grass cover and percentage grass occupancy in the three habitats of Mudumalai Tiger Reserve. I also determine the association of *L. camara* with the most common elephant browse species that contributed the most to these differences, in each of the three habitats.

In Chapter Three, I investigate the association of *L. camara* with elephant habitat use across the three habitats in Mudumalai, and within habitats separately, particularly the dry deciduous habitat, where the interaction term between *L. camara* and habitat was significantly associated with elephant habitat use to determine the type of association.

Chapter Four deals with elephant behaviour in the dry deciduous forest. In this chapter, I studied elephant feeding in different levels of *L. camara* invasions, and determined if there was an association of *L. camara* with elephant feeding behaviour and whether *L. camara* modified elephant feeding behaviour. The results are discussed along with suggested factors that could potentially contribute to improving a future study.

Chapter Five summarises the main findings of my research and synthesises and integrates the work, discusses the overall implications and provides management recommendations and further research ideas.

Chapters Two, Three and Four are written with the intention of publication as independent manuscripts. All the work undertaken in this dissertation was carried out under permits (see Research permits under Supplementary Material) provided by the Principal Chief Conservator of Forests & Chief Wildlife Warden, Tamil Nadu, India (Ref. No. WL5/57210/2008) and Conservator for Forest and Field Director, Mudumalai Tiger Reserve, Tamil Nadu, India (Ref. No. T/7240/2008). As per the terms and conditions set out by the Conservator of Forests and Field Director of the reserve, my study was restricted to observational work and I was not permitted to conduct experimental manipulation.

CHAPTER TWO

Lantana camara is associated with a variation in floral species assemblage, richness, selected elephant browse plant species and grass cover in Mudumalai Tiger Reserve, southern India

2.1 ABSTRACT

Exotic plant invasions are often associated with native floral species declines. Invasive exotic plants like *Lantana camara* have spread extensively across tropical dry forests of southern India. However, there is a lack of information on the association of invasive weeds and their interaction with habitat on native floral species assemblage and richness in areas such as India. Floristic changes may occur due to anthropogenic disturbance to the habitat or by exotic plant invasion of the habitat, or both leading to changes in native floral species assemblage and richness and in turn on forage availability. To assess floral species assemblage and richness, stem densities of shrubs and saplings were measured within 10 × 1-m plots defined every 100-m to sample at 11 plots, from 67 randomly located transects, 1-km in length, in Mudumalai Tiger Reserve, India, along with *L. camara* abundance. Along with biotic and abiotic environmental covariates, I first compared *L. camara*-invaded and uninvaded plots along each transect. I then tested for an association between *L. camara* abundance with three elephant browse plants that were present in all three habitats of the reserve and contributed most to the average dissimilarity in floral species assemblage; and finally, I tested the association of *L. camara* abundance and invasion (age of the stand, defined by average stem girth) with percentage grass cover and percentage grass occupancy, respectively. Of the 737 plots, 59% (n = 432) of the sampling plots were invaded with *L. camara* and more *L. camara*-invaded plots were present in the thorn forest (TF). A multivariate analysis revealed a significant association of all environmental covariates with floral species assemblage and richness. Pair-wise tests indicated that *L. camara* abundances were significantly associated with floral species assemblage and richness within the moist deciduous forest (MDF) and dry deciduous forest (DDF), but not in the TF. The association of *L. camara* abundance with elephant browse plants varied with species. *Randia* spp. was negatively associated with *L. camara* abundance in the MDF (P = 0.049) and contributed to 14% of the average dissimilarity between habitats and between plots with and without *L. camara* overall, followed by *Phyllanthus* spp. (9.2%) and *Shorea* spp. (7.5%). *Lantana camara* abundance was significantly associated with percentage grass cover in the MDF and DDF but not in the TF. Linear regression indicated that *L. camara* invasion was the only significant predictor of percentage of grass occupancy (P = 0.0001). While it is likely that additional contributing factors may exist, my results suggest that *L. camara* is

capable of altering floral species assemblage and richness in the MDF and DDF. However, permit conditions did not allow experimental work to be conducted to test whether *L. camara* is a 'driver' or a 'passenger' of changes in the floristic assemblage and richness. While it appears that *L. camara* is associated with a significant change in the floral species assemblage and richness, some elephant browse plants, percentage grass cover and percentage grass occupancy, further studies are required to experimentally test the role of *L. camara* in this important conservation site.

Keywords: anthropogenic disturbance, floral species assemblage, grass cover, invasive weeds, *Lantana camara*, richness

2.2 INTRODUCTION

Exotic plant invasions are often characterized by the replacement of local biotas with non-indigenous species, and the spread of a particular species over large areas (Hengeveld 1988, McKinney & Lockwood 1999). Exotic species may modify native communities by altering soil properties such as nutrient cycling (Belnap & Phillips 2001, Ehrenfeld *et al.* 2001, El-Ghareeb 1991, Vivrette & Muller 1977), hydrology (D'Antonio & Mahall 1991, Melgoza *et al.* 1990), be allelopathic (Achhireddy & Singh 1984, Gentle & Duggin 1997a), and compete with native species for light and nutrients (Braithwaite *et al.* 1989, Woods 1993). Native forage species used by herbivores as food may receive only limited resources due to competition with exotic plants, thus causing native species to persist at very low densities (Bedunah 1992, Belcher & Wilson 1989). Changes to the vegetation community through a decline of native forage species brought about by exotic weeds could have the potential to precipitate food-web-level, bottom-up meltdown (sensu Terborgh *et al.* 2001).

Exotic plants often require some disturbance for them to establish (Buckley *et al.* 2007, Duggin & Gentle 1998, Larson *et al.* 2001). In addition to the impact of exotic plant invasions on native plant communities, a number of studies have shown that anthropogenic disturbances can also alter plant communities (Angold 1997, Godefroid & Koedam 2004, Räsänen *et al.* 2007). Biotic factors such as tree density, canopy cover and grass cover and abiotic factors such as fire, distance to roads and settlements are responsible for changes to the vegetation community (for example, Morrison *et al.* 1995, Oliveira-Filho *et al.* 1998, Sullivan *et al.* 2005). While exotic plants have been known to displace native plants through competition or allelopathy (D'Antonio & Mahall 1991, Gentle & Duggin 1997a, Melgoza *et al.* 1990), some studies have suggested that invasion of exotic plants could just be an opportunistic response or a consequence of disturbance to a habitat (Gooden *et al.* 2009a, Gurevitch & Padilla 2004). Further to this concept, MacDougall and Turkington (2005) empirically showed that invasive exotic plants are often ‘passengers’ rather than ‘drivers’ that influence community structure. Nevertheless, it is often difficult to distinguish between the impacts of exotic invasive plants and other biotic and abiotic factors that drive changes to the floral species assemblage and richness.

Megaherbivores such as the Asian elephant (*Elephas maximus*) are adapted to live in diverse habitats and feed on a variety of plant species (Baskaran *et al.* 2010a, Owen-Smith 1988). However, despite their ability to exploit a wide range of forage species, elephant may be influenced by the establishment and spread of exotic invasive plants especially if these exotic plants are not eaten by elephant and replace native forage species. The establishment of exotic invasive plants often leads to displacement and decline of native forage species (Lym & Kirby 1987).

Mudumalai Tiger Reserve (hereafter Mudumalai) in southern India hosts a range of herbivores that depend on the vegetation community (see study area in Chapter One). Changes to the vegetation community brought about by both invasive weeds and anthropogenic pressures could impact the herbivore community (Prasad 2010) including elephant. In Mudumalai, one study estimates that browse forms 15% of elephant diet with *Acacia intsia*, Bamboo spp. and *Kydia calycina* forming 5%, 4% and 2% respectively, while grass forms nearly 85% of elephant diet of which *Themeda cymbaria* and *T. triandra* contribute 40% and 11% respectively to elephant diet in this reserve (Baskaran *et al.* 2010a). The physical impact *L. camara* has on grass is the reduction of grass cover (Kumar *et al.* 2012). As *L. camara* spreads, grass cover declines. This reduction in major elephant food source could lead to detrimental effects on elephants and their habitats (Baskaran *et al.* 2011a, Prasad 2012). For large herbivores, whose populations are not regulated through natural predation, it is likely that the availability of food is the limiting resource (Owen-Smith 1988, Sinclair 1975). Thus food resources are vital to maintaining a population.

Foraging behaviour by herbivores is expected to be influenced by both available biomass and plant chemical composition (Kuijper *et al.* 2009). Foraging decisions by herbivores are frequently based on the selection of patches that produce the highest protein and nutrient intake resulting from spatial variation in nutritional quality (Fryxell 1991). Exotic invasive plants have also been shown to significantly lower the available biomass and density of native species (Kohli *et al.* 2004, Kumar 2011, Luna *et al.* 2009). Thus, the reduction in available forage biomass brought about by invasive weeds and changes in chemical composition and palatability of plants as they grow (Jachmann 1989, Ramakrishnan *et al.* 1981) could result in a reduction of the overall carrying capacity of elephant (Sivaganesan 1991). Despite concerns over the reduction in forage

plants, previous studies in Mudumalai have raised concerns that the elephant population has been growing although their habitats have declined in extent and quality (Baskaran *et al.* 2010b, Daniel *et al.* 1987).

Lantana camara L., listed as amongst the world's 100 most invasive species (Lowe *et al.* 2000), has invaded India's tropical dry forests and appears to be associated with a reduction in the food species of native herbivores (Prasad 2012). Elsewhere, sites invaded by *L. camara* generally have lower plant species richness and diversity (Prasad 2010, Sharma & Raghubanshi 2007), and the weed is also thought to impede the growth of grass and native seedlings (Fensham *et al.* 1994, Gooden *et al.* 2009b, Kumar *et al.* 2012). For these reasons, many reserves manage habitat by investing resources in *L. camara* removal, especially by cutting and uprooting plants (Srivastava 2009).

In an attempt to understand what drives floral species assemblage and richness, I tested whether *L. camara*, along with other biotic and abiotic environmental covariates, was significantly associated with: 1) floral species assemblage and richness; 2) three elephant browse plants present throughout the reserve and that contributed most to the dissimilarity in floral species assemblage and richness in *L. camara*-invaded and uninvaded plots; and 3) grass cover. Grass cover was examined because of the importance of grass in elephant diet (Baskaran *et al.* 2010a, Sivaganesan & Johnsingh 1995). Permit restrictions prevented me from harvesting grass to estimate its biomass in the sampling sites and hence I used grass cover as an estimate of grass available. I use the term 'association' here because this is not a manipulative experiment. Instead, it is effectively a snapshot in time, for which I am unable to confidently state if *L. camara* is a 'driver' or a 'passenger' in community change for this system. The terms '*L. camara*-invaded' and 'uninvaded' are interchangeably used with '*L. camara*-presence' or 'absence'.

2.3 METHODS

2.3.1 Study site

The study was conducted in Mudumalai Tiger Reserve (Figure 2.1) situated at the foot hills of the Nilgiri District in Tamil Nadu State, southern India. The three broad

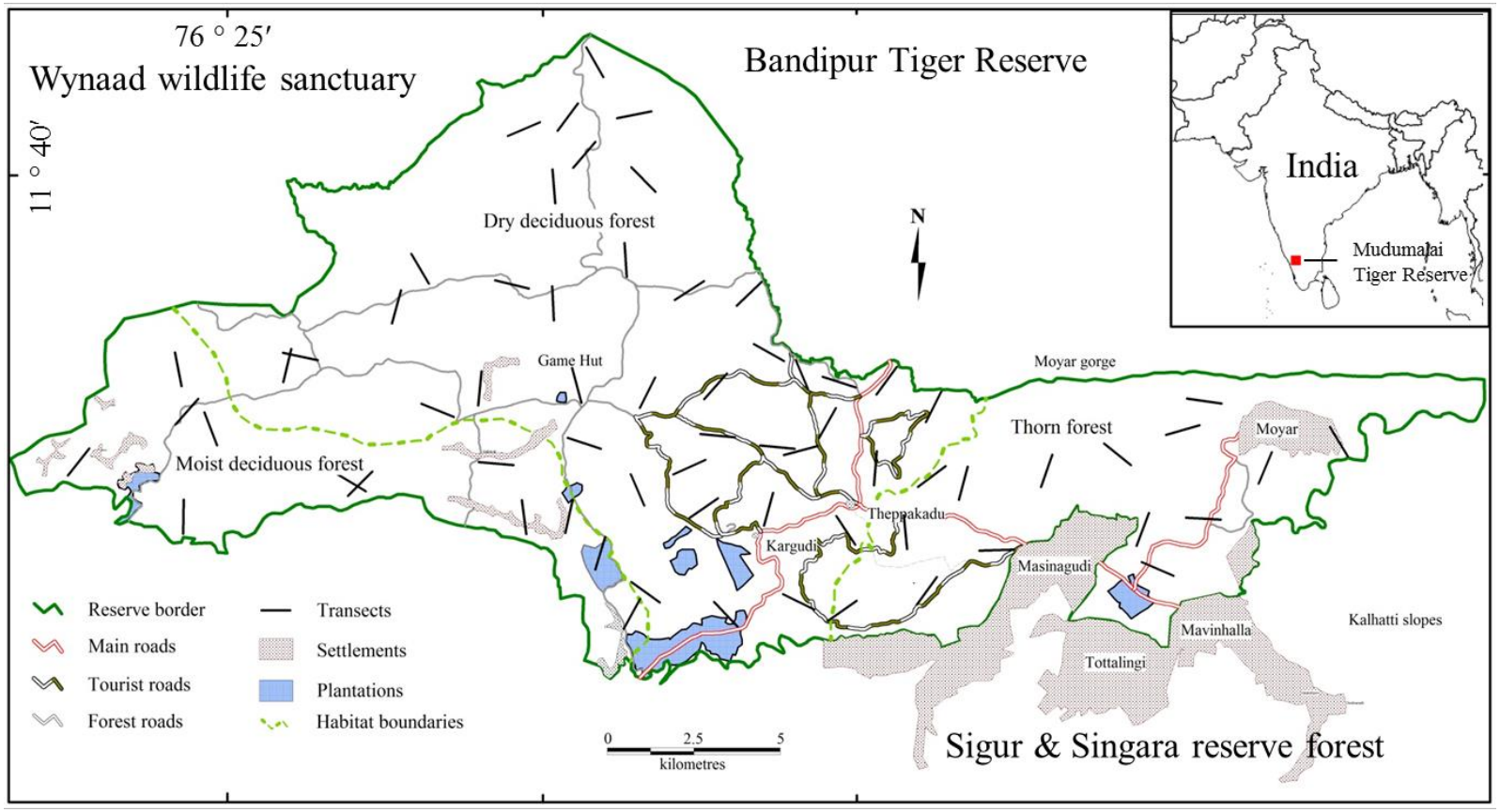


Figure 2.1: Mudumalai Tiger Reserve and its location in India showing the layout of 67 transects across the reserve within the three habitats. Habitat boundaries are delimited by bright green dashed lines: moist deciduous, dry deciduous and thorn forest. Plantations are shown as blue patches and settlements as brown patches. The road network distinguished as main, tourist and forest roads is shown by double lines.

vegetation types described by Champion and Seth (1968) in Mudumalai, moist deciduous forest (MDF), dry deciduous forest (DDF) and thorn forest (TF) were used to sample floral species assemblage and abundance of sites with and without *L. camara*. Data were collected between January and May 2009, and November 2009 and May 2010. Ground-surveyed topographic maps (1:50,000) of Mudumalai were divided into 94, 2 × 2-km cells using MapInfo Professional 7.8 (MapInfo Corporation, Troy, New York, USA). A 1-km transect was placed in 67 randomly selected cells, from a total of 94 cells. Start coordinates of each transect were randomly located within each cell. End coordinates were determined from a randomly selected compass direction 1-km away from the start coordinates, uploaded on to a hand held GPS (Garmin 60) using Garmin MapSource 6.11.6 (Garmin Ltd. Olathe, USA), and located on foot (see Supplementary Table 2.1 for georeferenced data of the start and finish locations of each transect and Supplementary Method 2.1 that was used to create an interpolated surface map of *L. camara* distribution in Mudumalai, Supplementary Figure 2.1).

2.3.2 Sampling floral species assemblage and richness

Floral species (shrubs and saplings, between 10 and 150-cm) were identified and counted in plots measuring 10 × 1-m located every 100-m along each transect in order to measure floral species assemblage and richness at each plot.

2.3.3 Sampling *Lantana camara* abundance and invasion and other environmental covariates

I first recorded *L. camara* presence or absence in the plot. To measure *L. camara* abundance, stem density of *L. camara* in each plot was recorded. To estimate *L. camara* invasion, the age of the stand, defined by average *L. camara* girth of all stems in a plot was used because in my field observations, I noted that older stands had less *L. camara* plants (as few individuals dominate while others die out) as has been noted elsewhere (Swarbrick *et al.* 1998). By contrast, younger stands had more individual plants. The girth of all *L. camara* stems were measured at ground level within 10 × 1-m plots and recorded in 1-cm categories. An average girth for each plot was derived. An alternative measure of *L. camara* invasion was the use of basal area which shows *L. camara*

dominance in space, obtained by multiplying the number of stems by average stem girth in a plot (see Supplementary Method 2.2 and Supplementary Figure 2.2 (a - c) for the relationships between the three measures).

Biotic and abiotic environmental covariates that could potentially be associated with *L. camara* abundance and invasion and floral species assemblage and richness were measured in each plot. Biotic covariates included tree density, canopy cover, and grass cover. Tree density along each 1-km transect was estimated every 100-m using the point centred quadrant method as described by Croze (1974) to sample at 11 points. Briefly, a cross is placed on the ground at fixed intervals along a transect and oriented in a fixed direction. Distance from the nearest tree to the centre point of the cross is measured in each of the four quarters. Absolute density (D) of the stand is calculated from the distance of the tree to the centre of the cross given by

$$D = \frac{K}{\bar{\bar{d}}^2}$$

Where $\bar{\bar{d}}$ = the mean of all distances and K a constant.

Canopy cover along each 1-km transect was estimated every 100 m using a 24 × 16 cm convex mirror divided into 24 equal cells (6 × 4 cells) and placed on the ground to reflect the canopy. Viewing directly above the centre of the mirror, if a cell reflected > 50% canopy cover then it was counted as having canopy cover and was ignored if a cell reflected < 50% canopy cover. The percentage of grass cover (area of grass cover per 10 m^2) present in each plot was visually estimated. All grass species were grouped together without distinguishing the various species. The percentage of bare ground, other vegetation (trees, herbs, shrubs) and rocks, was also visually estimated at the same site. The percentage of grass occupancy[1] (area of grass cover / area available to grass after deducting native vegetation, bare ground and rocks) was also calculated to provide a measure of the area in a plot that was actually occupied by grass or *L. camara*.

[1] For example, if 30% of a plot was occupied by trees, 20% herb cover, 30% bare earth or rock, 15% grass and 5% *Lantana camara*, then effectively, only 20% of the area is available to grass or *L. camara*. Thus in this example, 75% is occupied by grass (percentage grass occupancy) and 25% of the area is occupied by *L. camara.*

Abiotic environmental covariates related to anthropogenic disturbances, included distance to roads and settlements, and time since last fire burn. Linear distances between each sampling plot and the closest road and settlement were measured from 1:50,000 topographic maps, using MapInfo Professional 7.8 (MapInfo Corporation, Troy, New York, USA). As the size and thus potential impact of roads and settlements varied throughout Mudumalai, I used three categorical factors for settlements: 1) if a plot fell more than 2-km from a minor settlement (≤ 0.1 km^2); 2) if a plot fell within 2-km from a minor settlement; and 3) if a plot fell within 2-km of a major settlement (≥ 0.1 km^2). Similarly, for roads: 1) if a plot fell more than 2-km from a forest road (grey lines, Figure 2.1) beyond the tourism zone; 2) if a plot fell within 2-km from a forest road within the tourism zone (green and white double lines, Figure 2.1) where tourists to the reserve are allowed in forest department vehicles; and 3) if a plot fell within 2-km of a main/public road (red double lines, Figure 2.1). Within Mudumalai, smaller forest roads that were used only by the forest department's tourist vehicles were assumed to have less impact than the main/public road while forest roads (indicated by grey lines, Figure 2.1) beyond the roads in the tourism zone (indicated by green and white double lines, Figure 2.1) were presumed to have minimal impact on weed distribution.

Data on anthropogenic fire during the six years prior to the study (2003 to 2008) on each plot were obtained from the Tamil Nadu Forest Department Management Plan (Srivastava 2009), as monitored by Centre for Ecological Sciences, Indian Institute of Science, Bangalore. In addition, I recorded fire burns during the year of sampling. Sampling plots were overlaid on fire maps to assess its influence by calculating the time in years since the last burn occurred in the area sampled by each plot. A value of zero indicated that a plot had burned in the year of sampling.

2.3.4 Statistical analyses

2.3.4.1 Are floral species assemblage and richness associated with *Lantana camara* presence, abundance, habitat and environmental covariates?

To assess differences in floral species assemblage and richness in plots that were invaded and uninvaded by *L. camara* including *L. camara* abundance and

environmental covariates, I used PERMANOVA+ using 9999 permutations implemented in PRIMER v 6.1.11 (Clarke & Gorley 2006). The data were log-transformed (log x + 1) to account for the effects of rare and abundant species. A Bray-Curtis index was used as a similarity measure for floral species assemblage (Clarke & Warwick 2001). For floral species richness, a resemblance matrix was derived using Jaccard similarity coefficients which use presence-absence data. To further investigate the association of *L. camara* presence/absence with floral species assemblage and richness, I examined the output of PERMANOVA which includes pair-wise tests within each habitat comparing plots with and without *L. camara*. As there were a large number of interactions between various factors, I only examined the interaction between habitat and *L. camara* presence/absence, which was my primary interest. All P-values are quoted from permutation tests (either *F*-statistics or *t*-tests). I acknowledge that spatial autocorrelation may be an issue with these data as in many previous studies, but at this stage I am unable to incorporate any analyses to account for this issue.

2.3.4.2 Which elephant browse plants are associated with *Lantana camara* presence, abundance, habitat and environmental covariates?

In order to determine how individual species contributed to the differences in floral species assemblage between *L. camara*-invaded and uninvaded plots, I used SIMPER subroutine (analysis of per cent similarity) (PRIMER v 6.1.11) based on a Bray-Curtis similarity measure, with a log transformation of the data (log x + 1). The top three elephant browse food plants (saplings) that contributed most to the dissimilarity from the SIMPER analysis were then used to examine the slope of the relationship with *L. camara* abundance. The effect size of *L. camara* on each of the species that contributed to the average dissimilarity among habitats and between invaded and uninvaded plots, were derived using 'adonis' function in the 'vegan' package in R (see Supplementary Method 2.3 for R code; R Development Core Team 2013).

2.3.4.3 Is percentage grass cover associated with *Lantana camara* presence, abundance, habitat and environmental covariates?

Given the importance of grass in elephant diet (Baskaran *et al.* 2010a, Sivaganesan & Johnsingh 1995), I first conducted an analysis on percentage grass cover to study the association of *L. camara* abundance and other environmental covariates with percentage grass cover. A Bray-Curtis index was used as a similarity measure for percentage grass cover. PERMANOVA+ was used to run 9999 permutations to test for an association of *L. camara* abundance and biotic and abiotic environmental covariates with percentage grass cover. Biotic and abiotic factors used as environmental covariates were *L. camara* presence/absence and abundance, tree density, canopy cover, impact of roads, settlements and fire. PERMANOVA was used to conduct pair-wise tests to compare plots with and without *L. camara* within each habitat to examine these differences. As above, only interactions between habitat and *L. camara* presence/absence were examined and not all factor interactions.

2.3.4.4 Is percentage grass occupancy significantly predicted by *Lantana camara* invasion?

A linear regression was conducted on percentage grass occupancy, which was used as the outcome variable conducted in SPSS Statistics, release version 20.0 (IBM SPSS Inc., Chicago, IL, USA). I tested for an association of *L. camara* invasion[2] (average girth per plot) along with other environmental covariates, which included impact of roads, settlements, canopy cover, fire, tree density, DDF × *L. camara* interaction and MDF × *L. camara* interaction term with the percentage grass occupancy. The TF was used as the dummy variable and hence its interaction term with *L. camara* was not included in the model. Percentage grass occupancy per plot which was the outcome variable was arcsine-square root transformed for normality.

[2] I also used an alternative measure of *Lantana camara* using the basal area which shows dominance in space derived by multiplying the number of stems in a plot by the average stem girth.

2.4 RESULTS

Lantana camara has invaded large areas of Mudumalai (see Supplementary Figure 2.1). Overall, 59% of the sampling plots (n = 737) were invaded by *L. camara* throughout the reserve. The thorn forest (TF) (n = 165) had more *L. camara*-invaded sampling sites than the other habitats as only 12% of the sites were not invaded by *L. camara*. Of the sites sampled in the moist deciduous forest (MDF) (n = 132), 43% remained uninvaded while 52% in the dry deciduous forest (DDF) (n = 440) were uninvaded by *L. camara*. The density of *L. camara* varied throughout the reserve in different habitats from no *L. camara* to 39 stems per 10 × 1 m plot with an interquartile range of 4 stems per 10 × 1-m plot (25^{th} percentile = 0 stems; 75^{th} percentile = 4 stems).

2.4.1 Are floral species assemblage and richness associated with *Lantana camara* presence, abundance, habitat and environmental covariates?

While *L. camara* presence was clearly associated with the floral species assemblage, all environmental covariates were also statistically significant, P = 0.0001 (Table 2.1a). The largest component of variation was from habitat (13%), followed by roads, *L. camara* presence/absence on its own, and the interaction of habitat and *L. camara* presence/absence (each 7%). The component of variation of *L. camara* abundance was 5%. The lowest component of variation was grass cover (4%).

Pair-wise tests indicated that in both the MDF (t_{122} = 1.51, P = 0.008) and DDF (t_{429} = 3.49, P = 0.0001), the presence of *L. camara* was significantly associated with differences in floral species assemblage, while there were no significant differences in the TF (t_{156} = 0.89, P = 0.610) whether *L. camara* was present or not.

Lantana camara along with environmental covariates were significantly associated with floral species richness (P ≤ 0.0003, Table 2.1b). The highest components of variation were habitat (12%) followed by roads and *L. camara* presence/absence (both 7%), while the component of variation for *L. camara* abundance was 5%. Tree density had the lowest component of variation (2%).

Table 2.1: Results of PERMANOVA (permutation analysis of variance) examining the association of *Lantana camara* abundance (count per plot) and environmental covariates with floral species (a) assemblage and (b) richness. All environmental covariates were statistically significant. PERMANOVA also gives a component of percent variation for each predictor which is equivalent to the sum of the squared fixed effects divided by the degrees of freedom from standard ANOVA.

(a)

Source	df	Pseudo-F	P(perm)	Estimate	Percent variation
Lantana camara abundance	1	16.6	0.0001	41.51	5.28
Canopy cover	1	19.9	0.0001	50.97	5.85
Grass cover	1	7.4	0.0001	19.06	3.58
Fire	1	18.5	0.0001	50.11	5.80
Tree density	1	3.9	0.0001	7.83	2.29
Habitat	2	20.9	0.0001	251.36	13.00
Lantana camara (presence/absence)	1	9.7	0.0001	72.84	7.00
Roads	2	7.5	0.0001	78.40	7.26
Settlements	2	5.8	0.0001	65.56	6.64
Habitat × *Lantana camara* (presence/absence)	2	3.5	0.0001	71.78	6.95
Residuals	722			1965.40	36.35
Total	736				

(b)

Source	df	Pseudo-F	P(perm)	Estimate	Percent variation
Lantana camara abundance	1	12.6	0.0001	41.84	4.96
Canopy cover	1	13.8	0.0001	46.70	5.24
Grass cover	1	5.9	0.0001	19.58	3.39
Fire	1	16.0	0.0001	58.03	5.84
Tree density	1	2.6	0.0003	5.65	1.82
Habitat	2	15.5	0.0001	248.66	12.09
Lantana camara (presence/absence)	1	8.2	0.0001	80.94	6.90
Roads	2	6.5	0.0001	89.41	7.25
Settlements	2	4.8	0.0001	71.58	6.49
Habitat × *Lantana camara* (presence/absence)	2	2.9	0.0001	71.85	6.50
Residuals	722			2655.20	39.51
Total	736				

The significant interaction term between habitat and *L. camara* presence/absence indicated different effects of *L. camara* in different habitats. Pair-wise

tests indicated that the association between *L. camara* presence and floral species richness in the MDF and DDF were significant (MDF, t_{122} = 1.45, P = 0.006; DDF, t_{429} = 3.17, P = 0.0001). However, there was no association between *L. camara* presence and floral species richness in the TF (t_{156} = 0.79, P = 0.807).

2.4.2 Which elephant browse plants are associated with *Lantana camara* presence, abundance, habitat and environmental covariates?

SIMPER analysis indicated that *Randia* spp. (family: Rubiaceae) contributed 14.8% to the average similarity between habitats and between plots with and without *L. camara*, followed by *Phyllanthus* spp. (family: Phyllanthaceae) (9.2%), *Shorea* spp. (family: Dipterocarpaceae) (7.5%) and *Grewia* spp. (family: Malvaceae) (6.8%) (Table 2.2). All these plants are elephant browse food plants and the most important species in differentiating those plots with and without *L. camara*. Of the browse species that were estimated to contribute most to elephant diet by Baskaran *et al.* (2010a), Bamboo spp. (family: Gramineae) and *Kydia calycina* (family: Malvaceae) contributed only 3% to the average similarity, and only Bamboo spp. was found in all three habitats.

The association between *L. camara* presence/absence and *Randia* spp. in the MDF was significant (MDF, t_{121} = 1.93, P = 0.049) while there was no significant association between *L. camara* presence/absence and *Randia* spp. in the DDF (t_{428} = 0.25, P = 0.881) or TF (t_{155} = 1.42, P = 0.162) (Figure 2.2a). However, *L. camara* abundance was negatively associated with *Randia* spp. in the DDF only ($t_{1,439}$ = -3.03, P = 0.003).

Lantana camara presence was significantly associated with *Phyllanthus* spp. in the DDF (t_{428} = 6.34, P = 0.0001), but not in the MDF (t_{121} = 6.62, P = 0.947) or TF (t_{155} = 1.16, P = 0.222) (Figure 2.2b). *Shorea* spp. was present only in the DDF, but was absent in the MDF and TF.

Lantana camara presence was significantly associated with *Grewia* spp. in the DDF (t_{429} = 3.78, P = 0.0002), but not in the MDF (t_{122} = 0.47, P = 0.649) or TF (t_{156} = 0.41, P = 0.699). *Lantana camara* presence was significantly associated with Bamboo spp. in the MDF (t_{122} = 2.02, P = 0.043), but not in the DDF (t_{429} = 1.55, P = 0.119) or TF (t_{156} = 1.11, P = 0.266) (Figure 2.2c).

Table 2.2: Results of the SIMPER analysis showing the relative and cumulative contributions of various species that contributed to 86.56% of the average dissimilarity among habitats and between invaded and uninvaded plots. The effect of *Lantana camara* on each of these species is shown as coefficients. Elephant browse food species are represented by a star.

Species	Average abundance		Average Dissimilarity	%		Coefficient
	Invaded	Uninvaded		Contribution	Cumulative	
**Randia* spp.	0.56	0.71	12.79	14.77	14.77	-0.025
**Phyllanthus embellica*	0.09	0.46	8.00	9.24	24.02	-0.004
**Shorea roxburghii*	0.04	0.35	6.50	7.51	31.53	-0.005
**Grewia* spp.	0.24	0.30	5.89	6.80	38.33	0.010
Cassia spp.	0.26	0.21	5.73	6.62	44.95	-0.008
**Dalbergia* spp.	0.15	0.14	3.84	4.43	49.38	0.001
**Tectona grandis*	0.11	0.10	3.32	3.83	53.21	-0.002
Anogeisis latifolia	0.02	0.20	3.00	3.46	56.68	0.000
**Terminalia* sp.	0.01	0.18	2.75	3.17	59.85	0.001
**Diospyros montana*	0.10	0.10	2.71	3.13	62.98	0.004
**Ziziphus* spp.	0.14	0.13	2.68	3.10	66.08	0.002
**Kydia calycina*	0.11	0.18	2.61	3.01	69.09	-0.001
**Bambusa arundinacea*	0.18	0.07	2.46	2.84	71.94	-0.001
**Syzygium cumini*	0.07	0.07	1.69	1.95	73.89	-0.003
**Olea* sp.	0.05	0.16	1.56	1.80	75.69	6.180e-04
**Sclicheria oleosa*	0.06	0.04	1.50	1.73	77.43	0.005
**Pterocarpus marsupium*	0.02	0.08	1.47	1.70	79.12	3.076e-04
Glycosmis pentaphylla	0.14	0.13	1.34	1.55	80.67	0.004
Zingiberaceae	0.11	0.00	1.21	1.39	82.06	-0.004
Casearia esculenta	0.03	0.09	1.17	1.35	83.41	6.253e-05

Table 2.2 (continued……)

Species	Average abundance		Average Dissimilarity	%		Coefficient
	Invaded	Uninvaded		Contribution	Cumulative	
Cordia wallichii	0.04	0.03	1.13	1.31	84.72	0.001
**Helicteres isora*	0.08	0.08	1.01	1.16	85.88	-0.004
**Lagestroemia*	0.03	0.02	0.93	1.08	86.96	0.000
**Solanum* spp.	0.07	0.01	0.65	0.76	87.71	3.102e-03
Oujenia ojenensis	0.01	0.04	0.64	0.74	88.45	0.002
Bridelia sp.	0.01	0.03	0.56	0.64	89.09	7.752e-04
Argyreia cuneata	0	0.02	0.46	0.53	89.62	2.697e-04
Sterculia guttata	0	0.03	0.41	0.47	90.09	-0.000

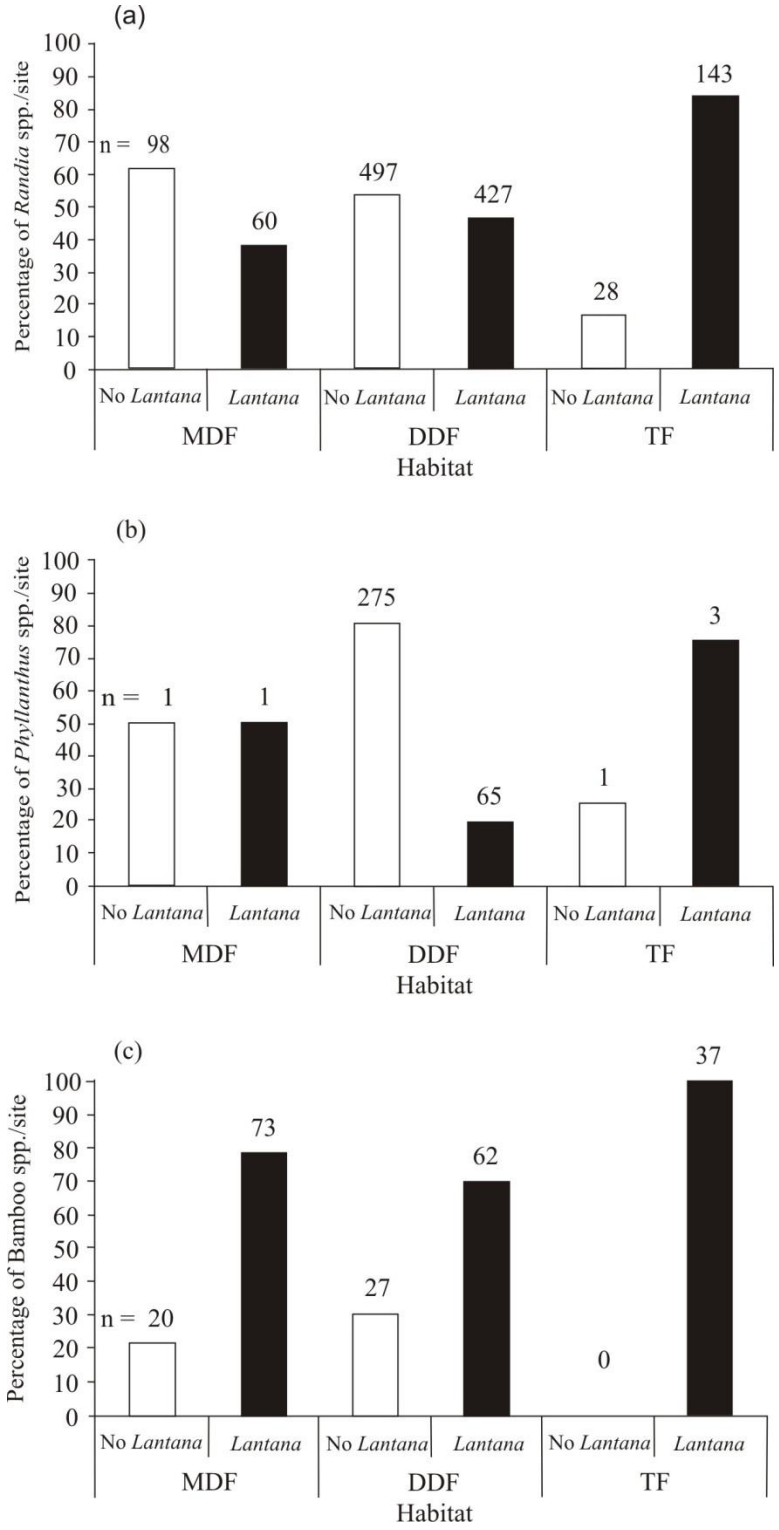


Figure 2.2: Percentage of the total number of elephant food plants (saplings) selected from the SIMPER analysis (a) *Randia* spp., (b) *Phyllanthus* spp., and (c) Bamboo spp. in *Lantana camara* invaded and uninvaded plots in three habitats [Moist deciduous forest (MDF); Dry deciduous forest (DDF) and Thorn forest (TF)] of Mudumalai Tiger Reserve. n refers to the number of individual plants of each species in each habitat.

2.4.3 Is percentage grass cover associated with *Lantana camara* presence, abundance, habitat and environmental covariates?

The PERMANOVA analysis indicated that percentage grass cover did not differ significantly according to whether a plot was invaded or uninvaded by *L. camara* (P = 0.543, Table 2.3). Tree density and fire were also not significant predictors of percentage grass cover (P > 0.121). However, all other environmental covariates were significantly associated with percentage grass cover (P < 0.009, Table 2.3). In fact, the highest component of variation was *L. camara* abundance (19%), followed by the interaction term between habitat and *L. camara* presence/absence (12%), and habitat (7%).

Pair-wise tests indicated that percentage grass cover significantly differed in the MDF (t_{120} = 3.51, P = 0.003) and DDF (t_{424} = 1.97, P = 0.034) depending on whether *L. camara* was present or absent. However, the presence of *L. camara* made no difference to the percentage grass cover in the TF (t_{153} = 0.80, P = 0.441). Thus it is difficult to generalise on the common effects of *L. camara* across the different habitats.

Table 2.3: Results of PERMANOVA (permutational analysis of variance) examining the association of *Lantana camara* abundance (count per plot), and environmental covariates on percentage grass cover. The component of percent variation (equivalent to the sum of squared fixed effects divided by the degrees of freedom from standard ANOVA) for each predictor is given. *Lantana camara* abundance, canopy cover, habitat, roads, settlements and the interaction term between habitat and *L. camara* (presence/absence) were significant predictors of percentage grass cover.

Source	df	Pseudo-F	P(perm)	Estimate	Percent variation
Lantana camara abundance	1	160.4	0.0001	98.65	19.47
Canopy cover	1	17.5	0.0001	10.32	6.30
Fire	1	2.2	0.1217	0.79	1.74
Tree density	1	2.1	0.1262	0.72	1.66
Habitat	2	5.2	0.0040	12.08	6.81
Lantana camara (presence/absence)	1	0.4	0.5428	-1.08	2.04
Roads	2	4.3	0.0097	9.16	5.94
Settlements	2	4.5	0.0099	11.04	6.51
Habitat × *Lantana camara* (presence/absence)	2	6.5	0.0007	35.87	11.74
Residuals	723			456.00	41.87
Total	736				

2.4.4 Is percentage grass occupancy significantly predicted by *Lantana camara* invasion?

The linear regression of the *L. camara* invasion (average girth per plot) and environmental covariates on percentage grass occupancy across habitats was statistically significant ($F_{8, 736} = 6.7$, $R^2 = 0.07$, P = 0.0001). *Lantana camara*[3] was the only significant predictor of the percentage grass occupancy (P = 0.0001, Table 2.4), possibly indicating competition for the same space. There was a significant negative correlation between percentage grass occupancy and *L. camara* in all three habitats indicating that as *L. camara* invasion increased, grass cover declined.

Table 2.4: Results of the linear regression of environmental covariates including *Lantana camara* invasion (average girth per plot) predicting percentage grass occupancy. *Lantana camara* invasion was the only significant predictor of percentage grass occupancy. The interaction terms, moist deciduous forest (MDF) and dry deciduous forest (DDF) with *L. camara* are included in the model. The interaction term thorn forest (TF) and *L. camara* was set to zero because of redundancies in the model.

	Coefficients			t	P
	Unstandardized		Standardized		
	B	SE	Beta		
(Constant)	77.778	4.494		17.306	0.0001
Lantana camara	-1.849	0.494	-0.193	-3.743	0.0001
Canopy cover	-0.087	0.047	-0.074	-1.846	0.065
Fire	-0.155	0.772	-0.008	-0.2	0.841
Tree density	-5.862	22.508	-0.009	-0.26	0.795
Roads	-0.18	1.933	-0.004	-0.093	0.926
Settlements	-2.303	2.064	-0.054	-1.116	0.265
MDF × *Lantana camara*	-0.834	0.628	-0.066	-1.329	0.184
DDF × *Lantana camara*	-0.509	0.87	-0.025	-0.585	0.559

[3] The model that used the alternative measure of *Lantana camara* invasion using an index of the basal area created from the number of stems multiplied by the average stem girth within the plot was also statistically significant. See Supplementary Table 2.2 for significant predictors in the model which included canopy cover and the interaction terms (MDF × *L. camara* and DDF × *L. camara*).

2.5 DISCUSSION

My results found a significant association between *L. camara* and floral species assemblage and richness in some habitats of Mudumalai. Nevertheless, the association of *L. camara* on floral species assemblage and richness is not simple, as the significance of the association differs in different habitats of Mudumalai. Further, I was also interested in the association of *L. camara* with elephant browse plants and grass cover. The constraints of sampling in this reserve did not enable me to experimentally determine if *L. camara* was the 'driver' or 'passenger' of these changes.

2.5.1 Are floral species assemblage and richness associated with *Lantana camara* presence, abundance, habitat and environmental covariates?

While the three habitats in Mudumalai are clearly different in terms of their floral species assemblage and richness, PERMANOVA pair-wise tests of the interaction between habitat and plots with and without *L. camara* indicated that *L. camara* made a significant difference only to the MDF and DDF of Mudumalai and not the thorn forest (TF). In the MDF, 43% of the sampled sites had *L. camara* present while in the DDF, 48% of the sampled sites were invaded by *L. camara*. The MDF has the highest shrub and sapling density and diversity compared to the DDF and TF in Mudumalai (Kumar 2011). It is likely that *L. camara* is capable of changing the diversity and density of shrubs and saplings and hence we see an association of *L. camara* in the MDF because of the higher diversity and density of shrubs and saplings. The MDF is a closed canopy forest and closed canopy is known to hamper *L. camara* growth (Duggin & Gentle 1998, Fensham *et al.* 1994). However, *L. camara* was recognised as a problem taking over the understory and spreading rapidly in the Benne and Mudumalai blocks of the MDF and affecting the growth rate of teak in its early stages as early as 1924 in Mudumalai when timber extraction was carried out (Ranganathan 1941). The timber extractions may have opened up the canopy and facilitated *L. camara* invasion suggesting that *L. camara* may be the 'passenger' here, but further studies are required to confirm its role here. Nevertheless, *L. camara* abundance has contributed significantly to the floral species assemblage and richness in the MDF.

Similarly, there is an association between *L. camara* presence and floral species assemblage and richness in the DDF, where timber extraction continued until a ban on logging in the 1980s (Srivastava 2009). Anthropogenic disturbances such as logging may have opened up the canopy which has increased the amount of light penetrating into the forest floor. Opening up of the forest canopy and allowing more light however, is an advantage to exotic invasive species such as *L. camara* that are known to germinate with an increase in light availability (Gentle & Duggin 1997b, Totland *et al.* 2005). Anthropogenic disturbances have also been known to facilitate exotic plant invasions (Buckley *et al.* 2007, Duggin & Gentle 1998, te Beest *et al.* 2012). Therefore, we see a significant association of *L. camara* with floral species assemblage and richness in the DDF.

In addition to logging, fire has also been regarded as having a major impact of native sapling regeneration in the DDF (Sivaganesan & Sathyanarayana 1995). Fires, have been shown to facilitate the spread of *L. camara* (Hiremath & Sundaram 2005). Fires suppress native saplings and facilitate germination and spread of *L. camara* (Berry *et al.* 2011, Raizada & Raghubanshi 2010) in the DDF. It is likely that the association of *L. camara* with floral species assemblage and richness is seen in the DDF because of the impact of logging and fire in the DDF. Grasses can be fuel loads that influence fire frequency and intensity (Scholes & Archer 1997). In the MDF, however, fire has been suggested to have much less impact on native species regeneration because grasses in the MDF retain their moistness even in the dry season, which reduces fire frequency and intensity (Sivaganesan 1991). In the TF a lack of litter accumulation and cattle grazing results in reduced fire frequency and intensity (Daniel *et al.* 1995, Sivaganesan 1991). However, when interpreting the response of native species distribution and abundance to infestations of exotic plants, caution must be exercised because infrequent plants may just be rare because of their nature of being rare, or may have been displaced by weed invasions (Butler & Cogan 2004).

In addition to *L. camara*, the results of my study also show that biotic and abiotic environmental covariates such as tree density, canopy cover, grass cover, impact of roads, settlements and fire are also significantly associated with floral species assemblage and richness. Elsewhere, the association of environmental covariates with floral species assemblage and richness have also been documented indicating the role

that biotic and abiotic factors have in the floristic assemblage and richness. For example Angold (1997) investigated the effect of a road on adjacent heathland vegetation in the UK, and found that there was an increase in the abundance of grasses in the vegetation near the road. In Australia, fire frequency apparently accounted for 60% of the floristic variation (Morrison *et al.* 1995) while in a central Brazilian deciduous dry forest, plant species abundance and distribution was significantly correlated with canopy gaps (Oliveira-Filho *et al.* 1998). Thus, other environmental covariates are also responsible for changes in the floral community.

2.5.2 Which elephant browse plants are associated with *Lantana camara* presence, abundance, habitat and environmental covariates?

Plant species are likely to respond to *L. camara* invasion differently, depending on different stages of its invasion (Gooden *et al.* 2009b). While some native species are excluded more easily than others from invaded communities, the resistance of native species to invasion varies (Standish *et al.* 2001). For example, *Randia* spp. that forms only 0.15% of elephant diet in Mudumalai (Baskaran *et al.* 2010a) was significantly associated with the presence of *L. camara* only in the MDF, but not in the DDF and TF, while the slope of the relationship between *L. camara* abundance and *Randia* spp. was negative only in the DDF and not in the MDF or TF. Further, Bamboo spp. did not appear to be associated with *L. camara* presence in the DDF and TF but was significantly associated with *L. camara* presence in the MDF. In fact, the percentage of Bamboo spp. saplings available was greater where there was more *L. camara* in all three habitats, and no Bamboo spp. saplings were found in the thorn forest where *L. camara* was absent. While this result does not indicate that this species requires *L. camara* to grow, it does appear to indicate that *L. camara* is affecting species composition by supressing some species and facilitating the expansion of others like Bamboo spp. (A. A. Desai, pers. comm.). Such changes in the vegetation composition may have a cascading impact on the ecosystem and would potentially impact all biodiversity. Further, it is hypothesised that greater Bamboo spp. sapling numbers occur within *L. camara* areas possibly because herbivores are unable to access these saplings. Other studies have shown that native floral species can benefit from invasive floral species by growing inside stands of the invasive species thereby experiencing lower

levels of herbivory (Atwater *et al.* 2011). This would allow these saplings to grow but herbivores may be feeding more on certain species where there is less *L. camara* thereby depleting their food resources in areas without *L. camara*. Although Bamboo spp. is often suggested as being important elephant food plant, one estimate indicates that it made up just 4.44% of elephant diet in Mudumalai (Baskaran *et al.* 2010a). Therefore, my results suggest that *L. camara* presence and abundance, habitat and environmental covariates are associated with some elephant food plants but this association varies depending on the species and in which habitat these species are found.

2.5.3 Is percentage grass cover associated with *Lantana camara* presence, abundance, habitat and environmental covariates?

The presence of *L. camara* did have a significant negative association with grass cover in the MDF and DDF. The DDF was reported to have the maximum grass species richness, followed by the TF (Kumar 2011). In addition, the annual net primary productivity of grass was estimated to be highest (720 g/m^2) in the DDF, 352 g/m^2 in the TF and 110 g/m^2 in the MDF (Baskaran *et al.* 2010a). The association of *L. camara* may not be seen in the TF due to the lower grass biomass in this habitat when compared to the MDF and DDF.

In addition, there are other factors that could potentially contribute to the absence of any association of *L. camara* in the TF. For example, cattle grazing has been regarded as one of the causes of the depletion of grass in the TF, and the TF has been considered as sub-optimal habitat for elephant due to low productivity of grass (Daniel *et al.* 1995) allowing *L. camara* to invade these sites (Silori & Mishra 2001) yet not have a significant association with grass cover in the TF. Cattle dung as an index of cattle use was considered for inclusion as a factor in this study. I was unable to obtain a reliable measure of cattle foraging via dung or another index and cattle use may have been underestimated because dung in the TF is removed by the local people and sold as manure to tea and coffee plantations (Silori & Mishra 2001, Tyagi 1995). Hence it was not included as an environmental covariate in my study.

2.5.4 Is percentage grass occupancy significantly predicted by *Lantana camara* invasion?

The most visible association of *L. camara* on elephant habitat is the loss of grass cover. My analysis indicated a significant negative association between percentage grass occupancy and *L. camara.* This result possibly indicates competition for the same space, nutrients or water. A previous study in Mudumalai indicated that in the DDF, 85% of elephant diet was grass, while 78% and 53% of elephant diet consisted of grass in the MDF and TF was respectively (Baskaran *et al.* 2010a). The reduction in grass cover could lead to food limitation for elephants and other herbivores that depend on grass in the reserve. Reduced grass cover could lead to a reduced carrying capacity of herbivores in the reserve. Any adverse impact on herbivores that are dependent on grass would in turn impact large carnivores like tigers which are dependent on them (Prasad 2010).

Overall the replacement of grass by *L. camara* could have serious conservation implications for both herbivores and on their predators. Unpalatable weeds such as *L. camara* may render some areas unsuitable to elephant through reduced forage, limiting food to fewer patches. Such changes in carrying capacity and distribution of food resources of the reserve could also result in elephants being forced to move out in search of better forage. Managers in particular need to recognise that reduced carrying capacity through loss of grazing areas can force elephants to move out of the reserve and come into increased conflict with the surrounding human settlement (Ishwaran 1993). It is important that managers take this into account and address this situation. For example, seeds of grass species such as *Axonopes* sp. that compete well with *L. camara* could be sowed to help increase forage for grazers (Kumar *et al.* 2012).

2.5.5 Conclusions

It appears that *L. camara* invasion is not associated with floral species assemblage and richness, elephant browse plants and grass cover in the TF despite the TF having the highest number of invaded sites. These results suggest that *L. camara* may not be responsible for any changes brought about to the floral community. This lack of association also suggests that managers may instead focus on *L. camara* management in the MDF and DDF of Mudumalai where *L. camara* does have a significant association

with the floral community. Nevertheless, as in many invaded systems, there is still uncertainty as to whether *L. camara* is the 'driver' of community changes or is just a 'passenger' that appears to be less affected by disturbance or environmental stressors and may just be an opportunistic invader (MacDougall & Turkington 2005). Given the fundamental correlative approach used in this study, due to constraints in sampling in a protected reserve, I do not know if *L. camara* is the 'driver' that is predominantly responsible for the changes in floristic composition or a 'passenger' of changes in environmental conditions and disturbance regimes. While some studies suggest that *L. camara* fits the 'driver model', and limits or excludes native species by competition or allelopathy (Achhireddy & Singh 1984, Gentle & Duggin 1997a, Osunkoya & Perrett 2011), other studies suggest that the 'passenger model' also describes *L. camara* dominance (Gooden *et al.* 2009a, Gooden *et al.* 2009b), although the 'passenger' and 'driver' model are not always exclusive (MacDougall & Turkington 2005). Further studies are required to empirically test whether *L. camara* is the 'driver' of floral community changes or just a 'passenger' that is a consequence of a disturbed habitat.

CHAPTER THREE

The influence of the invasive weed *Lantana camara* on elephant habitat use in Mudumalai Tiger Reserve, southern India

3.1 ABSTRACT

Invasive weeds like *Lantana camara* have a range of effects on animals such as elephant. These plants are not edible by the Asian elephant (*Elephas maximus*). They also compete for space with elephant food plants and take over large areas of elephant habitat. I tested whether the addition of *L. camara* to a model consisting of measured environmental variables improved predictions of habitat use by elephant in Mudumalai Tiger Reserve, India. Elephant dung density was used to assess elephant habitat use from 62 line transects 1-km in length. Results indicated that habitat and impact of human settlements significantly influenced elephant habitat use across habitats. However, I found no evidence for the hypothesis that the addition of *L. camara* significantly predicted elephant habitat use at the landscape level. I then tested the association of *L. camara* on elephant habitat use in the dry deciduous forest (DDF) where there was a significant interaction between DDF and *L. camara*. In the DDF, *L. camara* significantly predicted elephant habitat use. I conclude that while no significant effects of *L. camara* were seen at the level of an entire reserve, at a finer level and in specific habitats negative effects of this invasive plant on elephant habitat use were observed.

Keywords: Anthropogenic disturbance, *Elephas maximus*, elephant, habitat, invasive weeds, *Lantana camara*

3.2 INTRODUCTION

Invasive weeds are transformative, changing the character of natural ecosystems over substantial areas (Richardson *et al.* 2000), often resulting in homogenized biospheres of non-indigenous species (McKinney & Lockwood 1999). Empirical studies have shown that invasive weeds can negatively impact habitat selection and use by both wild and domestic ungulates (Hein & Miller 1992, Trammell & Butler 1995). For example, elk (*Cervas elephas nelsoni*) in Western Montana were attracted to habitats where the invasive knapweed (*Centaurea* spp.) had been removed (Thompson 1996). Invasive weeds compete with and replace native forage species (Belcher & Wilson 1989), thereby reducing the amount of food available to herbivores (DiTomaso 2000) through reduced forage production (Lym & Messersmith 1985).

One invasive weed of international significance is *Lantana camara* L., which was introduced to India from South America at the Indian Botanic Garden, Calcutta, as an ornamental plant in 1809 (Thakur *et al.* 1992). This widely invasive species grows particularly well in unshaded, anthropogenically disturbed habitat (Gentle & Duggin 1997b, Sharma *et al.* 2005).

The Asian elephant (*Elephas maximus*) is a wide-ranging species traversing human-made administrative boundaries (Baskaran *et al.* 1995, Desai 1991). Humans have converted and developed forest habitat for agriculture or urban development (Desai & Baskaran 1996) making the conservation of large herbivores such as the elephant challenging. In addition to illegal logging, cattle grazing, collection of fuel wood and non-timber forest produce, weed invasion appears to threaten many conservation areas including elephant habitat in the Nilgiri Biosphere Reserve, southern India (Desai & Baskaran 1996, Silori & Mishra 2001).

Elephants are megaherbivores that require large amounts of forage to survive (Owen-Smith 1988). The primary impact that *L. camara* is thought to have on elephant habitat is a reduction in grass cover. As *L. camara* spreads, grass cover appears to decline and is replaced by *L. camara* because both vie for the same space (Chapter Two). This reduction may be most pronounced in dry deciduous forest (DDF) where grass is the dominant food source for elephants, and where elephant density was

previously found to be highest in the dry season (Sivaganesan 1991, Sivaganesan & Johnsingh 1995).

In this study, I examined the influence of *L. camara* on habitat use by elephant across habitats and within habitats in Mudumalai Tiger Reserve, southern India. The following questions were examined: (1) Does the addition of *L. camara* significantly predict elephant habitat use across habitats at the landscape level? (2) Do models containing *L. camara* better explain elephant habitat use across habitats using an information-theoretic approach? (3) Because my results indicated a significant interaction between the DDF and *L. camara*, I tested whether *L. camara* significantly influenced habitat use by elephant within the DDF. I then used the same model to test whether *L. camara* significantly influenced elephant habitat use in the moist deciduous forest and thorn forest.

3.3 METHODS

3.3.1 Study site and methods

Mudumalai Tiger Reserve (here after Mudumalai; 11°32' and 11°42'N latitude, 76°20'and 76°45'E longitude) includes 321 km^2 of plains and foot hills of the Nilgiri district in Tamil Nadu state, southern India. The reserve is bounded to the north by Bandipur Tiger Reserve and to the west and north-west by Wynaad Wildlife Sanctuary. Singara and Sigur Reserve forests form the southern and eastern boundaries of Mudumalai (Figure 3.1a). Mudumalai and its surrounding reserves are part of the 5500 km^2 Nilgiri Biosphere Reserve (NBR) (Srivastava 2009). The wild elephant population in Mudumalai ranges from approximately 350 to 1000 elephants, depending on seasonal movement of elephants across the NBR (Baskaran *et al.* 2010b, Daniel *et al.* 1987).

Tropical forest types in Mudumalai include moist deciduous (MDF), dry deciduous (DDF) (mixed and *Shorea* vegetation) and thorn forest (TF) (Champion & Seth 1968) (Figure 3.1a). Teak (*Tectona grandis*) plantations and native trees were commercially logged in Mudumalai from the beginning of the 19th century and continued until the 1980s (Srivastava 2009). The presence of *L. camara* was described as a problem, affecting early growth rate of Teak in Mudumalai, Benne and Theppakadu

blocks of Mudumalai in 1924, in addition to its rapid spread and increased risk of fire (as fuel) in the DDF and *T. grandis* plantations (Ranganathan 1941).

Field observations and measurements were conducted between January and May 2009, and November 2009 and May 2010 to estimate elephant dung density and assess habitat characteristics. A topographic map (1:50,000) of Mudumalai derived from ground surveys was divided into 94, 2 × 2-km cells using MapInfo Professional 7.8 (MapInfo Corporation, Troy, New York, USA). Sixty-two cells were selected randomly to receive a 1-km transect. Transect locations are shown in Figure 3.1b. Each transect's start coordinates were randomly located within each cell. End coordinates were obtained from a randomly selected compass direction 1-km away from the start coordinates, uploaded on to a hand held GPS (Garmin 60) using Garmin MapSource 6.11.6 (Garmin Ltd. Olathe, USA), and located on foot.

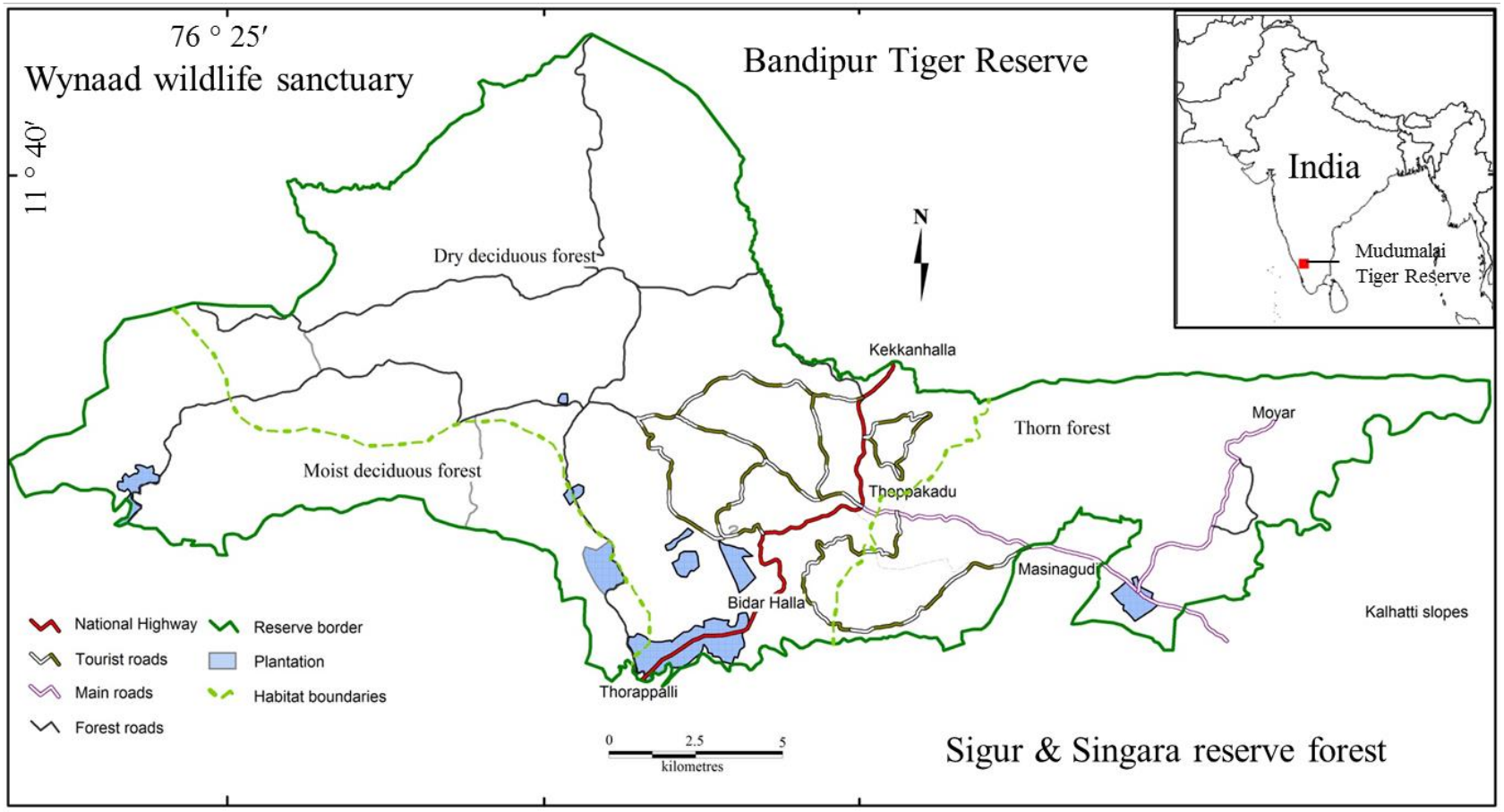
3.3.2 Elephant dung density as an index of elephant distribution and habitat use

I used elephant dung density to assess elephant habitat use. Elephant dung density has been used as an index of elephant distribution and habitat use for both African forest elephant (*Loxodonta africana cyclotis*) (Barnes *et al.* 1991, Fay 1991) and Asian elephant (Steinheim *et al.* 2005, Varma 2008). Line transects as described by Buckland *et al.* (2004) were used to estimate elephant dung densities and the data were analysed using the program DISTANCE 6.0 (Thomas *et al.* 2010). The perpendicular distance of all dung piles sighted from the line transect was measured using a measuring tape. Estimates of dung density were obtained from the perpendicular distances (Barnes & Jensen 1987).

3.3.3 Predictors of variation in elephant dung density

I reviewed the literature on elephant habitat use in Mudumalai (Daniel *et al.* 1987, Desai & Baskaran 1996, Sivaganesan 1991) to derive a set of likely environmental variables that have previously been suggested to influence elephant distribution and density.

(a)


76 ° 25′
Wynaad wildlife sanctuary
11 ° 40′
Bandipur Tiger Reserve
India
Mudumalai
Tiger Reserve
N
Dry deciduous forest
Moist deciduous forest
Kekkanhalla
Thorn forest
Moyar
Theppakadu
Masinagudi
Bidar Halla
Kalhatti slopes
Thorappalli
National Highway
Tourist roads
Main roads
Forest roads
Reserve border
Plantation
Habitat boundaries
0
2.5
5
kilometres
Sigur & Singara reserve forest

(b)

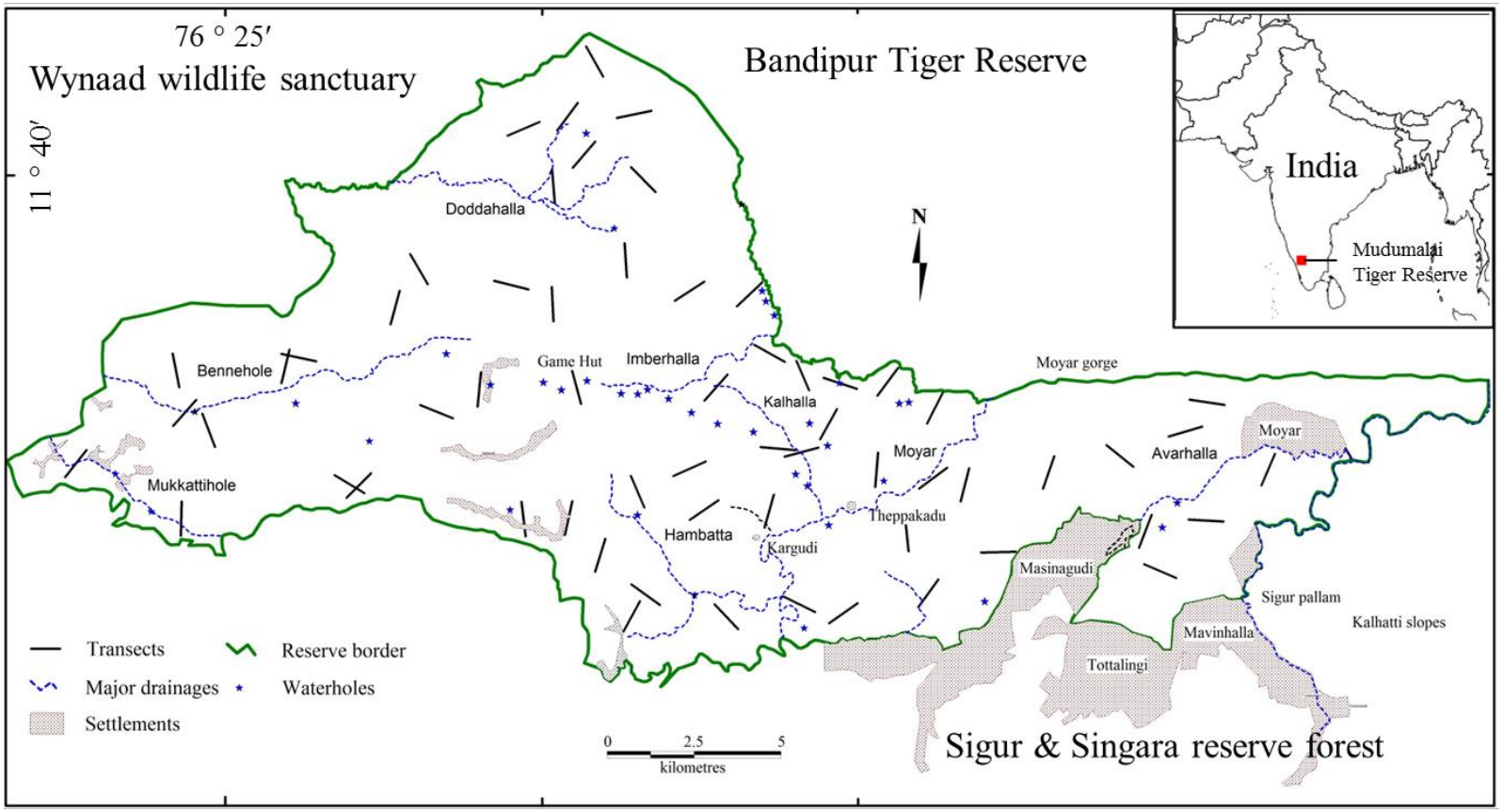


Figure 3.1: Mudumalai Tiger Reserve and its location in India showing (a) the major habitat boundaries: moist deciduous, dry deciduous and thorn forest delimited by bright green dashed lines. The road network distinguished as National highway, main road for public use, tourist roads where only forest department vehicles are permitted, and forest roads is shown. Plantations are shown as blue dotted patches; (b) layout of the 62 transects across Mudumalai. Major drainages are shown by blue dotted lines. The location of water holes is shown by stars. Settlements are shaded in brown.

To estimate *L. camara* invasion, the age of the stand, defined by the average girth of all *L. camara* stems measured at ground level within 10 × 1-m plots, defined every 100-m, to sample at 11 plots along each transect was used. The number of *L. camara* stems in each 1-cm category was recorded. The average *L. camara* girth for the 11 plots was averaged to give a *L. camara* invasion measure[4] for each transect.

Grass cover (forage for elephant) and canopy cover (shade for elephant) were estimated in each plot. A visual estimate of percentage grass cover to the nearest 5% cover was recorded in the plots. All grass species were grouped together without distinguishing the various species. The average of all values of grass cover for each plot was used as the estimate for each transect. Canopy cover along each 1-km transect was estimated every 100-m using a 24 × 16-cm convex mirror divided into 24 equal cells (6 × 4 cells) and placed on the ground to reflect the canopy. If a cell reflected > 50% canopy cover, it was counted as having canopy cover. If a cell reflected < 50% canopy cover, it was ignored. Percentage canopy cover at the point was estimated as an index of shade. The average value of canopy cover from all points along each transect was used as the estimate in the analysis.

The size and thus potential impact of settlements on elephant varied throughout Mudumalai. I therefore had three categories (1, 2 and 3) for the settlement variable, (1) if a transect fell more than 2-km from a minor settlement (≤ 0.1 km^2); (2) if a transect fell within 2-km from a minor settlement and (3) if a transect fell within 2-km of a major settlement (≥ 0.1 km^2). Similarly, the potential impact of roads on elephants differed with the greatest impact from the National highway passing through Mudumalai. This highway was considered to have the highest impact because vehicular traffic that included goods, passenger, tourist and private vehicles used the National Highway. The impact of roads were categorised as follows: (1) Kekkanhalla to Theppakadu and Theppakadu to Masinagudi; (2) Theppakadu to Bidderhalla; (3) Bidderhalla to Thorappalli; (4) Kalhatti slopes; (5) forest roads within the tourist zones in Mudumalai where only Forest Department vehicles are allowed; (6) all other roads within Mudumalai (Figure 3.1a). As the Moyar river runs parallel to the National

[4] An alternative measure of *Lantana camara* is basal area which shows dominance in space. Basal area was calculated by multiplying the number of stems with the average girth of the stems in the plot. The average girth of the plot was assumed to reflect the age while the basal area was assumed to reflect spatial dominance. (See Supplementary Method 2.2 and Supplementary Figure 2.2 (d - f) for the relationships between the three measures).

Highway between Theppakadu and Bidderhalla, this section of Mudumalai was considered to have the highest impact on elephants because elephants regularly tried to cross the road to drink from the river but were often stranded on the road sides because of vehicular traffic. Within Mudumalai, smaller forest roads that were used only by the forest department's tourist vehicles had less impact while roads beyond the tourism zone were considered to have minimal impact on elephant distribution and habitat use.

To measure water availability, linear distances between the midpoint of each transect and the closest waterhole (Figure 3.1b), were measured from 1:50,000 topographic maps using MapInfo Professional 7.8 (MapInfo Corporation, Troy, New York, USA). The influence of anthropogenic fire on each transect was assessed by calculating the time since the last burn occurred in the area sampled. Thus, a transect sampled in 2009 that had burned in the year 2008 was given a value of one indicating that it was at least 1 year since it last burned. If more than 50% of a transect length burned in a particular year, it was considered as burned that year. Data on fire burns between 2003 and 2008 were obtained from the Tamil Nadu Forest Department Management Plan (Srivastava 2009), as monitored by Centre for Ecological Sciences, Indian Institute of Science, Bangalore. I recorded whether the transect burned in the year of sampling. Transects were overlaid on these fire maps and assessed.

3.3.4 Statistical methods

DISTANCE program 6.0 was used to analyse estimates of elephant dung density along the transects (Thomas *et al.* 2010). Data filters and models were performed at various levels of truncation to improve the model fit (Buckland *et al.* 2004). The fit of the best possible model was determined by using Akaike's Information Criterion (AIC) (Akaike 1973) values that were generated by the program as well as by visually judging the fit of the proposed model to the observed distance data close to the line transect.

Dung density was first examined for normality. The skewness and kurtosis were both within the limits of normality and so normal theory models were used. Throughout, I used the Generalized Linear Model approach (McCullagh & Nelder 1983), with normally distributed errors and the identity link, as this allowed comparable analyses between the Generalized Linear Models and the information–theoretic (I-T) approach.

To investigate multicollinearity between the predictor variables, a correlation analysis was conducted. The largest correlation across habitats was between grass cover and *L. camara*, and was -0.360. I therefore concluded that multicollinearity was not a significant issue with these data, and the parameter estimates and P-values were valid. SPSS Statistics, release version 20.0 (IBM SPSS Inc., Chicago, IL, USA) was used to analyse the data.

My first question examined whether the addition of *L. camara* to other environmental variables significantly predicted habitat use by elephant across habitats in Mudumalai. I used a Generalized Linear Model (with a normal distribution and identity link) to predict elephant usage (based on dung density estimates).

My second question determined whether models containing *L. camara* better explained elephant habitat use across habitats. I used an I-T approach (Burnham & Anderson 2002) to develop the best model using available environmental (predictor) variables to explain elephant habitat use based on dung density estimates across Mudumalai. The I-T methods provide formal measures of the strength of evidence for alternative models, given the data (Hegyi & Garamszegi 2011). The I-T approach allows ranking and weighing multiple competing models. I used a second-order Akaike's Information Criterion (AIC_c) as my I-T statistic because models were large (i.e., with up to 51 explanatory variables; Burnham & Anderson 2002). Models with $\Delta AIC_c \leq 2$ were considered to have substantial support from the data and models with $\Delta AIC_c > 10$ to have no support or be implausible (Burnham & Anderson 2002).

In order to understand the relationship between elephant habitat use and *L. camara* in the three different habitats, I included habitat as a factor in my analysis. My third question examined whether *L. camara* along with significant environmental variables predicted habitat use by elephant within the moist deciduous forest (MDF), dry deciduous forest (DDF) and Thorn Forest (TF) separately. A Generalized Linear Model (with a normal distribution and identity link) was used to predict elephant usage (based on dung density estimates) using the main effect of *L. camara* and significant environmental variables from the model 1 and tested for overall significance.

3.4 RESULTS

3.4.1 Elephant dung density and *Lantana camara* invasion

The number of elephant dung piles counted along 1 km line transects varied between zero and 32 dung piles in Mudumalai. Estimates of dung pile density based on the DISTANCE algorithm ranged from zero to 6650 dung piles km^{-2} with an interquartile range of 2265 dung piles km^{-2} (25^{th} percentile = 1196 dung piles km^{-2}; 75^{th} percentile = 3461 dung piles km^{-2}). *Lantana camara* density per 10 × 1-m plot varied from 0 to 39 individuals and average stem girth per 10 × 1-m varied from 0.14 cm to 11.8 cm. There was a significant negative correlation between elephant distribution and *L. camara* at the landscape level ($R^2 = 0.064$, n = 62, P = 0.047, Figure 3.2a).

3.4.2 Influence of *Lantana camara* on elephant habitat use at the landscape level in Mudumalai

I first fitted a model (Model 1) which included habitat, impact of settlement, impact of roads, canopy cover, grass cover, fire, distance to water, and second-order interactions between factors. This model overall did not significantly predict dung density (χ^2 = 28.6, df = 23, $R^2 = 0.37$, P = 0.191, AIC_c = 1440.56). Impact of settlement (P = 0.007), impact of roads (P = 0.035) and habitat by impact of settlement interaction (P = 0.030) were individually significant.

To examine my first question whether the addition of *L. camara* significantly predicted dung density across all habitats, I added *L. camara* to Model 1, to give Model 2. This model, overall did not significantly predict dung density ($\chi^2 = 30.4$, df = 24, R^2 = 0.39, P = 0.172, AIC_c = 1582.19). Only impact of settlement (P = 0.003) and habitat by impact of settlement interaction (P = 0.024) were significant predictors of dung density.

Model 3 included habitat, impact of settlements, impact of roads, canopy cover, grass cover, fire, water, *L. camara* and its interaction with habitat (dry deciduous forest (DDF) by *L. camara*, moist deciduous forest (MDF) by *L. camara*). Model 3 did not significantly predict dung density (χ^2 = 21, df = 16, $R^2 = 0.81$, P = 0.178, AIC_c = 1130.02). The only significant predictor in the model was DDF by *L. camara*

interaction term (P = 0.038, Table 3.1) that predicted elephant dung density[5]. I also used the basal area as an alternative measure of *Lantana camara* invasion derived from the number of stems multiplied by the average stem girth (see Supplementary Table 3.2).

Examining the association of *L. camara* with elephant habitat use in the three habitats separately, *L. camara* was significantly related to dung density only in the DDF (Figure 3.2b), but there was no association of *L. camara* with dung density in the MDF and TF ($P \geq 0.05$).

3.4.3 Comparison of models using the information-theoretic (I-T) approach

My second question determined whether models containing *L. camara* better explained elephant habitat use across habitats. I used the I-T approach to select the most informative of the three models. Model selection using the I-T approach indicated that the model explaining elephant habitat use based on elephant dung density estimates was Model 3 which included habitat, impact of settlement, impact of road, canopy cover, grass cover, fire, distance to water, *L. camara* and its interaction with DDF ($\Delta AIC_c \leq 2$; $\omega_i = 1.000$). This was the only model to receive any support. The two other models (Model 1 and Model 2) received no support and were considered implausible (i.e. $\Delta AIC_c > 10$, Table 3.2).

3.4.4 Influence of *Lantana camara* on elephant habitat use within the dry deciduous forest (DDF), moist deciduous forest (MDF) and thorn forest (TF) of Mudumalai

My third question examined whether *L. camara* significantly influenced habitat use by elephant within habitats. I analysed the data for the DDF separately given that the interaction term DDF by *L. camara* was significant in Model 3. I also analysed the data

[5] Some authors have utilized a conversion factor to convert elephant dung density estimates to elephant density estimates (for example, Ishwaran 1993, Sukumar 1989b). This may be appropriate in some circumstances because conversion of elephant dung density estimates to elephant density estimates incorporates seasonal and habitat dung decay and defecation rates (Supplementary Method 3.1). In Mudumalai, Daniel *et al.* (2008) showed that mean decay rates (days) in micro-habitats varied from 81.5 SE = 2.5 days to 121 SE = 11.2 days. Using elephant density estimates, these data were analysed and produced the same significant predictors (Supplementary Table 3.1) when using dung density estimates.

for the MDF and TF to examine whether *L. camara* significantly predicted elephant habitat use within these habitats.

The model included impact of settlement, impact of road and *L. camara* which significantly predicted dung density in the DDF (χ^2 = 8.6, df = 3, P = 0.040). *Lantana camara* was the only significant predictor (χ^2 = 4.6, df = 1, P = 0.030, B = - 300 ± 140). There was a significant negative correlation between elephant distribution and *L. camara* in the DDF (R^2 = 0.18, n = 36, P = 0.009, Figure 3.2b). There was also a significant negative correlation between per cent grass cover and *L. camara* (r = -0.565, n = 36, P < 0.05) in the DDF.

The models with the same predictors, i.e., impact of roads, impact of settlements and *L. camara* also significantly predicted elephant dung density in the MDF (χ^2 = 17.5, df = 5, P = 0.004) and TF (χ^2 = 14.5, df = 5, P = 0.013). However, the only significant predictor in the MDF was the impact of settlement (χ^2 = 27.98, df = 2, P < 0.001) while the only significant predictor in the TF was the impact of roads (χ^2 = 20.13, df = 3, P < 0.001). The relationships between *L. camara* and elephant dung density in the MDF (P = 0.801, Figure 3.2c) or TF (P = 0.241, Figure 3.2d) were not significant.

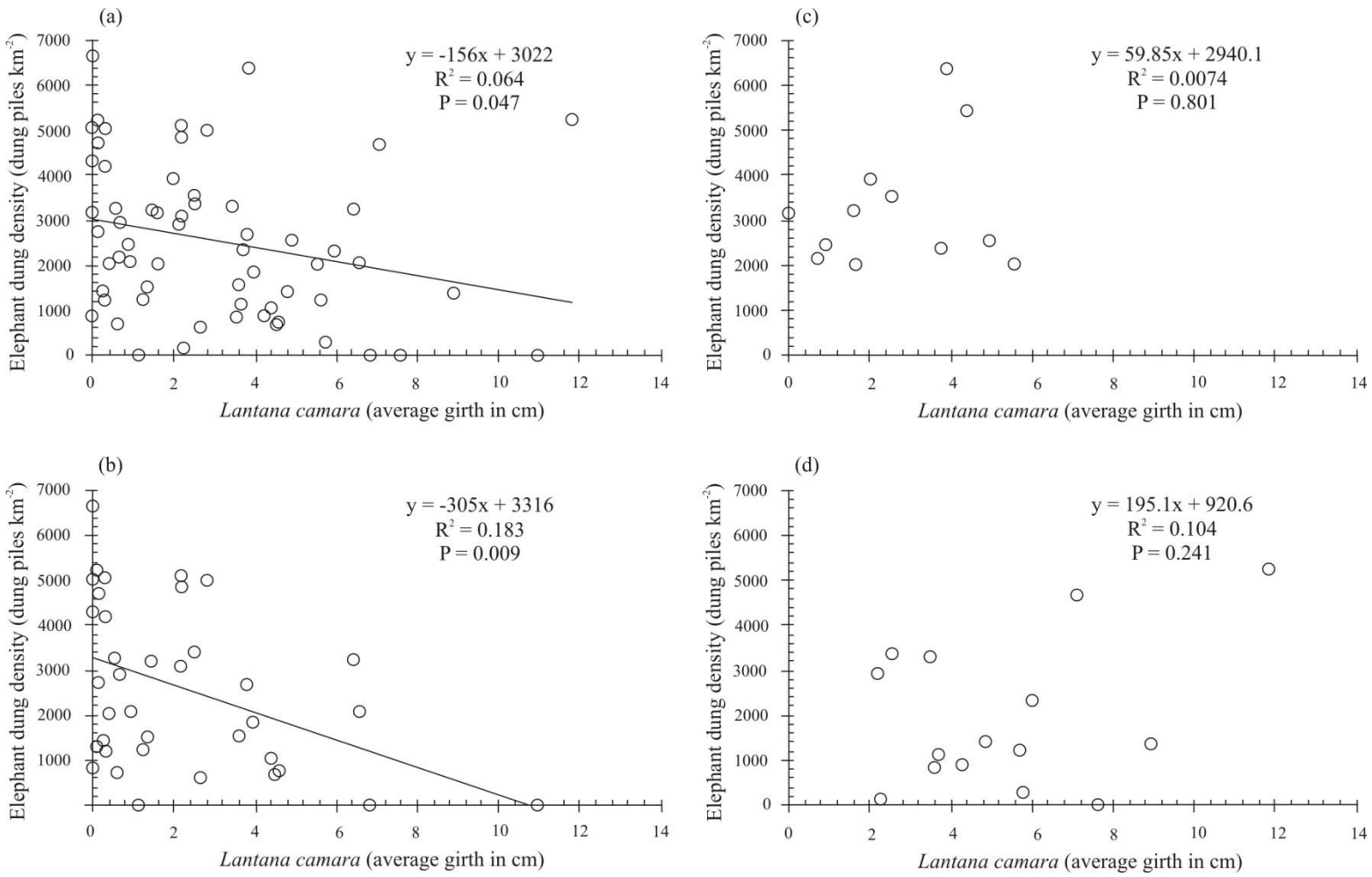


Figure 3.2: The relationship between elephant dung density (dung piles km^{-2}) and *Lantana camara* (a) across habitats (b) in the dry deciduous forest (c) moist deciduous forest and (d) thorn forest in Mudumalai Tiger Reserve.

Table 3.1: Model 3 with *Lantana camara* on its own, the interaction terms of *L. camara* with the dry deciduous forest (DDF) and moist deciduous forest (MDF) and environmental variables predicting elephant dung density estimates across habitats in Mudumalai Tiger Reserve. The Beta Coefficients, SE, Wald Chi-Square and levels of significance with main effects of environmental variables measured are shown. Factors (habitat, impact of settlements and roads) are entered as multiple dummy variables. For categorical factors with greater than two levels, the ranges of Beta Coefficients and SE are given.

Source	B	SE	Type III		
			Wald Chi-Square	df	P
(Intercept)	-314.5	1740	4.9	1	0.027
Habitat	2355.1 – 3173.7	1850 – 1997.4	2.5	2	0.282
Impact of settlements	1444.4 – 1490.6	805.5 – 896.9	3.6	2	0.162
Impact of roads	-875.9 – 749.2	617.4 – 1201.4	4.8	5	0.443
Canopy cover	-14.2	17.6	0.7	1	0.419
Grass cover	4	10.2	0.2	1	0.695
Fire	105.5	140.4	0.6	1	0.453
Water	49.8	325.8	0.0	1	0.878
Lantana camara	265.8	191.6	1.9	1	0.165
MDF × *Lantana camara*	-262.3	343.1	0.6	1	0.445
DDF × *Lantana camara*	-518.4	249.8	4.3	1	0.038

Table 3.2: Three statistical models for elephant habitat use in Mudumalai Tiger Reserve between January and May 2009 and November 2009 and May 2010. The models are in descending order based on the second-order Akaike's Information Criterion (AIC_c). The model consisting of *Lantana camara* and its interaction with habitat along with other environmental variables was the leading model and only model to receive substantial support. *K* is the number of parameters in each model which includes the intercept.

Model	Predictor variables	K	AICc	Δ AICc	ω
3	Habitat, impact of settlement, impact of roads, canopy cover, grass cover, fire, distance to water, *Lantana camara,* MDF × *Lantana camara,* DDF × *Lantana camara*	20	1130.02	0.00	1.000
1	Habitat, impact of settlement, impact of roads, canopy cover, grass cover, fire, distance to water, habitat × settlement, habitat × roads, settlement × roads	48	1440.56	310.54	0.000
2	Habitat, impact of settlement, impact of roads, canopy cover, grass cover, fire, distance to water, habitat × settlement, habitat × roads, settlement × roads, *Lantana camara*	51	1582.19	452.17	0.000

3.5 DISCUSSION

3.5.1 Influence of *Lantana camara* on elephant habitat use at the landscape level in Mudumalai

My first question determined whether the addition of *L. camara* had an influence on elephant habitat use in Mudumalai. The results of my study found no evidence that the addition of *L. camara* did influence elephant habitat use at the landscape level, however, I did find support for the hypothesis that *L. camara* negatively influenced elephant habitat use within the dry deciduous forest (DDF) at a lower spatial scale.

My study shows that habitat and the impact of settlements are associated with elephant habitat use in Mudumalai and appear to have substantially more of an influence on elephant distribution and habitat use at the landscape level than *L. camara*. Although elephants are known to use all habitats throughout the year in Mudumalai, their densities vary across habitats (Sivaganesan 1991). Movement across different habitats is governed by seasons and home ranges (Baskaran 1998, Sukumar 1989a). Elephants have large home ranges in excess of 550 km^2 in the study area (Baskaran *et al.* 1995) and hence they move across multiple habitats based on movement patterns established by individual clans and bulls. Consequently, habitat use at the landscape level is largely governed by seasonal changes in resource availability (Baskaran 1998). Additional problems to detecting the influence of *L. camara* on elephant distribution at the landscape level originate because elephants may have used *L. camara* areas just for resting or to pass through while looking for suitable feeding grounds and feeding on available grass patches around *L. camara* and during this time may have defecated. Such habitat use would make the influence of *L. camara* less visible, especially at the landscape level.

Invasive weeds such as *L. camara* on the other hand, would potentially influence elephant habitat use at lower scales covering smaller patches within a given habitat. *Lantana camara* patches currently appear substantially smaller than settlements (pers. obs.). Additionally, *L. camara* patches are not uniformly distributed and hence the influence of *L. camara* for different transects could vary, unlike settlements which are avoided by elephants (Desai & Baskaran 1996) and their impact therefore is uniform for a given distance from the settlement. However, *L. camara* on the other hand has an

influence on a much smaller spatial scale which represents smaller areas within a habitat. This is indicated by the significant interaction term, DDF by *L. camara,* in Model 3. Hence, analysing the influence of *L. camara* within individual habitats is more appropriate, as on a larger spatial scale, variables such as habitat and settlements confound the results.

3.5.2 Comparison of models using the information-theoretic (I-T) approach

My second question investigated whether models containing *L. camara* better explained elephant habitat use across habitats by using the I-T approach to compare models explaining elephant habitat use. The only model that received strong support was Model 3 that included habitat, impact of settlements, impact of roads, canopy cover, grass cover, fire, water, *L. camara* and its interaction with habitat (DDF by *L. camara,* MDF by *L. camara*). The only significant predictor in this model was the interaction term, *L. camara* by DDF, indicating that *L. camara* may in fact have an association with elephant habitat use within the DDF. Models 1 and 2 which included interaction terms between habitat, impact of settlements and impact of roads were not supported nor was the *L. camara* variable a significant predictor by itself in Models 2 and 3. This indicates that *L. camara* had an association with elephant habitat use only in certain habitats.

3.5.3 Influence of *Lantana camara* on elephant habitat use within the dry deciduous forest (DDF) of Mudumalai

My third question examined whether *L. camara* significantly influenced habitat use by elephant within the DDF, since the interaction between *L. camara* and DDF was significant. Given that habitat and impact of settlements may confound the results at larger spatial scales, one would therefore expect that an analysis on a smaller spatial scale, within individual habitats, would show that *L. camara* has an influence on elephant distribution; especially within habitats. My results indicated a significant influence of *L. camara* in the DDF. These results are supported by other empirical studies that have shown a negative impact of invasive weeds on ungulates (Hein & Miller 1992, Trammell & Butler 1995). Typically the elephant is more dependent on grass in the DDF and the thorn forest (TF) than in the moist deciduous forest (MDF)

(Baskaran 1998, Sivaganesan & Johnsingh 1995). However, the negative correlation between *L. camara* and grass cover suggests that the elephants may be avoiding areas where there is more *L. camara* due to the loss of grass. The negative correlation between elephant distribution and *L. camara* was statistically significant in the DDF but was not statistically significant in the TF and MDF. Grass is not a major food source in MDF but is a dominant food in both DDF and TF (Baskaran *et al.* 2010a). Thus, analysis at the landscape level results in the major predictors for movement at larger scales (habitat and impact of settlements) to be detected but *L. camara* drives habitat selection at a far smaller scale of a few ha to a few km^2 and hence its influence is more easily detected when within habitat assessment is performed.

3.5.4 Implications for conservation

Invasive weeds such as *L. camara* influence elephant at different spatial scales and have different influences in different habitats. My study finds no evidence that *L. camara* has affected elephant habitat use at the larger spatial scale of a landscape, but I did find support for the hypothesis that *L. camara* does have an influence at the smaller spatial scale of a single habitat. Since *L. camara* patches are not uniformly distributed and elephants do not eat *L. camara,* they are forced to selectively graze within and around *L. camara* patches (pers. obs.). The primary influence *L. camara* has on the elephant habitat is the reduction of grass cover (Prasad 2012). This is also seen from the negative correlation *L. camara* has with grass in the dry deciduous forest. The presence and spread of *L. camara* can therefore be considered as being adverse to elephants and other grazing herbivores. Selective grazing can reduce available forage and possibly favour the spread of invasive weeds (Lym & Kirby 1987, Vavra *et al.* 2007) such as *L. camara.* This selective grazing in turn could reduce the overall carrying capacity of elephants in Mudumalai. In North Dakota, leafy spurge (*Euphorbia esula*)-infested areas represented an annual herbage loss of 35% (Lym & Kirby 1987). A similar loss to grass and other native tree species may be occurring within Mudumalai. Lym & Kirkby (1987) reported an increased use of sites by cattle not infested by leafy spurge, which decreased preferred herbage and decreased species diversity. An increased use of non-infested sites would reduce the carrying capacity as a result of over-grazing and over-browsing of sites free of infestations (Trammell & Butler 1995). Managers could prioritise the

removal of weeds in the DDF, and thereby increase forage production in order to maintain habitat suitability for elephants and other grazing herbivores.

As *L. camara* densities vary in different vegetation (Chapter Two) and the evidence that *L. camara* influences habitat use at different spatial scales, it would be important that further studies at different spatial scales within each habitat be conducted to assess the true impact of *L. camara* on elephant and their habitat use. My study indicates that the effect of *L. camara* is not uniform, and thus *L. camara* management could focus on specific habitats, enabling managers to use their limited resources where they are most required.

CHAPTER FOUR

Lantana camara invasion is associated with a change in elephant feeding behaviour in Mudumalai Tiger Reserve, southern India

4.1 ABSTRACT

Lantana camara is a widespread exotic invasive species in India that is capable of dominating and displacing native forage species. However, information on how exotic invasive species affect the behaviour of megaherbivores such as *Elephas maximus* is limited. I investigated whether *L. camara* was associated with variation in elephant feeding behaviour in Mudumalai Tiger Reserve, southern India. Fifty-seven elephants were observed for a total of 64.3 hours using the focal-animal sampling method. Sampling plots measuring 10 × 1-m plots spaced 50-m apart were used to measure site characteristics where elephant were observed feeding. The behavioural response of elephant to *L. camara* was assessed from feeding and stepping rates. Grass was a major component of elephant diet (88%) while the remainder was browse (12%). Elephant were never observed to feed on *L. camara*, but rather fed on grass and browse that was present within and around *L. camara* patches. Feeding rates (number of trunksful· min^{-1}) were negatively associated with *L. camara* invasion ($F_{1, 55} = 4.26$, $\beta = -0.27$, $P = 0.044$). Path analysis indicated that the total effect of *L. camara* on feeding rates was 11% ($\beta = -0.24$) less than the direct negative association ($\beta = -0.27$) owing to a positive indirect association of *L. camara* with feeding rates through grass cover and browse density ($\beta = 0.03$). *Lantana camara* was not significantly associated with stepping rates (number of steps·min^{-1}). Rather, grass cover and browse density were associated with stepping rates ($F_{2, 55} = 11.16$, $P = 0.0001$, $R^2 = 0.30$). Path analysis indicated that stepping rates were negatively associated with grass cover ($\beta = -0.39$, $P = 0.003$) and positively associated with browse density ($\beta = 0.38$, $P = 0.001$). While this study was of a correlational nature based on observational data, my results indicate that *L. camara* is potentially capable of modifying certain aspects of elephant behaviour, likely through a loss of grass areas due to *L. camara* invasion. Experimental work is needed to test for causal relationships among the variables I measured, over multiple seasons and in different habitats to enhance our understanding of how invasive weeds modify elephant behaviour.

Keywords: Dry deciduous forest, elephant behaviour, feeding rates, *Lantana camara*, stepping rates

4.2 INTRODUCTION

Foraging decisions are guided by behavioural predisposition and inherited skills that are refined through experience and accumulation of knowledge (Launchbaugh & Howery 2005). According to the rate maximizing foraging theory, animals make choices that maximize the net rate of energy intake while foraging (Le Rossignol *et al.* 2011, MacArthur & Pianka 1966, Nagarajan *et al.* 2002). In order to meet their metabolic requirements, herbivores must make these food-choice decisions while maintaining an adequate nutrient intake (Owen-Smith 1979). However, unpalatable invasive weeds may render some areas unsuitable to herbivores through reduced forage, limiting food resources to fewer patches (Atwater *et al.* 2011), particularly if the weed is not eaten. In some cases, substantially lower leaf herbivory was experienced by highly invasive exotic plants when compared to non-invasive exotics (Cappuccino & Carpenter 2005). Weed invasion, therefore, is expected to modify herbivore feeding behaviour through an increase in unpalatable or low nutritional value food species.

Biological invasions are characterised by the spread of exotic species in areas newly inhabited by the species (Hengeveld 1988). Invasive plants have been shown to modify habitat use by a wide range of wild and domestic herbivores (Hein & Miller 1992, Thompson 1996, Trammell & Butler 1995), alter abundances of birds, reptiles (Aravind *et al.* 2010, Kutt & Fisher 2011, Scheiman *et al.* 2003), and even grizzly bears (*Ursus arctos horribilis*) (Reinhart *et al.* 2001). Invasive plants may even have toxic effects on various mammals (Heemstra *et al.* 1999, Sharma *et al.* 1981). Further, invasive plants may have a direct negative effect on native plants that may be herbivore food. Depending on the interactions among competitors and consumers, indirect interactions between invasive and native plants may also decrease the direct negative effects of invasive plants on native plants because of indirect positive effects such as reduced competition from other native plants and lower levels of herbivory (Atwater *et al.* 2011). Thus, investigating direct and indirect pathways may help understand the role of invasive weeds and their interaction with native plants and consumers.

It is particularly challenging to demonstrate the mechanism of impact of invasive weeds on wild megaherbivores such as elephant where no direct outcomes can be easily measured. For example, in the livestock industry, the impact of poisonous

range weeds has been shown to have an indirect impact on cattle and sheep in terms of reduced reproduction, and lower milk quality and wool production (Frandsen & Boe 1991). One way to examine the mechanism of influence of invasive weeds is through studying herbivore behaviour (for example, feeding rates and other associated behaviours like stepping rates while feeding) in habitat which varies in levels of weed invasion.

The Asian elephant (*Elephas maximus*) has been known to have a major effect on ecosystem functioning and vegetation dynamics and structure (Sivaganesan & Sathyanarayana 1995, Sukumar 1989a). Elephants feed on large quantities of vegetation that is consumed on a daily basis and are able to switch between grass and browse depending on season and availability (Baskaran 1998, Sukumar 1989a). In terms of its biomass, the elephant is a major contributor to total large herbivore biomass (Sukumar 1989a). It is also recognised as a *flagship species* of conservation interest (Blake & Hedges 2004, Johnsingh & Joshua 1994, Venkataraman *et al.* 2002).

A number of studies have been conducted on the ecology of elephants in Mudumalai Tiger Reserve (here after Mudumalai) in southern India, some of which include ranging and habitat use (Baskaran *et al.* 1995, Desai 1991), foraging behaviour and time activity budget of elephant (Baskaran 1998, Sivaganesan 1991). While these studies have drawn attention to the proliferation of exotic weeds, there has been a lack of published studies that evaluate the influence of these weeds on elephant in Mudumalai. Elephants have been shown to spend between 60% and 74% of their day foraging on grass (graminoids) and browse (dicotyledons) in Mudumalai depending on season and habitat (Baskaran *et al.* 2010a, Sivaganesan & Johnsingh 1995). The basic classification in terms of plant species that are eaten is the graminoid:dicotyledon proportions (including non-graminaceous monocots with dicots) (Owen-Smith 1988). Grass has been shown to form a major component of elephant diet (85%) while browse accounted for about 15% of elephant forage in this reserve (Baskaran *et al.* 2010a). Thus elephant in this reserve are predominantly grazers. If the proliferation of weeds did influence elephant by either occupying space or displacing native forage species (grass and browse), it is possible that elephant may modify their feeding behaviour depending on the level of invasion.

An increase in exotic plant species such as *Lantana camara*, an alien invasive weed in Mudumalai, has caused concern about its effects on native floral communities and in turn on the herbivore community (Subramanian *et al.* 2001). Given, the significant association of *L. camara* with floral species assemblage and richness, percentage grass cover and occupancy in the dry deciduous forest (DDF) (Chapter 2), and elephant habitat use in the DDF of Mudumalai (Chapter 3), I tested the hypotheses that variation in elephant feeding behaviour is associated with variation in *L. camara* invasion in the DDF. Elephant feeding behaviour was examined from feeding and stepping rates while feeding at different levels of *L. camara* invasion.

4.3 METHODS

4.3.1 Study site and elephant population

Mudumalai is located at the tri-junction of the 5500 km^2 Nilgiri Biosphere Reserve, in the state of Tamil Nadu, Southern India (Srivastava 2009). Bandipur Tiger Reserve lies to the north and Wynaad Wildlife Sanctuary lies to the west and northwest of Mudumalai. Singara and Sigur Reserve forests form the southern and eastern boundaries (Figure 4.1). The wild elephant population in Mudumalai was estimated at 768 (95% lower and upper confidence interval = 536-1001) (Baskaran *et al.* 2010b). Mudumalai has been classified into three major habitats based on vegetation types (Champion & Seth 1968). For this study, only the DDF (≈ 195 km^2) was chosen for a finer spatial scale study. Due to permit restrictions, I was unable to regularly visit the moist deciduous and thorn forests in search of elephant. However, a focus on the DDF allowed increased replication and sampling.

4.3.2 Elephant behavioural observations (focal animal sampling)

Wild elephants were used to study the behavioural response of elephant to *L. camara* invasion while feeding. Field observations and measurements were conducted between January and May 2009, and November 2009 and May 2010. Observations of sub-adult and adult elephants were made during daylight between 0600 hours and 1800 hours. These elephants typically occurred in groups. Elephants were located from the road and

approached on foot, downwind, to minimize disturbance from observers. The first individual seen, or the closest elephant at the beginning of data collection was selected from the herd and focal animal sampling method (Altmann 1974) was adopted to sample its feeding. Observations were carried out from ground level and/or the vantage of a tree's branch (6 to 8-m above ground and above an elephant's reach). Locations of the feeding sites were taken where the sampling observation of an elephant began (Figure 4.1) using GPS (Garmin 60).

Observation periods varied from 10 minutes to five hours depending on the length of time the elephant was visible and normal feeding behaviour was observed (i.e. no disturbance from people, vehicles or other elephant groups). Viewing distance ranged from 10-m to approximately 50-m. Standard 7 × 50 binoculars were used for observations and care was taken to minimise disturbance to the group. When the focal elephant was not visible during the observation period, recording stopped and the interval was noted so that these minutes could be deducted from the sampling period. Recording of feeding behaviour (trunksful and steps, see below) resumed when the focal elephant reappeared. If a focal elephant remained out of view for more than five minutes, the next closest elephant seen at the time of observation was chosen for another sample, if changing the observer location did not address the situation. Fifty-seven elephants were sampled for a total of 64.3 hours.

To assess the behavioural response of elephant to *L. camara* invasion, I used feeding rates derived from observations of the number of trunksful·min^{-1}. This measure of feeding rate has previously been used to study the food intake of elephant (Baskaran 1998, Sivaganesan 1991). I followed their methodology in order to make studies comparable. Feeding rates, defined as the number of trunks of grass or browse that the focal elephant gathered with its trunk and put into its mouth, were recorded every minute until the elephant was no longer visible. Browse and major grass species that were eaten were identified and recorded.

To further assess the behavioural association between elephant and *L. camara* invasion, I also assessed stepping rates while feeding, derived from the number of steps·min^{-1} during the period of observation. One step was defined as the movement of one back foot from one place to another followed by the second foot, without placing the first foot back where it came from.

4.3.3 Sampling environmental covariates

The sites' characteristics (environmental covariates) between the start and end points of each sampling observation were measured from straight line transects. Transect lengths varied from 50 to 500-m depending on the distance the elephant moved during the sampling period. Environmental covariates of the feeding sites, measured from 10 × 1-m plots, spaced 50-m apart along each transect were *L. camara* invasion, tree density, canopy cover, browse density and percentage grass cover.

To estimate *L. camara* invasion, an index of the age of the stand defined by stem girth was derived. The girth of all *L. camara* plants at ground level were measured and recorded in 1-cm categories. An average girth for each plot was obtained. The average *L. camara* girth for each plot was averaged over all plots along each transect, to give an estimate of *L. camara* invasion for each transect, as the number of plots within each transect varied, depending on the distance the elephant moved. I also used the basal area as an alternative measure of *L. camara* invasion derived by multiplying the number of stems in a plot by the average stem girth (see Supplementary Method 2.2 and Supplementary Figure 2.2 (g - i) for the relationship between the different measures). The basal area measurement represents *L. camara* invasion dominance in space. Browse density (shrubs and saplings measuring 10 to 150-cm in height) was derived from the same plots measuring 10 × 1-m along each transect. A visual estimate of percentage grass cover to the nearest 5% cover was recorded in each plot. All grass species were grouped together without distinguishing the various species. The percentage grass cover was averaged over all plots and was used as the estimate for each transect.

Tree density[6] along each transect was estimated every 50-m using the point centred quadrant method, as described by Croze (1974). Canopy cover along each transect was estimated every 50-m using a 24 × 16-cm convex mirror divided into 24 equal squares (6 × 4 cells) similar to a densiometer and placed on the ground to reflect

[6] Absolute density (D) of the stand is calculated from the distance of the tree to the centre of the cross given by $D = \frac{K}{\bar{\bar{d}}^2}$ where $\bar{\bar{d}}$ = the mean of all distances = $\frac{\sum_{i=1}^{4n} di}{4n}$ where di is the distance of the i^{th} tree to the centre point, n is the number of stations, and K a constant.

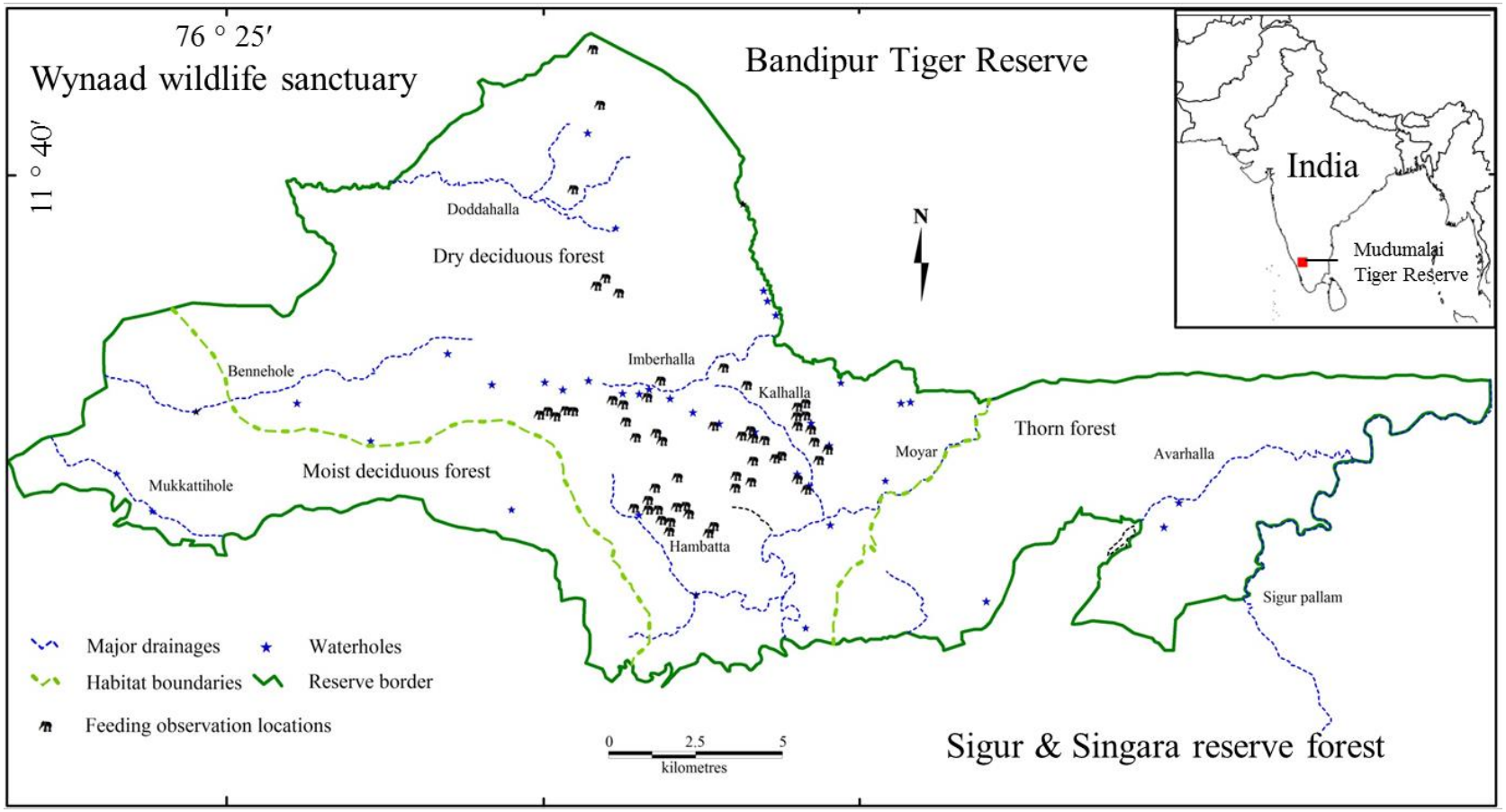


Figure 4.1: Mudumalai Tiger Reserve and its location in India showing locations of elephant feeding observations in the reserve within the dry deciduous forest. Major forest types: moist deciduous and thorn forest delimited by bright green dashed lines are also shown. Major drainages are shown by blue dotted lines and the locations of waterholes are shown by stars.

the canopy cover. A cell reflecting > 50% canopy cover was counted as having canopy cover while a cell reflecting < 50% canopy cover was ignored. The percentage canopy cover that was estimated at the point served an index of shade. The average value of canopy cover from all points within each transect was used as the estimate in the analysis.

4.3.4 Data analysis

Linearity was examined by plotting the relationship between the response variable (feeding and stepping rates) and each predictor variable (environmental covariates) using Minitab's lowess plot (smoothening parameter 0.5), Minitab 15 (Minitab, State College, PA, USA). To investigate multicollinearity between the environmental covariates, a correlation analysis was conducted. Because multicollinearity was a potential problem as tree density and canopy cover were significantly correlated, only canopy cover (and not tree density) was used in the stepwise multiple regression to assess the relationship between the response variable and predictor variables thereby providing valid parameter estimates and P-values. Feeding and stepping rates were tested against measured environmental covariates (*L. camara* invasion, percentage canopy cover, percentage grass cover and browse density) using stepwise multiple regression. The data were analysed using SPSS Statistics, 20.0 (IBM SPSS Inc., Chicago, IL, USA). Prior to analysis, all variables were transformed for normality using $\log_{10}$ and arcsine-square root transformations as appropriate.

To examine for relative direct and indirect effects of environmental covariates on feeding and stepping rates, I used a path analysis (Sokal & Rohlf 1981, Wright 1968). The process involves an analysis amongst a set of variables for a hypothesized causal structure or path model. A path analysis assumes linear relationships between variables with normal distributions. All variables were transformed to conform to this assumption, and analyses were conducted using AMOS 19.0 (Arbuckle 2010). Path analysis tests whether the total observed covariance structure is reflected in the covariance structure of a subset of relationships among a group of variables. If the covariance structure of the path diagram does not differ from the total observed covariance structure, then a statistically insignificant result will be obtained, indicating a good fit to the data (Arbuckle 2010). A hypothesised subset of relationships between

variables (path diagrams), one for feeding rates and one for stepping rates were constructed (Figure 4.4). In constructing the final model, I used logical inference rather than model selection.

4.4 RESULTS

The average number of *L. camara* stems seen was three per observation site and the largest average number of *L. camara* stems in a sample was 16. Ten sampling sites out of 57 had no *L. camara* present. *Lantana camara* girth ranged from no *L. camara*, to 9.50 cm, with an interquartile range of 3.06 cm, mean of 3.17 ± 2.31 cm (SD) (25^{th} percentile = 1.50 cm; 75^{th} percentile = 4.57 cm), in areas where elephant were observed feeding.

Fifty-seven elephants were observed over 64.3 hours. Elephants were never observed to feed on *L. camara*, but utilised grass species such as *Setaria intermedia*, *Digitaria* sp. and *Eragrostis* spp. growing on the edges of *L. camara* patches. These grass species appeared green (based on colour) and moist even in dry season. When feeding on tall grass species such as *Themeda cymbaria*, elephants were observed dusting the mud off the roots on their front feet and then feeding on the lower portion of the plant, discarding the upper portion and roots. Grass was a major component of elephant diet (88%, or 4399 of 4981 trunksful), while the remainder was browse (12%, or 582 of 4981 trunksful) which included shrubs and saplings. The tall grass *T. cymbaria* contributed 76.2% (3352 of 4399 trunksful) of diet, while *Pennisetum hokanackeri* found in the swamps, other tall grass species such as *Cymbopogon flexuosus*, *Imperata cylindrical* and short grass species such as *T. triandra* and *S. intermedia* constituted the rest (23.8%, or 1047 of 4399 trunksful).

4.4.1 Multiple regression

Stepwise multiple regression indicated that of the environmental covariates measured, *L. camara* was the only environmental covariate that significantly predicted feeding rates ($F_{1, 55} = 4.26$, P = 0.044), though, explained only 7% of the variability in feeding rates. The relationship between *L. camara* and feeding rates was negative ($\beta = -0.27$, $t =$

-2.06, P = 0.044, Figure 4.2). Canopy cover, grass cover and browse density were not associated with feeding rates (P ≥ 0.05). Using the basal area measure of *L. camara* as an alternative measure of *L. camara* dominance in space, there were no significant predictors in the model.

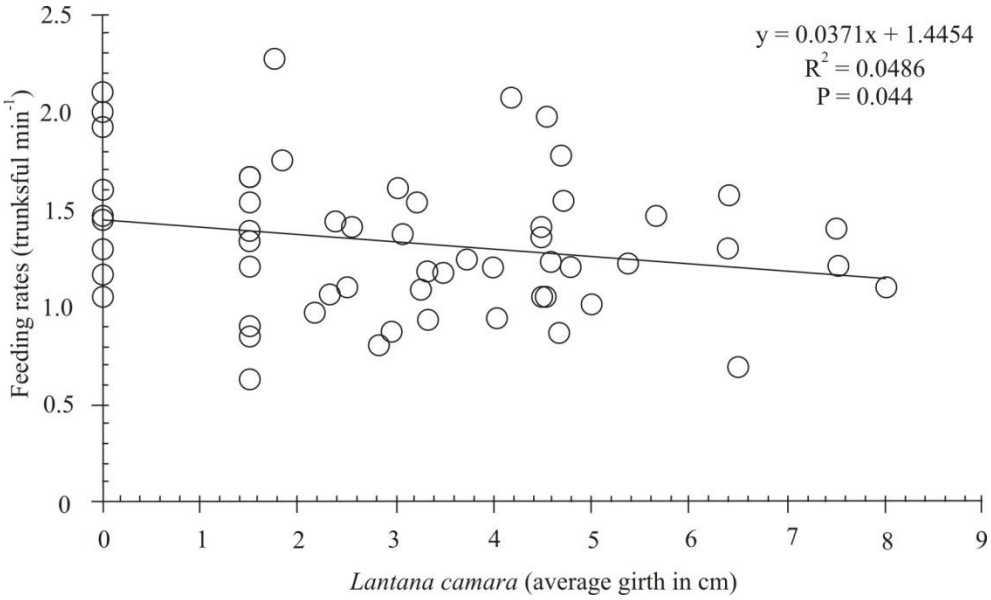


Figure 4.2: The relationship between *Lantana camara* and elephant feeding rates (trunksful·min^{-1}) in the dry deciduous forest of Mudumalai

Stepwise multiple regression was also used to predict stepping rates of elephant while feeding in different *L. camara* invasions. *Lantana camara* did not enter into the final model. The final model included grass cover and browse density ($F_{2, 55}$ = 11.16, P = 0.0001, R^2 = 0.30). These variables together significantly predicted stepping rates, and explained 30% of the variability in stepping rates. Stepping rates were negatively associated with grass cover (β = -0.35, *t* = -3.05, P = 0.004, Figure 4.3a) and positively associated with browse density (β = 0.39, *t* = 3.40, P = 0.001, Figure 4.3b). The use of the basal area as an alternative measure of *L. camara*, derived by multiplying the number of stems in plot by the average stem girth, produced the same significant predictors; grass cover (β = -0.41, *t* = -3.53, P = 0.001) and browse density (β = 0.36, *t* = 3.12, P = 0.003) as the use of average stem girth.

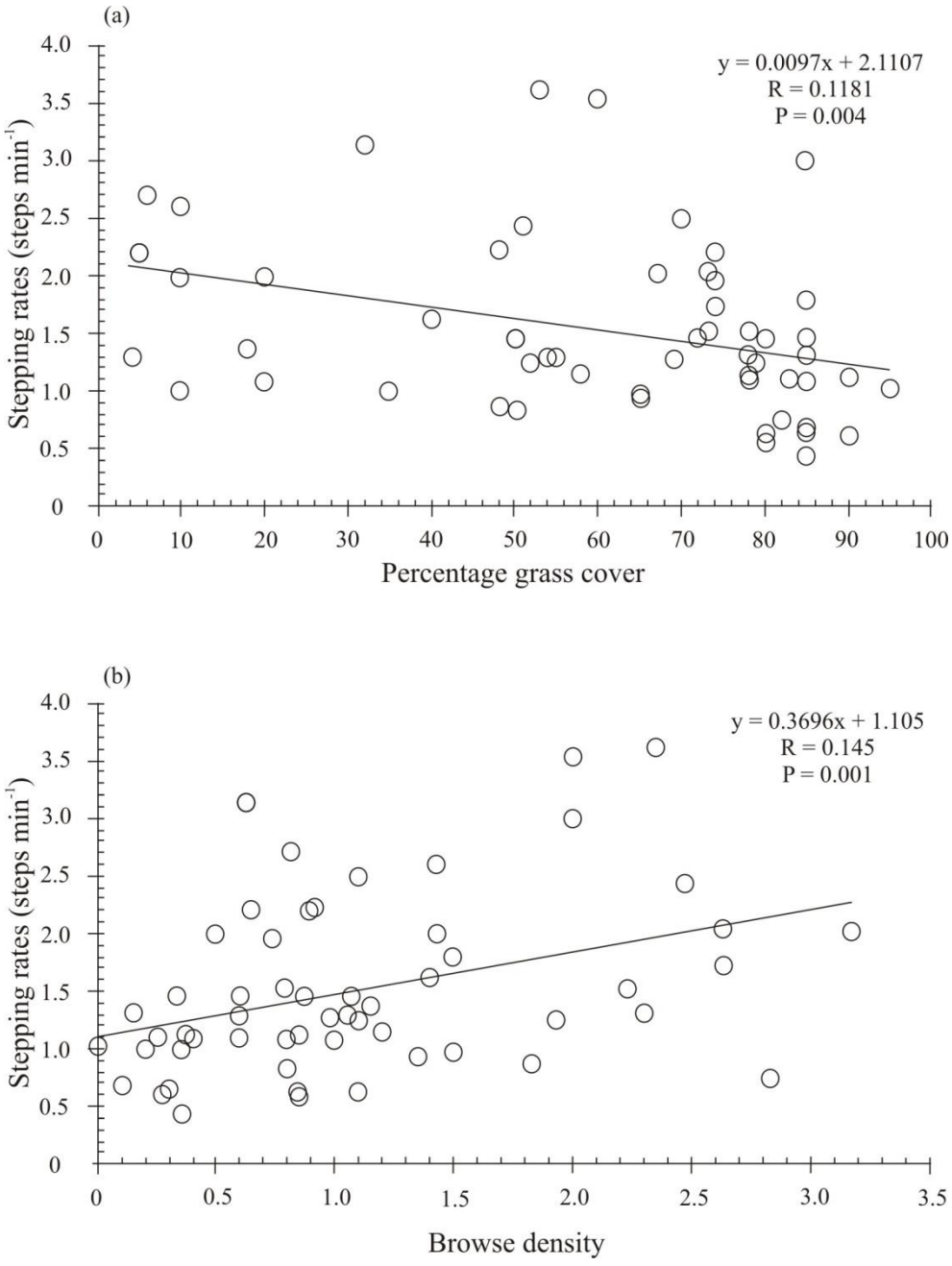


Figure 4.3: The relationship between elephant stepping rates and (a) percentage grass cover and (b) browse density.

4.4.2 Path analysis

In addition to the multiple regression analyses, I used a path analysis to estimate the relative importance of direct and indirect effects of *L. camara* and other potential

variables on feeding and stepping rates. Given that elephant feed on grass and browse, the path diagram predicted that grass cover and browse density had a direct effect on feeding rates, while *L. camara* had both direct and indirect effects on feeding rates mediated by grass cover and browse density (Figure 4.4a). The path diagram reflecting the relationship between stepping rates and environmental covariates predicted that grass cover and browse density have direct effects on stepping rates, while *L. camara,* which was my primary interest had both direct and indirect effects on stepping rates mediated by grass cover and browse density (Figure 4.4b).

Results from the path analyses for feeding rates (Figure 4.4a) produced an insignificant likelihood ratio test (χ^2 = 0.77, df = 1, P = 0.381), indicating a good fit to the data. As in the multiple regression analysis, the path analysis also suggested that feeding rates were negatively associated with *L. camara* (β = -0.27, P = 0.048). A significant negative association was seen between *L. camara* and grass cover (β = -0.29, *t* = -2.07, R^2 = 0.07, P = 0.043, Figure 4.5) indicating that *L. camara* invasion therefore may have resulted in reduced grass cover. The total effect of *L. camara* on feeding rates was -0.24 (0.05 + -0.02 = 0.03 + -0.27) [indirect effects through grass cover (-0.29 × -0.16 = 0.05) and browse density (-0.17 × 0.11 = -0.02) and direct effect (β = -0.27) on feeding rates]. However, because *L. camara* also had a strong direct negative effect on grass cover (β = -0.29, P = 0.023) but no effect on browse density (β = -0.17, P = 0.197), the indirect effects of *L. camara* on feeding rates were positive. Consequently, the overall negative effect of *L. camara* on feeding rates was reduced by ≈ 11% (from -0.27 to -0.24). Nevertheless, these variables (*L. camara*, grass cover and browse density) together explained only 9% of the variation in feeding rate.

The path analyses on stepping rates (Figure 4.4b) produced an insignificant likelihood ratio test (χ^2 = 0.762, df = 1, P = 0.383), again indicating a good fit to the data. The analysis suggested that stepping rates were negatively associated with grass cover (β = -0.39, P = 0.003) and positively associated with browse density (β = 0.38, P = 0.001). In agreement with the multiple regression analysis, *L. camara* was not associated with browse density (β = -0.17, P = 0.202). The total effect of *L. camara* on stepping rates was -0.02 (0.11 + -0.06 = 0.05 + -0.07) [indirect effects through grass cover (-0.29 × -0.39 = 0.11) and browse density (-0.17 × 0.38 = -0.06) and direct effect (β = -0.07) on stepping rates]. Again, the indirect effects of *L. camara* on stepping rates

were positive. As a result, the overall negative effects of *L. camara* on stepping rates were reduced by ≈ 71% (from -0.07 to -0.02). These variables together explained only 28% of the variation in stepping rate which was less than the variation explained in the multiple regression (30%).

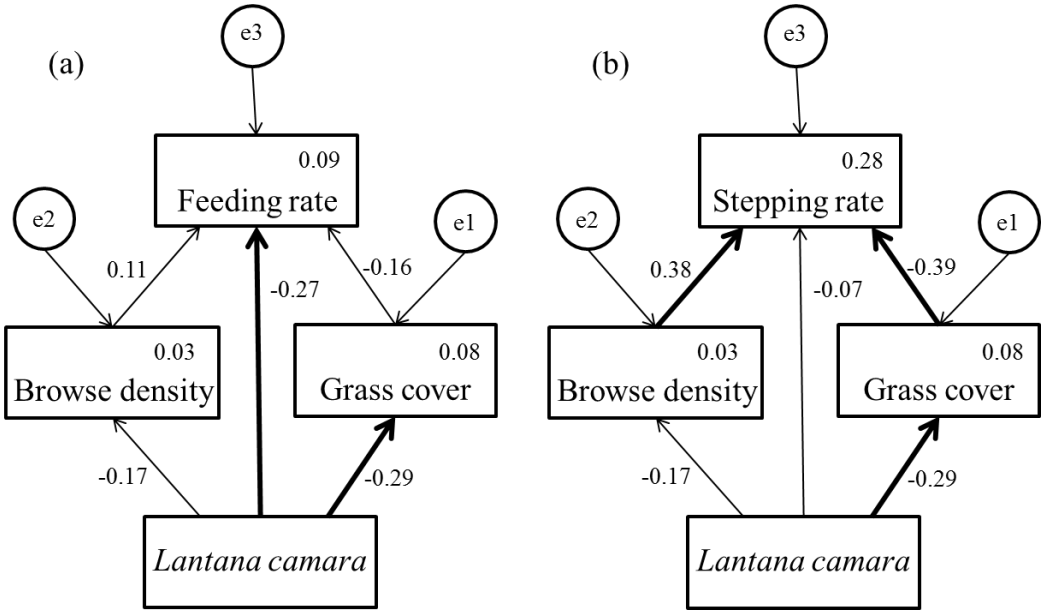


Figure 4.4: Path diagrams and path coefficients of (a) feeding rates and (b) stepping rates. The path diagram predicted that (a) grass cover and browse density had a direct effect on feeding rates while *Lantana camara* had direct and indirect effects on feeding rates through grass cover and browse density; (b) grass cover and browse density had direct effects on stepping rates while *Lantana camara* had direct and indirect effects on stepping rates through grass cover and browse density. Numbers in the boxes are R^2 values. Numbers near the arrows are path coefficients, and the circles labelled e1, e2 and e3 refer to error terms (n = 57). Significant relationships are shown by thick arrows. Path coefficients can be compared directly.

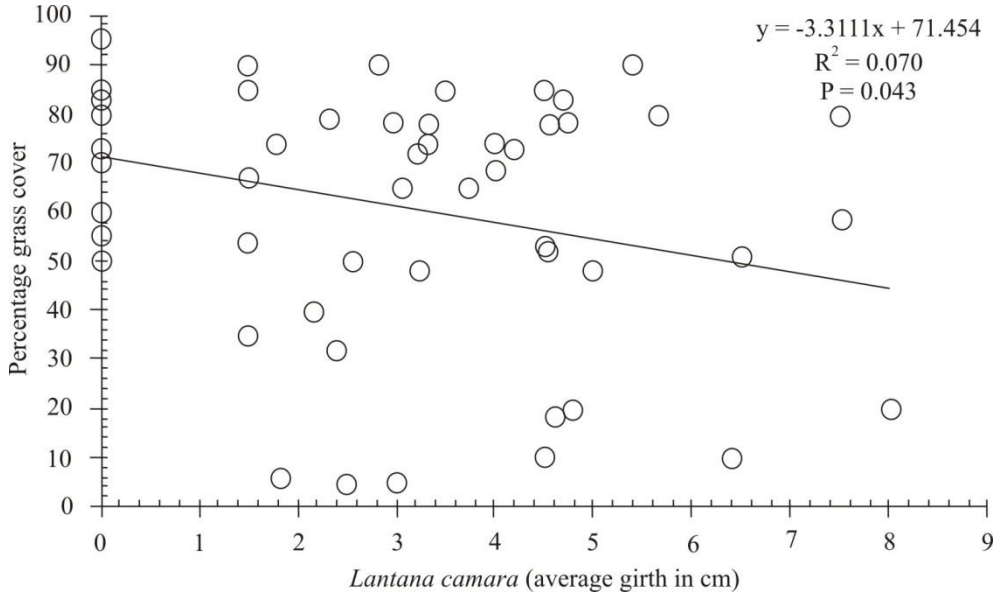


Figure 4.5: The relationship between percentage grass cover and *Lantana camara* in the dry deciduous forest of Mudumalai Tiger Reserve.

4.5 DISCUSSION

In this study, I examined the behavioural response of elephants to *L. camara* invasion while feeding in the dry deciduous forest (DDF) of Mudumalai. Previous studies have shown that invasive weeds can influence foraging strategies of mammals either through reduction in forage production or reduced utilization of invaded habitats (for example, Hein & Miller 1992, Trammell & Butler 1995). Elephants were never observed to feed on *L. camara*, and my results from the multiple regression indicated that feeding rates declined with an increase in *L. camara* invasion.

Path analysis indicated an overall negative association of *L. camara* on feeding rates. The direct negative association of *L. camara* on feeding rates were however reduced by 11% as a result of the indirect positive effect of *L. camara* on feeding rates through grass cover and browse. Most of the indirect positive effects of *L. camara* on feeding rates were because of reduced grass cover where *L. camara* was more prevalent and so elephants increased their feeding rates. Additionally, smaller trunksful size in areas with more *L. camara* but reduced grass cover (pers. obs.) may explain the positive association. Although indirect positive effects were observed, the overall effect was still

negative indicating that *L. camara* reduced feeding rates of elephants because of the negative association of *L. camara* with grass that forms major elephant food. Nevertheless, the indirect relationships remain to be tested. Thus, the positive indirect effects of *L. camara* through grass and browse as seen from the path analysis may be a consequence of elephant increasing their feeding rates because of lower grass biomass available, contrary to a site that is highly invaded and hence a direct negative association of feeding rates with *L. camara* where there was no grass. In contrast, elephants may increase the size of their trunksful (pers. obs.) where there is more grass biomass in uninvaded or lower *L. camara*-invaded sites. In my study however, trunksful size was assumed to be constant, although in reality trunksful size probably varied considerably. Any future assessment of feeding would ideally include measurement of the quantity of grass taken in each trunkful so as to better correlate feeding rates with *L. camara* invasion.

The variation in feeding rates explained by *L. camara*, grass cover and browse density was only 9% which suggests that a number of unmeasured environmental covariates could explain more of the variation in feeding rates. For example, grass species composition, height of grass stand, texture, palatability and nutrient content, none of which were measured in this study, have been shown to contribute to variation while feeding (Baskaran *et al.* 2010a, Sivaganesan & Johnsingh 1995, Sukumar 1989a). Lower feeding rates may also reflect a decline in forage quality and availability during the dry season (Ruggiero 1992) when this study was conducted or availability of unpalatable grass species growing near or within *L. camara* stands (Prasad 2012). In addition to these factors, terrain conditions and the uniform distribution of preferred food also contribute to variation in feeding patterns (Vanculenberg 1977) and warrants further investigation.

The negative association of *L. camara* with feeding rates most likely resulted from the reduction and decline of grass, a major elephant food source (88%). The decline in grass as *L. camara* invasion increased is supported by other studies (Fensham *et al.* 1994, Kumar *et al.* 2012, Prasad 2012) and it has been suggested that grass and *L. camara* may be almost mutually exclusive (Prasad 2012). Preferred elephant foraging areas of the DDF that were once covered with grass species like *T. triandra* and *T. cymbaria* and formed the bulk of elephant forage have now been heavily invaded by *L.*

camara (N. Sivaganesan, pers. comm.). While elephant appear to continue to use *L. camara*-invaded habitats (Chapter Three) and forage on the available grass within and around *L. camara* patches, there may be changes to their foraging strategy as a consequence of this invasive plant. In my study, elephants were observed to feed on grass species such as *Setaria intermedia, Digitaria* spp, and *Eragrostis* spp. growing on the edges of *L. camara* patches. Such use has previously been attributed to the soft texture and palatability of these grasses that also remained green and moist in the dry season (Sivaganesan & Johnsingh 1995) and were observed to be rich in nutrients (Daniel *et al.* 1995). It is possible that elephants may also be increasing the use of these species in their diet due to the reduction in the grass areas and remains to be tested.

Stepping rates were, however, not significantly associated with *L. camara* invasion. Instead, results from the multiple regression indicated that grass cover and browse density significantly predicted stepping rates and explained 30% of the total variation in the data. The path analysis allowed me to determine the importance of the direct and indirect associations of *L. camara* through grass and browse with stepping rates, which indicated a positive indirect association. The positive indirect association of stepping rates with *L. camara* may be again reflecting the reduction of grass cover, and that elephants are stepping more to find grass. Alternatively, the overall negative association of *L. camara* with stepping rates, as suggested by the path analysis, indicates that possibly *L. camara* may be restricting elephant movement confining feeding to the available grass, hence resulting in reduced stepping rates.

The significant negative correlation between stepping rates and grass cover that was observed is likely to be a reflection of the availability of the principal and bulk forage which is grass. In plant communities with higher densities of preferred forage, animals are known to stay longer (Senft *et al.* 1987). In addition, selection of plant parts eaten by elephant may have reduced movement rates. In the DDF, Sivaganesan and Johnsingh (1995) recorded elephants feeding on the lower parts of tall grass species while discarding the upper portion. This selection was attributed to the crude protein and palatability of the lower portion of these grass species in the dry season. Elephants in my study were also observed spending time dusting off the mud from the root section and chewing the lower portion and discarding the roots and top portions of grass. Such behaviour may have caused elephant to reduce their stepping rates as grass cover

increased because they spent more time in one area with grass, which is their preferred forage (Baskaran *et al.* 2010a), rather than moving constantly in search of more grass.

The positive correlation between stepping rates and browse density indicated that elephant appeared to seek out sites with greater availability of grass, since grass forms a major component of elephant diet. In addition, elephant may prefer to move out into more open areas (with less understory) perhaps to ensure protection and avoid ambush predators such as leopards (Blake 2004) and tigers, avoid or minimize insect bites (Sivaganesan, pers. comm.) and possibly to maintain visual and olfactory contact with other members of the herd, as has been suggested for the African elephant (*Loxodonta africana*)(Martin 1978, Poole *et al.* 1988). It is also likely that browse density can affect the availability of grass or the quality and composition of grass (Riginos *et al.* 2009), thereby contributing to an increase in stepping rates.

I used a path analysis because it allows pathways for several independent variables, in addition to ranking the evident influence of potential causal factors. While similar amounts of variation were explained by multiple regression and path analysis on feeding and stepping rates (feeding rates, 7% and 9% respectively; and stepping rates, 30% and 28% respectively), the path analysis also provided evidence of direct and indirect effects of *L. camara* on feeding and stepping rates. This evidence however, is correlational and does not explicitly indicate a cause-effect relationship between the variables. In order to untangle the effects of various factors and to properly test for causal relationships among the variables, an experimental approach, outside of the dry season and over multiple seasons is necessary. During the duration of my study, owing to the nature of the permits provided by the reserve managers, no experimental work could be conducted nor could the work be carried out over multiple seasons.

4.5.1 Conclusions

I found that wild elephants do not eat *L. camara* and this invasive plant is taking the place of elephant forage such as grass. The results of my study suggest that the association of invasive weeds such as *L. camara* with elephant behaviour is complex and that there are a number of variables that interact to determine elephant behaviour in a weed infested habitat. However, my data is suggestive of the possibility that invasive

weeds such as *L. camara* are capable of modifying certain aspects of elephant behaviour. Some behaviours, nevertheless, are apparently not associated with weed invasion, for example, stepping rates. My study suggests that if *L. camara* continues to spread or the existing stands increase in density, grass availability for elephants may become a constraint leading to an over-exploitation of the existing grass stands. Further studies are required to experimentally test whether *L. camara* is responsible for the displacement of grass or whether grass is displaced by other factors such as increased herbivory and fire, and *L. camara* is opportunistically invading. In addition, experimental studies should be conducted to assess other behavioural responses of elephant to weed invasion.

CHAPTER FIVE

GENERAL DISCUSSION

Exotic plant invasions are a cause for concern particularly in pristine ecosystems, which are storehouses for biodiversity (Blossey 1996, Higgins *et al.* 1999). Consequently, documenting the presence, spread and changes that invasive exotic weeds may bring about, becomes fundamental to managing these invasions (D'Antonio & Vitousek 1992). Invasive exotic plant species are often reported to alter native floral species' community composition either through competition for resources such as nutrients, light and water (Braithwaite *et al.* 1989, Walter 1972) or displacement of native species by allelopathic means (Fuerst & Putnam 1983, Heirro & Callaway 2003). Invasive exotic weed species are not only capable of altering native floral species composition, they are also capable of influencing habitat use by mammals either through a displacement of native forage or by acting as physical barriers (Rice *et al.* 1997, Trammell & Butler 1995). In my dissertation, I examined three main aspects of the exotic weed, *Lantana camara* and its association with changes in: 1) floral species assemblage and richness, elephant browse plants and grass cover, 2) elephant habitat use across habitats and at a finer spatial scale within habitats, and 3) elephant feeding behaviour.

A key finding of my research is that *L. camara* is presently not eaten by elephant and that it seems to displace native floral species such as grass, which is an important source of elephant forage (Chapter Two and Four). The results of my research also suggest that *L. camara* is significantly associated with differences in floral species assemblage and richness, and an altered percentage grass cover in the dry deciduous forest (DDF) and moist deciduous forest (MDF) of Mudumalai Tiger Reserve. Additionally, I found that *L. camara* invasion was associated with a decline in the percentage grass occupancy in all three habitats of the reserve (MDF, DDF and TF) suggesting direct competition for space. In the thorn forest (TF), however, I found no evidence that *L. camara* was associated with floral species assemblage, richness, and percentage grass cover (Chapter Two). I also found no evidence that *L. camara* was associated with elephant habitat use across the three forest types (MDF, DDF and TF). By contrast, I did find evidence that elephant habitat use, was significantly negatively associated with *L. camara* in the DDF, when assessed within habitat (Chapter Three). Lastly, I used feeding and stepping rates to examine for any evidence of modification of

elephant behaviour while feeding in different densities of *L. camara* invasion. My results indicated that *L. camara* invasion was significantly associated with decreased feeding rates, but no change in stepping rates. *Lantana camara* appears to be capable of modifying certain aspects of elephant behaviour, possibly through a reduction of grass and browse, owing to increased weed invasion (Chapter Four).

My study indicated a significant negative correlation between *L. camara* and grass cover (Chapter Two). This negative correlation suggests that as *L. camara* continues to spread, grass cover is reduced from many areas of the reserve. Reduction of grass cover is cause for concern as elephant are dependent on grass for the bulk of their diet, as my and previous studies on elephants in Mudumalai have demonstrated (Chapter Four, Baskaran *et al.* 2010a, Sivaganesan & Johnsingh 1995). In addition to the depletion of certain grass species, the overgrazing of existing grass areas by elephant and other herbivores could reduce the overall carrying capacity of elephant in Mudumalai. While the over-exploitation of grasses by elephants in the DDF was not observed during the present study, such a phenomenon may be inevitable in the future (N. Sivaganesan, pers. comm.), particularly if elephants are confined to the reserve due to loss of important habitat corridors (Sivasubramaniyan & Sivaganesan 1996).

Another line of evidence for the association of *L. camara* with elephant provided by this study is the apparent association of *L. camara* with elephant habitat use only at a finer spatial scale within the DDF and not the entire landscape scale (Chapter Three). African elephants appear to make top-down foraging decisions first by selecting landscapes and then habitats within those landscapes, and finally, species within habitats (Shrader *et al.* 2012). Therefore, in order to determine impacts of invasive weeds on elephant, fine scale studies appear to be better suited since foraging decisions appear to be made at the finer scale. My results not only indicate the importance of studying elephant habitat use at different scales, but also suggest that the association of *L. camara* with elephant is not uniform and may have different effects across habitats and within specific habitats (Chapter Three).

My results indicating no significant association of *L. camara* with elephant habitat use at the landscape scale could imply that there is actually no effect of *L. camara* at this scale. Given the patchy distribution of *L. camara* in Mudumalai, it may be that any effect of *L. camara* on elephant would not be seen across habitats, as

elephants have home ranges in excess of 500 km^2 in this part of South India (Baskaran *et al.* 1995). Furthermore, given that *L. camara* currently occupies a relatively small proportion of the larger landscape, one might not see landscape effects of *L. camara*. Alternatively, one of the reasons for no significant association of *L. camara* with elephant habitat use across habitats could possibly be because my study was conducted during the dry season, when elephants are expected to show a clumped distribution around water sources (Baskaran 1998, Sukumar 1989b). Thus, sampling during the wet season, when elephants may be distributed more evenly may reveal a relationship to the presence of *L. camara.* I was unfortunately not permitted by Indian conservation authorities to sample in the wet season. In addition, the lack of a relationship across habitat types may also be because the presence of dung that was used as a measure of elephant habitat use merely indicated the presence of elephants in the area but not what exactly elephants were using the habitat for (Chapter Three). Thus, we may not see a significant relationship between elephant habitat use and *L. camara* across habitat types at the landscape scale.

Additionally, studies on Asian elephants have shown fidelity to their home ranges (Baskaran *et al.* 1995, Desai 1991). This fidelity would restrict elephant to habitats available within their home ranges, which may not include all the different habitat types present in the larger landscape. Therefore, even if an adjoining habitat contains better forage, elephants may not necessarily use these habitats simply because they are out of their home ranges (Baskaran 1998). Furthermore, we do not know what role hierarchy plays in terms of elephant selecting their habitats. It has been suggested that elephant appear to apparently abide by the 'ideal-despotic distribution' rather than the 'ideal-free distribution' of habitat use (Baskaran 1998, Fretwell 1972, Fretwell & Lucas 1970). Thus, if certain areas of the reserve are dominated by *L. camara* but are a part of an elephant's home range, elephants may continue to go back to those areas despite reduced food resources. Food in the form of grass is present in and around *L. camara* patches. Elephant may still use the habitat to gain food, but take longer for harvesting so as to avoid consuming *L. camara*. Such habitat usage could possibly result in poorer body condition and reduced reproductive success, despite not showing a reduced use of the area (Baskaran 1998). Hence, it is likely that elephant habitat use may not be modified until the habitat is radically altered by invasive weeds such as *L.*

camara. The extent to which a vegetation community may be restructured, may vary with extent of change to the vegetation structure (Harris *et al.* 2003), and as long as there is a high proportion of indigenous vegetation, particularly in newly invaded areas, these sites will continue to be used by native fauna (Mgobozi *et al.* 2008). The lack of a significant association of *L. camara* invasion with elephant habitat use at the landscape scale could also indicate the importance of long term monitoring studies to assess the role that invasive weeds may have on changes in elephant home ranges and in turn on their habitat use. A limitation of my study was the short sampling period (extending over two dry seasons) which may not be sufficient to see any significant changes to elephant habitat use at the landscape scale that could possibly be brought about by *L. camara* over a period of many years.

5.1 Implications for other species

A number of studies on the impact of invasive weeds on native fauna have demonstrated the negative effects of invasive exotic plants either through the loss of native forage species, or because they act as a physical barrier or a deterrent due to the unpalatable nature of these weeds (for example, Bedunah 1992, Kutt & Fisher 2011, Maron & Lill 2005, Scheiman *et al.* 2003, Tyser & Key 1988). The significant negative association of *L. camara* with grass cover indicates a reduction of forage species for grazers in addition to elephant. In addition, changes to the floral species assemblage and richness brought about by weed invasion, can alter the availability of browse species (Chapter Two) for other herbivores. At the extreme end of the spectrum of herbivore responses, Baskaran *et al.* (2009) postulated that even small alterations in the vegetation physiognomy could potentially eliminate species such as the four-horned antelope (*Tetracerus quadricornis*) that prefer open patches over areas that are invaded by weeds or because of vegetation changes brought about by weed invasion. Higher abundance of four-horned antelope was found in sites with lower weed cover in Mudumalai, and a decline in this species' range was attributed to weed invasion that created dense undergrowth unsuitable for four-horned antelope (Baskaran *et al.* 2009, Baskaran *et al.* 2011b). So as *L. camara* continues to spread, uninvaded areas may be used more, creating increased herbivore pressure in smaller areas.

Lantana camara was negatively associated with elephant habitat use (Chapter Three) and feeding rates in the DDF (Chapter Four), despite elephant in the study area ranging over large areas (greater than 500 km^2) (Baskaran *et al.* 1995), and being capable of feeding on both grass and browse depending on season and availability (Baskaran 1998, Sukumar 1989a). For herbivores with more specialised diets and habitat requirements, it is possible that invasive exotic weeds such as *L. camara* can be more detrimental, particularly when the weeds are toxic or displace forage species and occupy space.

5.2 Future research directions

Despite the correlative approach used in this study, the results of my study have provided some baseline information on the association of invasive weeds with the floral species community, and on elephant habitat use and their feeding behaviour. I was unable to experimentally manipulate aspects of this system due to permitting and time issues. The lack of approval to conduct experimental manipulation in this reserve has by nature reduced my ability to conclusively determine the role of *L. camara* in altering native floral species assemblage and richness, elephant habitat use and elephant feeding in this reserve. Thus, further experimental manipulation and research is required and recommended to substantiate the findings provided here so we have a better understanding of the role of invasive weeds and define their role using the passenger-driver model proposed by MacDougall and Turkington (2005). Specifically, it is possible that *L. camara* invades and then causes habitat change and consequent feeding modification by elephant, or it may also be possible that *L. camara* can only invade sites that are disturbed. The management response to the 'passenger' or 'driver' model consequently varies. Correlational studies are useful, but experimental studies are necessary to determine the role of *L. camara* as a passenger or driver of changes in this system.

One way to demonstrate whether exotic plants are the 'driver' or 'passenger' of floral community change is to set up long term monitoring sites where there is no anthropogenic disturbance. Using a control site, seeds of an exotic plant such as *L. camara* can be sown at one site, and some form of anthropogenic disturbances such as cattle grazing or fire created in another site, and changes to the floral community

monitored over time and compared. With all variables equal at all experimental sites, and the exotic plant as the only variable at play, we can identify whether the exotic plant is the 'driver' or a 'passenger' of alterations in the plant community. Such longer term study sites have been useful in highlighting invasive species interactions elsewhere (for example, Duggin & Gentle 1998, Gentle & Duggin 1997b).

Some communities such as riparian vegetation have been shown to recover without consequences to species diversity after the removal of an invasive weed (Hejda & Pyšek 2006). However, where allelopathy is a mechanism that is used by an invader, it is also necessary to study the role of allelopathy to understand the long-term effects of exotics on native species regeneration. Monitoring and comparing the floral species composition before and after removal of exotic weeds is also essential. These types of experiments have been used elsewhere, such as in wet sclerophyll forests (Gooden *et al.* 2009a), dry rainforests-open forest ecotones in Australia (Duggin & Gentle 1998), and in tropical dry forests of India (Prasad 2010). In addition, species-specific and site-specific experiments may be required as the impacts of invasive species can be variable. For example, there was a significant increase in native floral species richness and diversity in the UK following the removal of an invasive plant *Impatiens glandulifera* (Hulme & Bremner 2006). However, removal experiments of *I. glandulifera* in the Czech Republic did not produce a significant increase in native floral species richness and diversity, and this difference was attributed to the difference in cover of the invader (Hejda & Pyšek 2006). Thus, further research on mechanisms used by various invaders and their consequent impacts to the native flora need to be monitored continuously as follow up procedures may be required for several years (DiTomaso 2000).

Lantana camara is an aggressive widespread invasive weed from South America that currently occupies around 13.2 million ha of pasture land besides forest and fallow areas in India (Sharma & Raghubanshi 2011). Efforts to eradicate and control *L. camara*, including the use of fire, physical, chemical and biological controls or a combination of these methods have been used in India, Australia and South Africa where *L. camara* is a problem (Babu *et al.* 2009, Bhagwat *et al.* 2012, Love *et al.* 2009, Vardien *et al.* 2012, Yeates & Schooler 2011). In India, successful restoration of *L. camara*-infested sites has been limited to a few sites (Babu *et al.* 2009, Love *et al.* 2009, Rana & Singh 1999). Limitations to controlling *L. camara* include cost, man-power,

accessibility to invaded sites, or even management intervention that may also facilitate further invasion because of disturbance in the process of weed removal (Buckley *et al.* 2007, Day *et al.* 2003). Furthermore, *L. camara* control via biological and chemical control methods are less favoured methods because of the potential adverse effects these methods may have on native biota (Love *et al.* 2009). Success in controlling *L. camara* invasion using classical biological control varies because biological control has been confounded by the diverse hybrid composition (many horticultural hybrids and wild species) of *L. camara* (Sanders 1987, Vardien *et al.* 2012). Further research is required on which methods of control are most effective, cost-efficient, and suitable depending on the extent and location of invasion.

There is a lack of information on the role of elephant in facilitating the spread of *L. camara* although their destructive feeding habits of pushing down trees, and opening up the canopy are well known (Sivaganesan & Sathyanarayana 1995, Sivasubramaniyan & Sivaganesan 1996). Canopy gaps facilitate *L. camara* invasion by allowing more light to enter in (Fensham *et al.* 1994, Totland *et al.* 2005). Studies on the African elephant have shown that high elephant density can lead to an increase in size and number of paths which open up dense vegetation and gives access to other herbivores (Kerley *et al.* 2004, Landman *et al.* 2007). Additionally, these elephant were also responsible for a reduction in floral species richness through herbivory, trampling and path formation (Landman *et al.* 2007), zoochory (Lewis 1987), and nutrient cycling (Paley & Kerley 1998). Thus, both elephant and exotic weeds may have dramatic consequences on the various species of flora and fauna. Therefore, the role of elephant in facilitating the spread of invasive weeds requires further research. This kind of research would be particularly important if elephant populations were to increase.

Now that we know *L. camara* has a significant negative association with elephants in terms of habitat use in certain habitats and modification of certain aspects of elephant feeding, it is important to assess how elephants are coping with changes that are brought about by weed invasion through a reduction of their food species. Are elephants broadening their range of food species to compensate for the loss of favoured food plants and are these new species of poorer quality? Or are elephant feeding more on rare and endangered food species leading to a further decline? In work that is not reported here, I observed captive elephant feeding occasionally on *L. camara*. However,

this was most probably because these elephant were frequently taken to areas around the elephant camps that are heavily invaded by *L. camara* and no other forage species were present (pers. obs.) and hence had no option but to feed on *L. camara*. Nevertheless, this does provide reason to believe that wild elephant could or might eventually include *L. camara* in their diet, should other food be limited. This feeding could lead to the further spread of *L. camara*, as elephant are well known for their seed dispersal capabilities in Asian forests (Campos-Arceiz & Blake 2011, Campos-Arceiz *et al.* 2008, Jothish 2013). Finally, what are the consequences of reduction of food species to elephant: will feeding on poorer quality of food lead to poor health and body conditions, and in turn reduced reproduction and relative fitness? A major issue that managers are currently facing is the change in elephant population size (Baskaran *et al.* 2010b). If the population is increasing, it creates more pressure on food such as grass and trees, which may further facilitate invasion. Thus monitoring the elephant population is also required.

In retrospect, it would be appropriate to incorporate covariates such as other competing herbivores like domestic cattle, goats and other wild ungulates into my thesis and the analyses of my data. Initially, I attempted to monitor variables like cattle use through dung deposition, but this was abandoned because dung is harvested and sold as manure. Consequently, estimating cattle grazing would have been underestimated by such methods. Estimating cattle and wild ungulate use was a time intensive approach and would have taken more time than I was able to invest. Should there be future research into this system, I would recommend some degree of change in the approach used or covariates that I examined to include measures of competing herbivores as a potential for alterations to the floral species assemblage, richness, elephant habitat use and feeding behaviour.

5.3 Management recommendations

Based on the findings presented in my dissertation, the following management recommendations may be suggested;

- Wild elephant do not appear to eat *L. camara* (Chapter Four). Since *L. camara* is negatively associated with grass indicating that *L. camara* takes the place of grass (Chapter Two, Prasad 2012), which is a major part of elephant diet in this

reserve (Chapter Four, Baskaran *et al.* 2010a, Sivaganesan & Johnsingh 1995), controlling the spread of *L. camara* would be appropriate to maintain food resources for elephant. This could include the use of fire, biological, physical, or chemical control, or a combination of these methods (but see limitations above).

- *Lantana camara* appears to be capable of altering the grass cover and floral community in the DDF and MDF (Chapter Two), changing elephant habitat use (Chapter Three) and some behavioural characteristics of elephant in the DDF (Chapter Four). Given the limited resources that managers are faced with, and the magnitude of the weed invasion problem in Mudumalai, all the research presented here indicates that more attention should be focused in controlling the spread of *L. camara* first in the DDF and then the MDF. Despite the TF having the most number of invaded sites, it appears that invasion here does not significantly impact floral species assemblage, richness and percentage grass cover (Chapter Two). Consequently, management of *L. camara* in the TF may therefore be considered low priority.
- If grass becomes scarce for elephants, tree-mortality may increase as elephants push down trees or damage the canopy (Sivaganesan & Sathyanarayana 1995) to obtain more food, thus opening up the canopy and perhaps even facilitating invasion. Previous studies on elephant populations have already cautioned an increase in the elephant population (Baskaran *et al.* 2010b). Thus, monitoring the role of elephant in facilitating invasion is important.
- Anthropogenic disturbances such as roads and settlements are capable of altering floral species assemblage and richness (Chapter Two, Mishra *et al.* 2004, Ramírez-Marcial *et al.* 2001) and also appear to influence elephant habitat use (Chapter Three). In addition, previous studies have also shown disturbance to be an important factor in promoting weed invasion (Berry *et al.* 2011, Butcher & Kelly 2011, Duggin & Gentle 1998, Gentle & Duggin 1997b). Management restrictions on anthropogenic disturbances to prevent collection of fuel-wood, non-timber forest products and anthropogenic fires should be enforced, and alternative livelihoods provided to villagers living on the fringes of the reserve.
- An inventory of invasive weeds and their current distribution would be useful to monitor and document their increase and spread, and subsequent changes brought about to the floral community (Chapter Two, D'Antonio & Vitousek

1992). This would also provide some indication of the rapidity of spread so that management checks could be put in place to curb the spread of invasive exotic weeds.

- Different habitats have varying floral species communities (Chapter Two). Habitat-specific management programs such as planting of native saplings or sowing seeds of native plants that are declining should be considered. More importantly, those that are able to resist exotic plant invasions and may be elephant food species like Bamboo spp. and grass species such as *Axonopes* sp. that can co-exist with or even out-compete *L. camara* (Chapter Two, Kumar *et al.* 2012) may be required. The habitat can thereby be managed to be productive and maintain the faunal community that depend on the habitat.
- The current fire management program may have to be revised and planned based on more scientific research. The current practices of controlling fires by cutting fire lines, or early burning may in fact not be ideal, as more litter accumulates and when fires do occur, they are more severe and cause great loss bringing about changes to both the floral community and promote the spread of exotic weeds, like *L. camara* (Chapter Two, Hiremath & Sundaram 2005).

5.4 Final conclusions

Lantana camara has spread substantially since its introduction into India at the beginning of the 19th century (Bhagwat *et al.* 2012, Kannan *et al.* 2012). It has been predicted to spread further due to its ability to thrive on nutrient poor soil and affect the physicochemical properties of the soil, and is capable of driving ecosystem changes either by out-competing native species or occupying vacant niches (Bhatt *et al.* 1994, Osunkoya & Perrett 2011). The combined impact of elephants and invasive weeds, together with other forces such as fires, can have a dramatic impact on the ecosystem, and communities of flora and fauna that live in these ecosystems (Mgobozi *et al.* 2008, Pellew 1983). The findings presented in this dissertation provide new insight into the biology and understanding of the interaction and association of invasive weeds and elephants. For example, we now have information on which habitats and which plant species within these habitats appear to be most affected by *L. camara*. Such information will enable managers to prioritize management decisions with limited funds available.

The interaction between elephants and invasive weeds (for example, Prasad & Williams 2010) has previously received very little attention. My work has contributed substantially as we now know that *L. camara* does have an association with variation in the floral species assemblage and richness and grass cover in the MDF and DDF. Further, the percentage grass occupancy significantly declines as *L. camara* invasion increases in the reserve. *Lantana camara* is associated with a decline in elephant habitat use within specific habitats. Finally, direct and indirect effects of *L. camara* and its interactions with other factors such as grass and altering browse species are also capable of modifying certain aspects of elephant behaviour in the DDF of Mudumalai. Together, my research findings increase our understanding of the complexity of the association between the invasive weed *L. camara* and the Asian elephant.

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SUPPLEMENTARY MATERIAL

Research permits: Copy of the terms and conditions of the permit provided by the Conservator of Forests and Field Director, Mudumalai Tiger Reserve, India to carryout research presented here.

Proceedings of the Conservator of Forests and Field Director, Mudumalai Tiger Reserve, Udhagamandalam.

PRESENT: Dr. Rajiv K. Srivastava, I.F.S.,
Conservator of Forests and Field Director.

Ref.No. T/7240/2008. **Dated 10-09-2009.**

Sub- Permission to carryout study on "Diet and Habitat use by Elephant in response to a prolific weed Lantana Camera at Mudumalai Tiger Reserve for a period of one year from May 2009 to April 2010" – Regarding.

Ref:- 1) Letter from Mr. Ajai A. Desai, Member, Steering Committee, Project Elephant (Govt. of India) B.C. 84, Camp, Belgaum lr. Dt. 05-10-2008.
2) This office Ref. No. 7240/2008-T, dated 17-11-2008.
3) Principal Chief Conservator of Forests and Chief Wildlife Warden, Chennai – Ref. No.WL5/57210/2008, dated 25-05-2009.

((((())))))

As per the above reference, permission is hereby granted to Mr.Gaius Wilson, South India Biblical Seminar, Bangarapet, Karnataka to carryout **Study on "Diet and Habitat use by Elephant in response to a prolific weed Lantana Camera at Mudumalai Tiger Reserve for a period of one year from May 2009 to April 2010",** subject to the usual terms and specific conditions laid down below:-

1. Study inside the Reserve Forests/Sanctuary/National Park will be allowed only between morning 6.00 AM and evening 6.00 PM.
2. This permission for entry inside the Sanctuary in only for the aforementioned persons and for the aforementioned period and also the permission is hereby granted for the vehicle No. KA 12 M 3477 for the purpose of study work only during the above period.
3. All the Rangers are to be informed in advance (atleast one week before) about the place of visit inside the Sanctuary and the Researchers shall enter into the Reserve Forests only with the assistance of a guide or field staff provided by the concerned Ranger.
4. At the end of every calendar month, following things should be submitted to this office with a copy to concerned Range Officer.
   - Progress Report for the last month (noteworthy findings, observations, sightings, etc.,) and
   - Next month's plan of action (planned places of visit, purpose or study in ensuing calendar month, etc.,)
   - Any suggestions relating to Conservation of nature or Management of Sanctuary/National Park.
5. At the end of work, the team shall furnish to this office and the concerned Range office, a detailed conclusive report about the results of his study / research / work.
6. Every member of the research shall abide by all the laws, rules, orders and guidelines, which are meant for Conservation of nature. He will be assumed to know the penal provisions of the acts like, Wildlife (Protection) Act, 1972, Tamil Nadu Forest Act, 1882, etc.,

Permits (continued……)

7. Following things are banned inside the Sanctuary :-
   - Carrying of Fire Arms.
   - Carrying liquor, plastic articles, cigarettes, tobacco and music system
   - Playing of music, making noise and shouting.
   - Littering the areas inside the Sanctuary.
   - Damaging the habitat by plucking leaves, cutting branches from trees kindling fire, erecting temporary of permanent shed etc.,
   - Teasing wild animals and birds.
   - Causing disturbance to tribals living inside the sanctuary.
   - Collection of capture of any samples including fauna, flora, soil, rock and minerals, etc., unless specifically sanctioned by Conservator of Forests and Field Director, Udhagai.

8. Any other instructions given by the Conservator of Forests and Field Director or the concerned Rangers shall be obeyed.

9. Permission for the visit is provisional and may be cancelled, by competent authority, due to the following reasons:-
   - Violations of any Laws, Rules, Orders, Guidelines, etc., (even found on a later date)
   - Any other administrative reasons.

10. After completion of the study work, the Researcher should make a presentation at the convenient date fixed by the Principal Chief Conservator of Forests. The Publication must duly acknowledge the assistance of field staff and Tamil Nadu Forest Department in the research project.

11. After completion of the above study period, the applicant should send both the hard copy and soft copy of the study report to this office.

12. The researcher has paid Rs.5,000.00 (Rupees Five Thousand Only) towards caution deposit vide Banker Cheque No. 021488, dated 09-09-2009 of State Bank of Travancore.

    A sum of Rs.300.00 has been collected vide C.F. 61 No. 657107 of 10-09-2009 for entering the Mudumalai Tiger Reserve.

Sd/-Rajiv K.Srivastava
Conservator of Forests and Field Director.

To
Mr.Gaius Wilson, South India Biblical Seminary, Post Box 20,Anandagiri, Bangarapet-563 114, Karnataka.
Copy submitted to the Principal Chief Conservator of Forests & Chief Wildlife Warden, Chennai
Copy to Dr.N. Kalaivanan, Forest Veterinary Assistant Surgeon, Theppakkadu to render necessary arrangement.
Copy to all Rangers for information and necessary action.

/ t. c. b. o. /

Superintendent
10-9-09

Sp/- (T/Research Permission) we : msw.
10/9/09

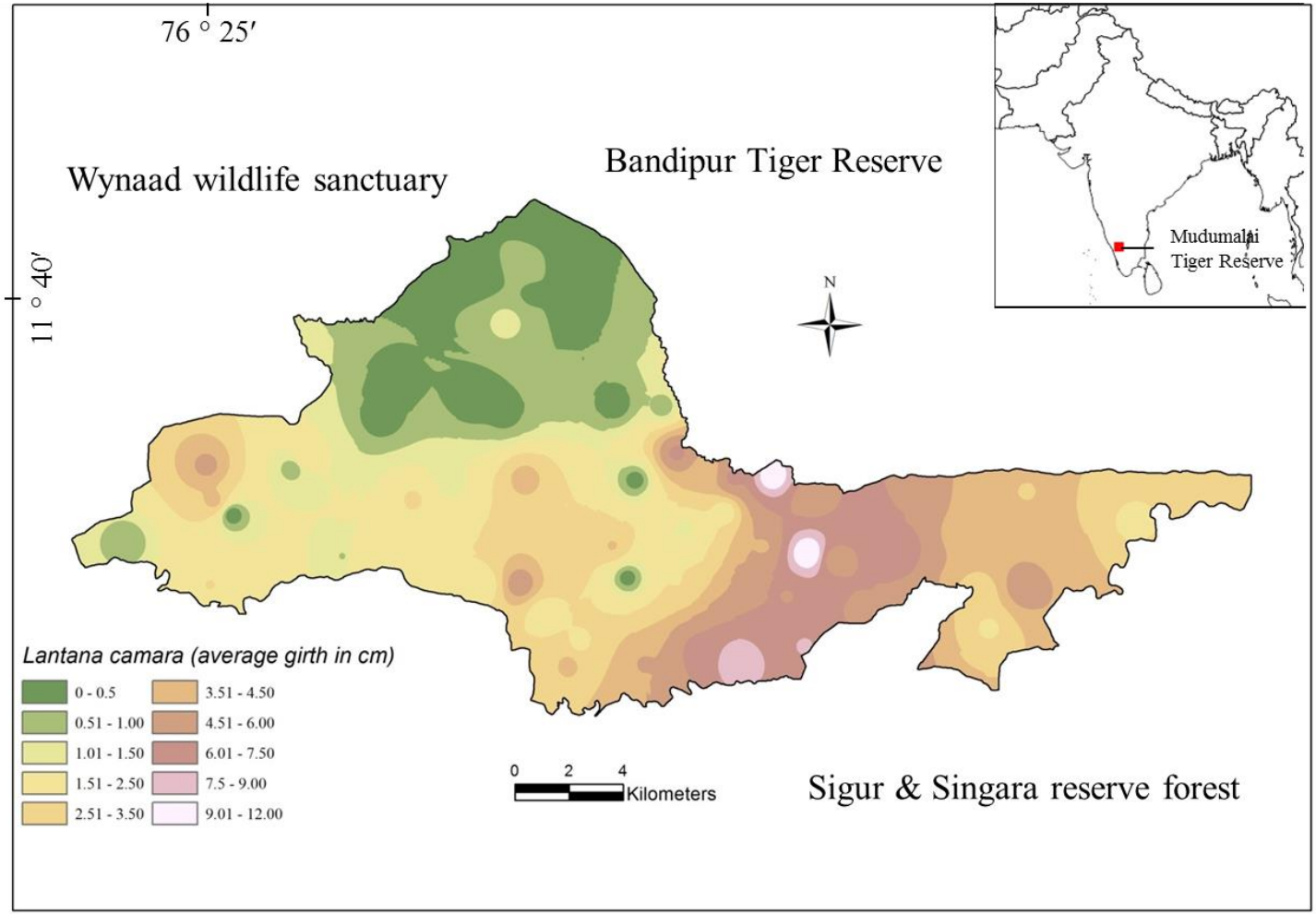
Supplementary Table 2.1: Georeferenced locations of transects laid across Mudumalai Tiger Reserve that were used to sample the vegetation community and elephant habitat use.

	Start		Finish	
Transect number	Longitude East	Latitude North	Longitude East	Latitude North
1	76.53354	11.58862	76.54204	11.59244
2	76.55755	11.57498	76.56000	11.58368
3	76.52580	11.58031	76.52228	11.58857
4	76.54984	11.59846	76.54074	11.59929
5	76.53787	11.57703	76.54540	11.58225
6	76.58173	11.56989	76.57677	11.57752
7	76.57224	11.59831	76.57661	11.60623
8	76.57173	11.59611	76.56285	11.59374
9	76.56927	11.61127	76.56600	11.61901
10	76.55035	11.63340	76.55688	11.63970
11	76.53391	11.63491	76.54159	11.63991
12	76.48183	11.60690	76.48271	11.61591
13	76.52122	11.64108	76.52069	11.65002
14	76.50697	11.66998	76.51293	11.67691
15	76.50689	11.58190	76.50486	11.57306
16	76.60927	11.58190	76.61155	11.59060
17	76.60049	11.60249	76.60453	11.61049
18	76.58744	11.59470	76.58676	11.58570
19	76.52469	11.60619	76.52866	11.61415
20	76.52034	11.54756	76.52471	11.55546
21	76.66420	11.59906	76.67296	11.60162
22	76.54175	11.60857	76.54769	11.61537
23	76.51549	11.57199	76.51287	11.56339
24	76.48632	11.64012	76.49523	11.63789
25	76.46879	11.63922	76.46414	76.46414
26	76.43927	11.61893	76.43012	11.62085
27	76.40153	11.60183	76.40755	11.60865
28	76.65482	11.59105	76.64786	11.59677
29	76.65777	11.56533	76.66618	11.56165
30	76.67862	11.57660	76.66943	11.57707
31	76.47528	11.60388	76.46673	11.60732
32	76.44730	11.58287	76.45371	11.58927
33	76.49456	11.57273	76.49339	11.58178
34	76.45895	11.62869	76.46129	11.63744
35	76.50142	11.63849	76.50189	11.62947
36	76.70757	11.60121	76.71233	11.59348
37	76.61469	11.56836	76.62384	11.56860

Supplementary Table 2.1 (continued……)

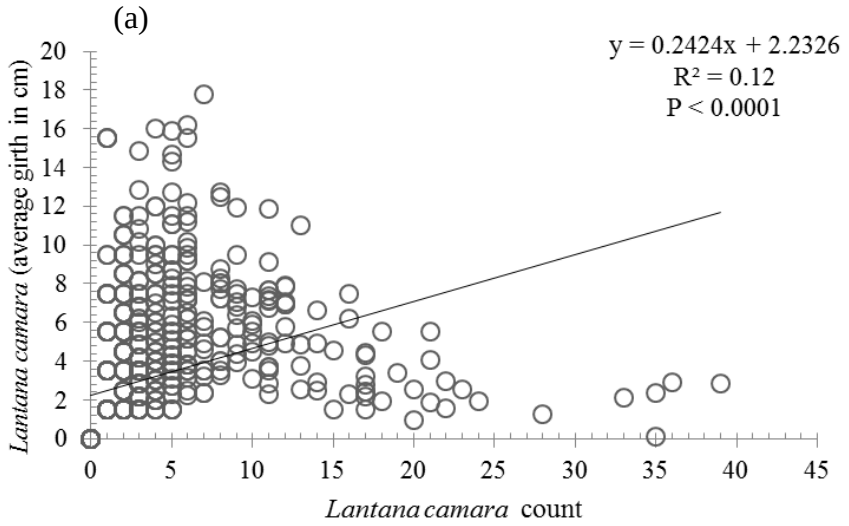
	Start		Finish	
Transect number	Longitude East	Latitude North	Longitude East	Latitude North
38	76.59278	11.61715	76.58740	11.60984
39	76.58190	11.61166	76.57314	11.61453
40	76.56286	11.61872	76.55491	11.62322
41	76.55060	11.54813	76.54434	11.55473
42	76.56269	11.55675	76.57089	11.55271
43	76.59465	11.57770	76.59551	11.56878
44	76.48197	11.59184	76.49109	11.59105
45	76.50917	11.60763	76.50669	11.61685
46	76.57461	11.54975	76.58208	11.55503
47	76.59810	11.55396	76.60339	11.56126
48	76.59839	11.58523	76.60567	11.59079
49	76.51865	11.68318	76.52765	11.68503
50	76.50828	11.68716	76.50284	11.67977
51	76.49815	11.68210	76.48977	11.67847
52	76.50150	11.66962	76.50225	11.66060
53	76.51048	11.70198	76.51496	11.69416
54	76.40313	11.61206	76.40142	11.62093
55	76.37865	11.59552	76.37308	11.58831
56	76.40374	11.58182	76.40357	11.57283
57	76.68868	11.58608	76.69219	11.59444
58	76.55655	11.59627	76.56568	11.59541
59	76.43011	11.61309	76.43217	11.62183
60	76.63102	11.58526	76.63396	11.59377
61	76.50555	11.59827	76.51432	11.59539
62	76.52241	11.56000	76.52990	11.55458
63	76.45199	11.58410	76.44416	11.58884
64	76.65637	11.56968	76.65964	11.57827
65	76.40925	11.60503	76.41251	11.59635
66	76.67884	11.60743	76.66981	11.60873
67	76.52236	11.67015	76.52879	11.66360

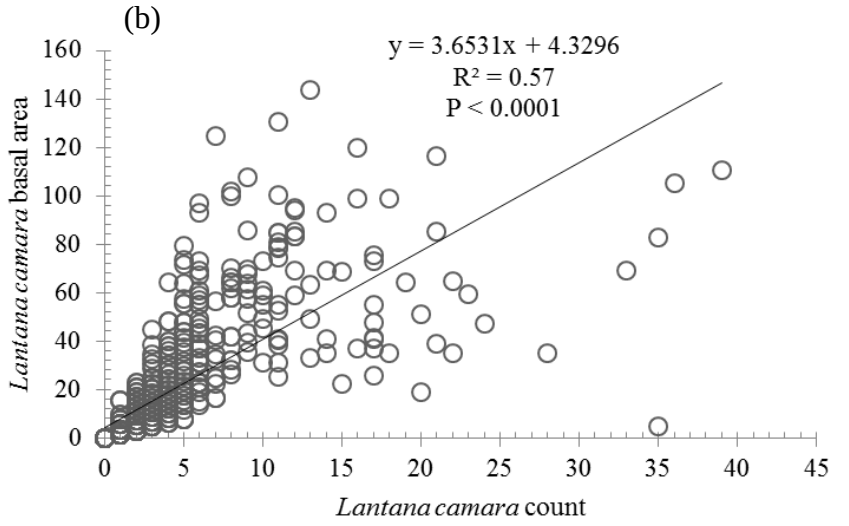
Supplementary Method 2.1: ArcMap 10.1 (ArcGIS 10.1, ESRI 2012) was used to create a thematic map of *Lantana camara* presence using the Spatial Analyst tool. The GPS locations along with their respective measures of *L. camara* invasion (average stem girth) were imported into ArcMap to generate a thematic map. Inverse distance weighting was used to create an interpolated surface of *L. camara.*

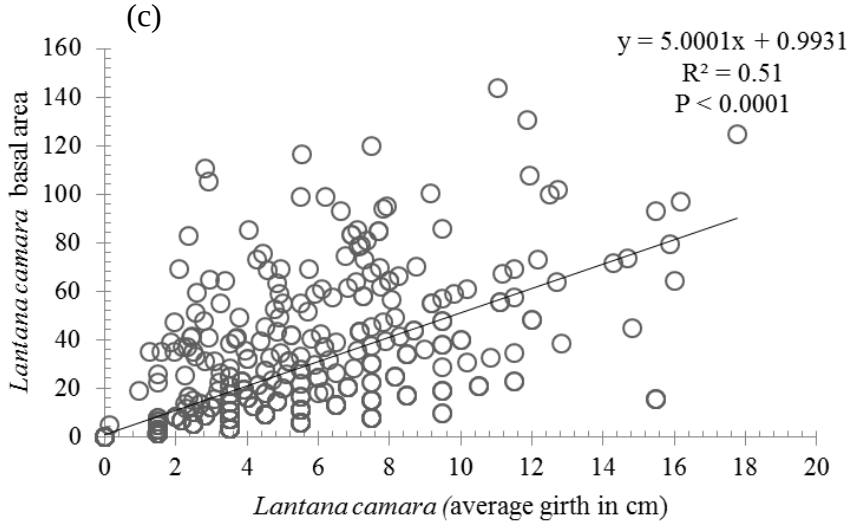


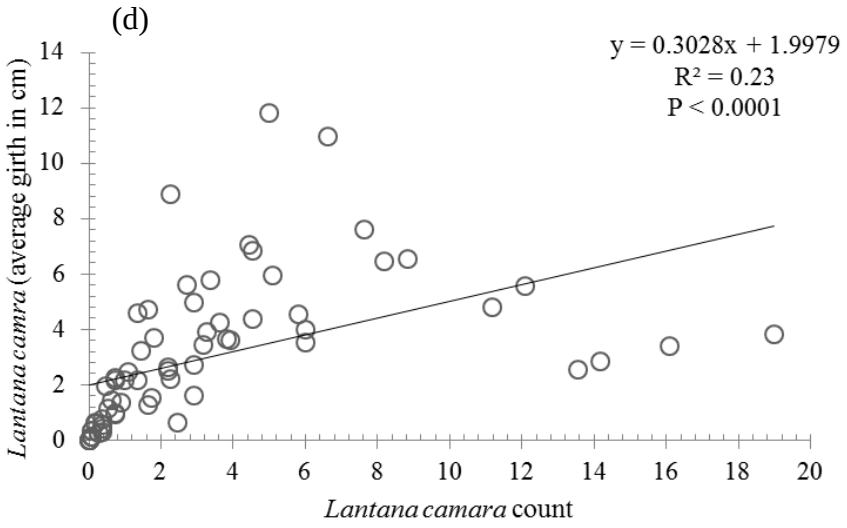
Supplementary Figure 2.1: The presence of *Lantana camara* (average stem girth of transects) in Mudumalai Tiger Reserve, southern India. The northern regions of the reserve have some areas that are free of *L. camara* invasion while the rest of the reserve has variations of low to high infestation.

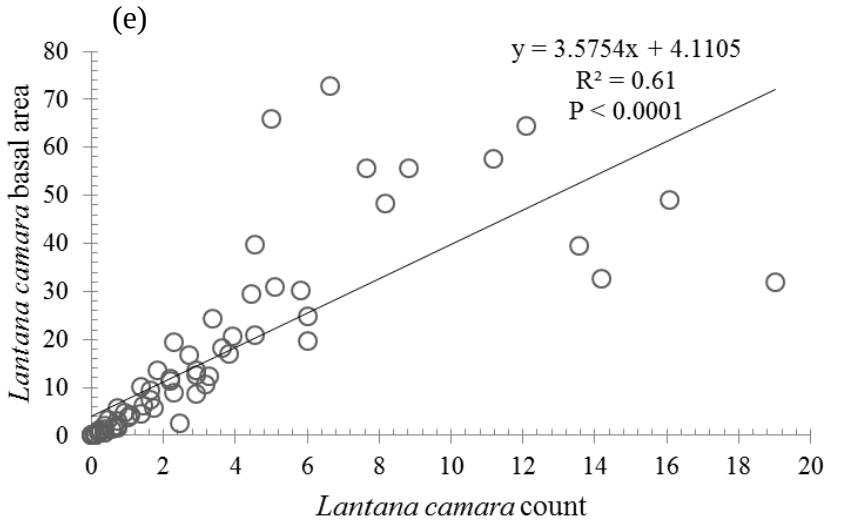
Supplementary Method 2.2: In my thesis, the three measures of *Lantana camara* invasion were stem counts of *L. camara* in each 10 × 1-m plot, average girth of *L. camara* in each plot and basal area derived by multiplying the stem count by the average girth of each plot. All three measures could be used to examine the relationship between *L. camara* and the vegetation community (Chapter Two), elephant habitat use (Chapter Three) and elephant behaviour (Chapter Four). The figures below show that all three measures were positively correlated ($P \leq 0.004$) with each other indicating that the use of any of the measures likely yielded similar results. However, contrary to my expectation, there was a positive correlation between the average stem girth and stem count (Supplementary Figure 2.2a, d and g). Nevertheless, this relationship was weak explaining only 12% (plot-wise), 22% (transect-wise) and 14% (feeding transect-wise) of the variation respectively. Given the large number of plots without *L. camara*, it was likely that the relationship between the average girth and count was positive. I therefore excluded the plots without *L. camara* and examined the relationship between the average stem girth and stem count. When examined plot-wise, I found that there was no significant relationship between the average stem girth and stem count of *L. camara*. However, when examined transect-wise, I found that there was still a significant positive relationship between the measures of girth and count. It appears that both older and young *L. camara* plants grow together and hence a positive relationship was observed between the average stem girth and stem count. Therefore, the age of the stand (presumed to be represented by the average stem girth) may be a better predictor of the changes brought about by *L. camara* to the vegetation community because plant communities take longer to respond as plants have to die off. Elephants on the other hand may be to responding to what they see at any particular time and the measure of the basal area of *L. camara* may be more immediate and indirectly predict habitat use. I expected a stronger relationship between elephant habitat use and the index of the basal area of *L. camara.* Instead I found that stem girth was a better predictor of elephant habitat use.

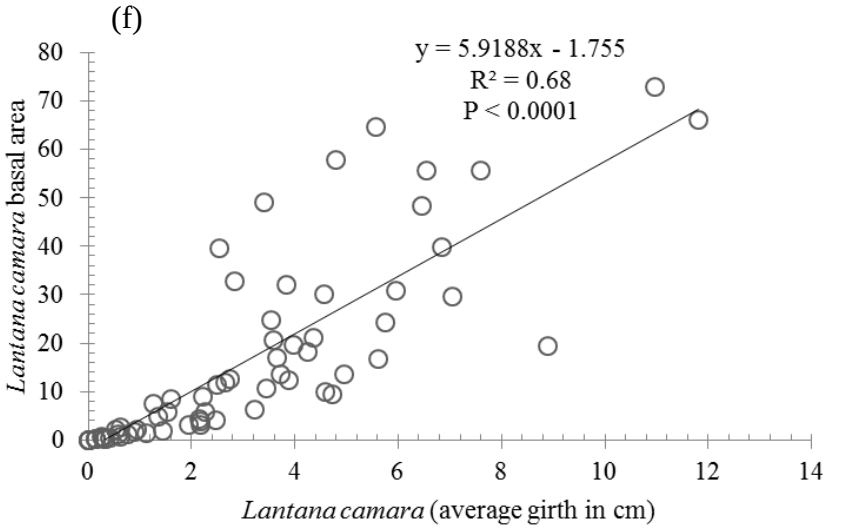

(a)
y = 0.2424x + 2.2326
R² = 0.12
P < 0.0001
Lantana camara (average girth in cm)
Lantana camara count


(b)
y = 3.6531x + 4.3296
R² = 0.57
P < 0.0001
Lantana camara basal area
Lantana camara count

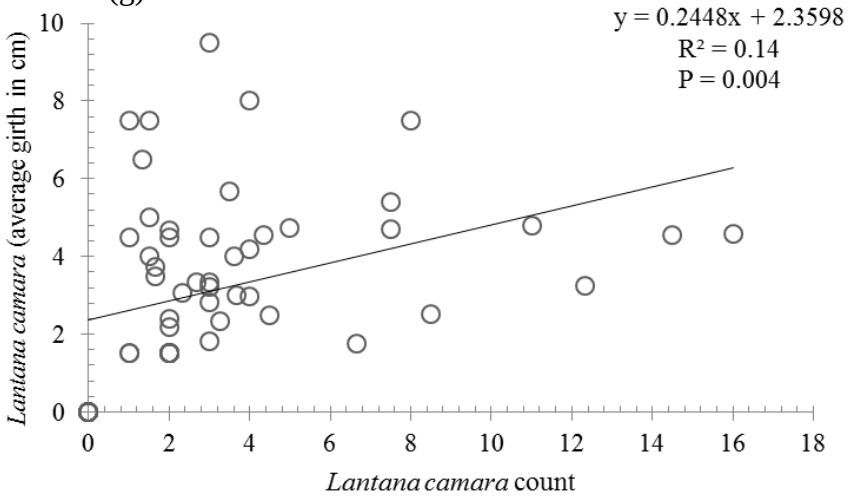

(c)
y = 5.0001x + 0.9931
R² = 0.51
P < 0.0001
Lantana camara basal area
Lantana camara (average girth in cm)


(d)
y = 0.3028x + 1.9979
R² = 0.23
P < 0.0001
Lantana camara (average girth in cm)
Lantana camara count

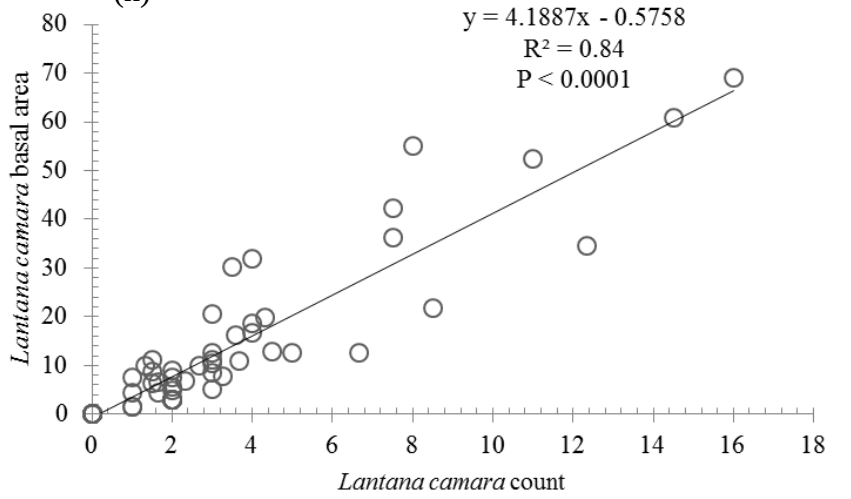

(e)
y = 3.5754x + 4.1105
R² = 0.61
P < 0.0001
Lantana camara basal area
Lantana camara count


(f)
y = 5.9188x - 1.755
R² = 0.68
P < 0.0001
Lantana camara basal area
Lantana camara (average girth in cm)

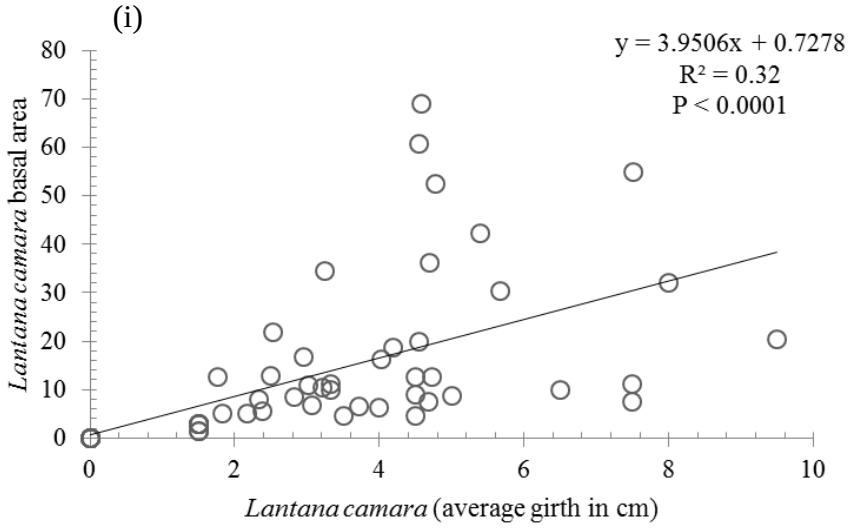
(g)


y = 0.2448x + 2.3598
R² = 0.14
P = 0.004
Lantana camara (average girth in cm)
Lantana camara count

(h)


y = 4.1887x - 0.5758
R² = 0.84
P < 0.0001
Lantana camara basal area
Lantana camara count

(i)


y = 3.9506x + 0.7278
R² = 0.32
P < 0.0001
Lantana camara basal area
Lantana camara (average girth in cm)

Supplementary Figure 2.2: The relationship between the three measures of *Lantana camara* per plot (a) average stem girth and stem count (b) *L. camara* basal area and stem count (c) *L. camara* basal area and average stem girth; and per transect (d) *L. camara* average stem girth and stem count (e) *L. camara* basal area and stem count (f) *L. camara* basal area and average stem girth; per (feeding) transect (g) average stem girth and stem count (h) *L. camara* basal area and stem count and (i) *L. camara* basal area and average stem girth.

Supplementary Method 2.3:

R code used to derive model coefficients

```
library(vegan)
Sdata<-read.csv("MTR_Final.csv")
summary(Sdata)

Sdata$roads<-as.factor(Sdata$roads)
Sdata$settlements<-as.factor(Sdata$settlements)
Sdata$Habitat<-as.factor(Sdata$Habitat)

summary(Sdata)
Y<-Sdata[2:80]
Yprime<-log(Y+1)
summary(Y)

model<-adonis(Yprime ~ Canopy + Grass + Fire + Habitat + Status +
roads + settlements + Count, Sdata, permutations=9999)
summary(model1)
model$coefficients
```

Supplementary Table 2.2: The linear regression of environmental covariates including the alternative measure of *Lantana camara* invasion from the basal area (number of stems × average stem girth in the plot) predicting percentage grass occupancy in Mudumalai Tiger Reserve. *Lantana camara* invasion, canopy cover and the interaction terms of habitat (moist deciduous forest [MDF] and dry deciduous forest [DDF]) with *Lantana camara* were statistically significant. The interaction term, Thorn forest (TF) with *Lantana camara* was used as the reference category.

	Coefficients			t	P
	Unstandardized		Standardized		
	B	SE	Beta		
(Constant)	78.177	4.228		18.491	0.0001
Lantana camara	-.330	.073	-.241	-4.498	0.0001
Canopy cover	-.091	.044	-.078	-2.065	0.039
Fire	-.357	.726	-.019	-.492	0.623
Tree density	-7.052	21.254	-.011	-.332	0.740
Roads	1.467	1.822	.036	.805	0.421
Settlements	-2.865	1.944	-.067	-1.474	0.141
MDF × *Lantana camara*	-.308	.139	-.088	-2.211	0.027
DDF × *Lantana camara*	-.317	.090	-.179	-3.524	0.0001

Supplementary Method 3.1: In Chapter Three, I used dung density as an estimate of elephant habitat use. Some authors have utilized a conversion factor to convert elephant dung density estimates to elephant density estimates (for example, Ishwaran 1993, Sukumar 1989b). This may be appropriate in some circumstances because conversion of elephant dung density estimates to elephant density estimates incorporates seasonal and habitat dung decay and defecation rates. In Mudumalai, Daniel *et al.* (2008) showed that mean decay rates (days) in micro-habitats varied from 81.5 SE = 2.5 days to 121 SE = 11.2 days. Nevertheless, 63 fresh dung piles (42 dung piles in the dry deciduous forest [DDF], 10 dung piles in the thorn forest [TF] and 11 dung piles in the moist deciduous forest [MDF]) were marked and monitored to ensure that previous published estimates were applicable during this study. These dung piles were revisited once every week until the dung piles disappeared. Elephant density *(E)* was calculated using equation (1)

$$E = (Y \times r) / D \qquad (1)$$

where *Y* is density of dung piles km^{-2}, *r* is dung decay rate day^{-1} (the daily rate of disappearance of dung piles) and *D* is defecation rate day^{-1}. A dung deposition rate of 14.98 (Daniel *et al.* 2008) was used to convert dung density to elephant density estimates. Dung piles monitored in this study had a mean decay time of 103 days (n = 42, SE ± 5.46, 0.0097 decay rate day^{-1}) in DDF and 72 days (n=10, SE ± 6.63, 0.0138 decay rate day^{-1}) in TF, similar to the rates described by Daniel *et al.* (2008). Dung piles marked in MDF could not be monitored and the decay rates were not analysed. Eleven dung piles in the DDF burned in a forest fire and were subsequently not used in the analyses.

Supplementary Table 3.1: Using elephant density estimates, these data were analysed and produced the same significant predictors when using dung density estimates with different B and SE values. Model 3 with *Lantana camara* on its own, the interaction terms of *L. camara* with the dry deciduous forest (DDF) and moist deciduous forest (MDF) and environmental variables predicting elephant density estimates across habitats in Mudumalai Tiger Reserve. The Beta Coefficients, SE, Wald Chi-Square and levels of significance with main effects of environmental variables measured are shown. Factors (habitat, impact of settlements and roads) are entered as multiple dummy variables. For categorical factors with greater than two levels, the ranges of Beta Coefficients and SE are given.

Source	B	SE	Type III		
			Wald Chi-Square	df	P
(Intercept)	-0.4	1.4	3.5	1	0.063
Habitat	1.68 – 2.06	1.44 – 1.56	5.7	2	0.334
Impact of settlements	1.09 – 1.12	0.63 – 0.70	1.8	2	0.406
Impact of roads	-0.73 - 0.73	0.48 – 0.94	3.4	5	0.181
Canopy cover	0.0	0.0	0.5	1	0.482
Grass cover	0.0	0.0	0.3	1	0.558
Fire	0.1	0.1	0.4	1	0.524
Water	0.1	0.3	0.1	1	0.764
Lantana camara	0.3	0.1	2.9	1	0.087
MDF × *Lantana camara*	-0.2	0.3	0.9	1	0.351
DDF × *Lantana camara*	-0.4	0.2	4.8	1	0.028

Supplementary Table 3.2: Model 3 using the basal area as an alternative measure of *Lantana camara*, derived by multiplying the number of stems in a plot with the average stem girth. The model included *Lantana camara* (basal area) on its own, the interaction terms of *L. camara* with the dry deciduous forest (DDF) and moist deciduous forest (MDF) and environmental variables predicting elephant dung density estimates across habitats in Mudumalai Tiger Reserve. However, the model overall was not significant and there were no statistically significant predictors when using the *L. camara* index invasion derived from the basal area. The Beta Coefficients, SE, Wald Chi-Square and levels of significance with main effects of environmental variables measured are shown. Factors (habitat, impact of settlements and roads) are entered as multiple dummy variables. For categorical factors with greater than two levels, the ranges of Beta Coefficients and SE are given.

Source	B	SE	Type III		
			Wald Chi-Square	df	P
(Intercept)	893.2	1514.8	4.6	1	0.033
Habitat	374.4 - 1651.7	1392.7 - 1481.2	2.1	2	0.342
Impact of settlements	1710.9 - 1767.2	797.0 - 849.5	5.6	2	0.061
Impact of roads	-1157.1 - 765.1	660.0 - 1274.3	5.7	5	0.332
Canopy cover	-11.8	17.0	0.5	1	0.485
Grass cover	8.2	11.0	0.6	1	0.455
Fire	76.6	143.1	0.3	1	0.592
Water	83.6	333.7	0.1	1	0.802
Lantana camara	20.7	24.0	0.7	1	0.390
MDF × *Lantana camara*	-14.4	38.1	0.1	1	0.706
DDF × *Lantana camara*	-37.3	30.4	1.5	1	0.220

Journal of Tropical Ecology publication: (Wilson *et al.* 2013)

Chapter Three was accepted for publication by the Journal of Tropical Ecology and published online on the 11th of April 2013 as below:

WILSON, G., DESAI, A. A., SIM, D. A. & LINKLATER, W. L. 2013. The influence of the invasive weed *Lantana camara* on elephant habitat use in Mudumalai Tiger Reserve, southern India. *Journal of Tropical Ecology* 29:199-207.

DOI: http://dx.doi.org/10.1017/S0266467413000205

The influence of the invasive weed *Lantana camara* on elephant habitat use in Mudumalai Tiger Reserve, southern India

Gaius Wilson, Ajay A. Desai, Dalice A. Sim and Wayne L. Linklater

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