

The influence of forest reserve protection on the structure, stability, and functioning of dung-associated invertebrate communities



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Thesis abstract

Communities are influenced by many factors, with anthropogenic impacts being one of the strongest. These factors can influence community structure and may cause non-random species loss by filtering certain traits of species, which may also determine how a species contributes to ecosystem functioning. The structure of a community can also be highly variable over short timescales and across seasons, as abiotic factors can alter a resource over the course of days and also alter intensity of competition within a community. These short-timescale influences are most noticeable in an ephemeral resource that is limited in both space and time. Changes in community structure and interactions can be represented as networks of interactions (links) among species (nodes). Interaction networks describe a community and incorporate non-trophic interactions, which can alter their structure. These are generally measured by counting the number of trophic interactions, ignoring non-trophic interactions such as competition. However, competitive interactions may be important for network dynamics, yet the most appropriate way to quantify competition remains unclear. The outcome of a competitive interaction could potentially be predicted by the body size of competing individuals, and this would remove the need to observe individual interactions. These ideas were tested using the dung-associated community in an Afromontane forest reserve in Nigeria across variation in seasons and in areas that were protected from anthropogenic impacts by fencing. Trapping and recording of interactions within the community was used to assess community structure, and experiments were run to test how dung removal and secondary seed dispersal changed across seasons and in protected areas of the forest. The influence of competition was determined by altering the size and number of dung beetles present at the resource. The community structure was influenced by forest protection and varied across seasons. Additionally, the size and number of dung beetles present was higher in protected areas in the wet season, resulting in higher dung removal and secondary seed dispersal and indicating non-random species loss in unprotected areas. The attractiveness of the dung resource changed over short timescales and desiccation occurred rapidly in the dry season, which resulted in decreased insect abundance and diversity over the course of days. Individual dung removal rates were not additive, and could only be used to predict community-level dung removal when taking into account competitive interactions. The body-size ratio between winners and losers of a competition was a good predictor of an

interaction outcome. Competition networks were highly connected and nested, with compartmentalisation occurring in the competition network. At the community level, effects of forest protection and changing seasons only altered network nestedness. Therefore, body size can be used to predict species responses to anthropogenic threats and community structure and function when taking into account density-dependent competitive interactions. Furthermore, when determining community responses to anthropogenic threats, sampling across changes in seasons and observing competitive interactions provides more information about a community structure and stability.

Chapter 1 Introduction

Ecosystems are influenced by many factors and of these, habitat loss is the single largest driver of biodiversity loss (Sala et al. 2000). Anthropogenic impacts on ecosystems typically result in habitat loss and/or habitat degradation (Brooks et al. 2002, Wright 2005). Anthropogenic impacts can take many forms, such as forest clearing for agricultural purposes, along with further encroachment of agricultural activities on remaining forest habitat (Sodhi et al. 2009). These impacts also often result in the degradation of any remaining forest as the vegetated edges can become more open, resulting in higher temperatures, lower humidity, and increased wind disturbance, which can further alter the affected forest communities (Didham et al. 1998). These effects are not ubiquitous in their influence on species, as some may be affected detrimentally whereas others can be affected positively, depending on their habitat preference (Didham et al. 1998). Additionally, forests that are impacted by anthropogenic activity can become more disturbance-prone as the frequency of natural disturbance events can be altered. For example, this could result in increased wind-fall events and drought occurrence (Chazdon 2003). The matrix habitat adjoining the forest also has an effect on the communities within, as the more degraded and contrasting the habitat, the harsher the environment it presents (Barnes 2011). A study by Watson et al. (2004) in Madagascar found that forest bird species richness was negatively affected by habitat loss and forest degradation and the effects were particularly strong due to the highly degraded matrix habitat. Conversely, in studies where the matrix was less degraded, bird species richness was not strongly altered (Saab 1999, Watson et al. 2004). While the combined impacts of habitat loss and further degradation have a detrimental effect on the communities within the adjacent forest habitat, protecting forest reserves by excluding anthropogenic threats may mitigate detrimental effects on communities (Benayas et al. 2009).

Communities that occur in areas with strong seasonality may be more susceptible to anthropogenic threats than communities that exist in areas with no strong seasonal changes (Bullock et al. 1995). Seasonally dry tropical forests exhibit dramatic changes between wet and dry seasons that can cause strong changes in the community present, mediated through fluctuations in abiotic factors such as rainfall and temperature (Bullock et al. 1995). Species within these forests respond differently depending on

their life history traits and resource requirements, with some invertebrates, such as dung beetles, exhibiting higher abundance during the wet season (Hanski and Cambefort 1991, Vernes et al. 2005). This occurs because during the dry season they are at high risk of desiccation, which can be fatal (Vernes et al. 2005). In addition, ephemeral resource patches are influenced by factors that act over shorter time scales than seasonal effects, as they may have a short life span or decompose rapidly (Finn 2001). For example, the longevity of carrion or dung resources is determined by decomposition, which affects, and is affected by, the associated community (Ives 1991, Finn 2001).

Functional traits mediate species responses to environmental change

Species responses to anthropogenically driven changes in habitat depend on their traits, as species that are better adapted to surviving in a harsh environment may persist longer than more vulnerable species (Lavorel et al. 1997, Slade et al. 2007, Ewers and Didham 2008). For example, disturbance from grazing in an alpine grassland leads to higher leaf toughness and dry matter content in the plants present, resulting in lower productivity (Quétier et al. 2007). Plant species that cannot adapt in this way may go locally extinct (Lavorel et al. 1997, Quétier et al. 2007). Traits have also been shown to predict how a species will respond in insect communities as large bodied bee and dung beetle species were the first to go locally extinct in response to anthropogenic disturbances (Larsen et al. 2005). This could be because larger bodied species may have smaller population sizes, lower reproductive rates and may require a larger home range, all of which could make them more susceptible to disturbance (Gaston and Blackburn 1995).

The traits that dictate how a species responds to habitat alteration, known as ‘response traits’, can also influence how important the species is for the providing ecosystem functioning (Larsen et al. 2005), and identifying these ‘effect traits’ enables a prediction of how trait-determined species responses will alter the ecosystem function of the species in question (Pakeman 2011, Norris 2012). For example, the study by Larsen et al. (2005) found that the large bodied dung beetle species were also more important functionally than smaller species as they removed more dung. Consequently, investigating species compositional changes and how species respond to habitat change enables a more detailed understanding than more traditional approaches that have typically relied on summaries of how overall diversity has changed in a community (Larsen et al. 2005, Lewis 2009).

Species interactions determine the structure and function of communities

Interactions between species can be disrupted by species losses as they are part of a larger network and this loss affects the species they interacted with (Ings et al. 2009). A network is made up of species that are all connected via interactions between them and that generally share a common resource (de Ruiter et al. 2005). These interactions are referred to as either trophic interactions (predator-prey) or non-trophic interactions (mutualist, competitive) between species (Pimm et al. 1991, de Ruiter et al. 2005). A food web is made up of predominantly trophic interactions. The structure of food webs are generally split by trophic levels, with energy flowing upwards through links between species with the resource at the bottom and predators at the top (Pimm et al. 1991). Within these levels, species at the base of the web (the resource) feed on nothing within the web and species at the top of the web (top predators) are not fed on by any other species. Also, species at intermediate trophic levels both predate on species at lower trophic levels and are also prey to species at higher trophic levels (Pimm et al. 1991). Additionally, the number of species and individuals within those food webs decreases with increasing trophic level as predators are generally larger than their prey and therefore their abundance is limited to the abundance of their prey species (Pimm et al. 1991, Cohen et al. 1993). How these interactions between species are arranged affects the structure of the community and studying these interactions can give information about how stable these networks are (Williams and Martinez 2000, Berlow et al. 2004).

Food web structure and stability

There are many metrics used to determine food web structure (Tylianakis et al. 2010). A common measure of describing a network or food web's structure is by measuring the strengths of interactions among species (McCann et al. 1998). A strong interaction is where two species strongly limit the abundance of the other and a weak interaction is where two interacting species have little impact on each other's abundances. The mixture of these strong and weak interactions within a community can influence a community's stability (Berlow et al. 2004) and are thus important for understanding the functional responses of networks to environmental change. Another common measure of a network or food web's structure is nestedness, which measures if

generalist species interact with specialist species and vice versa. A network is described as nested if the generalists interact with mainly specialists and specialists mainly interact with generalists (Atmar and Patterson 1993). Therefore, a high degree of nestedness can yield unstable networks as the loss of a generalist species can detrimentally influence its associated interacting specialist species. However, if a specialist is lost from the network then there will be very little impact on the community (Tylianakis et al. 2010). Also, a network that has many links between species is more connected and is more robust to habitat loss and disturbance (Dunne et al. 2002b). Measuring these network metrics gives important information on the stability of communities, as a highly connected community with many weak links and several strong links is more robust to global change drivers (Dunne et al. 2002b, Berlow et al. 2004).

The structure of a food web can be predicted in part by the size of its constituents (Woodward et al. 2005, Brose et al. 2006b). The size of predators constrains their feeding interactions, as predators have to be able to catch their prey (Cohen et al. 1993). Therefore, the links between species can be partly predicted by measuring the ratio between the body size of predators and that of prey species, which can also dictate the per capita interaction strength for predators and their prey (Emmerson and Raffaelli 2004, Brose et al. 2006a, Brose et al. 2006b). The distribution of predator-prey body size ratios can also predict the patterns and distribution of interaction strengths, which can determine food web stability (Emmerson and Raffaelli 2004). These structural patterns have mainly been tested in networks with only predator-prey interactions (Ings et al. 2009), however the same findings may also apply to interaction networks that include non-trophic interactions, such as mutualisms or competition.

Non-trophic interactions in size structured networks

Non-trophic interactions are common in communities, and can take the form of mutualism, facilitation, and competition, among others (Kéfi et al. 2012). Commonly studied examples are pollen transport and ant-plant networks (Ings et al. 2009), yet little is known about the general patterns and mechanisms involved in non-trophic interactions (Woodward et al. 2005, Goudard and Loreau 2008). These non-trophic interactions can influence the structure of a community, as competition between species determines how many organisms can exploit the same resource, and occurs when a

resource is limited in space and time (Davis 1996). Competition increases at high abundance levels and can have indirect benefits at the species and guild level as it regulates the numbers of competing organisms which may in turn promote coexistence of a diverse range of species (Hanski and Cambefort 1991, Finn and Gittings 2003). There are many adaptations for escaping competition and thus avoiding related fitness costs. These include temporal, spatial and seasonal segregation (Giller and Doube 1994, Krell et al. 2003, Vernes et al. 2005, Noriega et al. 2007). Additionally, resource partitioning among organisms and variation in morphological and behavioural adaptations facilitate species coexistence among organisms utilising a shared resource (Krell-Westerwalbesloh et al. 2004, Croomsigt and Olf 2006, Jacobs et al. 2008). Consequently, networks whose interactions include both non-trophic and trophic characteristics may have lower biomass and productivity due to competition, leading to a constraint in the total biomass and production of that system (Goudard and Loreau 2008). Therefore, studying non-trophic interactions helps to explain the structure and dynamics of an ecological community and how it functions within the ecosystem (Berlow et al. 2004, Goudard and Loreau 2008).

Biodiversity loss can directly result in a decrease in the functioning of the ecosystem as some of the species present become rare or locally extinct (Petchey 2000, Norris 2012). This can be predicted by body size as larger species are more likely to be lost first from a network (Petchey et al. 2004). Body size has been shown in non-trophic networks as for example the giant tortoises and lizards have all gone extinct from the Canary Islands and smaller lizard species still exist (Barahona et al. 2000, Woodward et al. 2005). Additionally, functional extinction can occur before a species is locally extinct as a reduction in a species' abundance to low levels can result in loss of the ecosystem functions it performs, consequently recording that a species is present does not necessarily mean that it is still functionally important within the community (Naeem and Li 1997, Crowder et al. 2010, Brown et al. 2011). Fundamentally, it is the loss of traits from a system that dictates how the ecosystem functioning provided by that community will change (Norris 2012). Therefore, it is of considerable importance to measure the traits of the remaining organisms to determine what impact the loss of species will have on ecosystem functioning (Lavorel and Garnier 2002, Norris 2012).

Network structure and function in dung-associated invertebrate communities

Insects are tightly linked with ecosystem processes, as they provide services such as secondary seed dispersal, decomposition and nutrient cycling (Lewis 2009). Dung-associated insects therefore provide an ideal study system for documenting how habitat change due to anthropogenic activities ultimately affects the functioning of that system (Lewis 2009). Also, a community based around an ephemeral resource is an ideal system for testing how the associated community responds to abiotic and biotic factors (Finn 2001). This thesis investigates how insect community structure can be influenced by reserve management aimed at protecting forest remnants from anthropogenic threats and how this influence is altered by abiotic factors over changing seasons. It also focuses on how the combination of these two effects alters the functioning of the entire ecosystem. This question is explored with an emphasis on how the community is structured by interactions between the species within it. I used a dung-associated invertebrate community in an Afromontane forest in Nigeria as my focal study system (see below). The dung resource is well defined in time and space and easily replicated and provides an ideal study system (Davis 1996, Finn 2001). Additionally, the dung-associated community is an ideal ecological indicator of ecosystem health as it is strongly influenced by ecosystem degradation (Andresen 2008).

Study site

The study area was located in an Afromontane forest system on the Mambilla Plateau, at Ngel Nyaki forest reserve in Nigeria. The forest reserve is located in Taraba State, within the Cameroon Highlands ecoregion, and contains a network of Afromontane forest fragments (Olson et al. 2001, WWF 2001). The plateau is made up of rolling hills mainly between the altitudes of 1400 and 1600 m (Chapman and Chapman 2001).

The total Ngel Nyaki reserve area is 4600 ha and includes the main forest area, with an area of 720 ha, as well as riverine fragments, small forest patches, and overgrazed exotic grasslands (Chapman and Chapman 2001, Matthesius et al. 2011). The forest type is most similar to dry tropical forest and has distinct wet and dry seasons. The wet season starts in mid March and extends until mid November, with

annual rainfall between 1600 and 2000 mm (Chapman and Chapman 2001). Climate in the wet season is humid, with rainfall occurring almost daily, and has an average temperature of $26^{\circ}\text{C} \pm 13^{\circ}\text{C}$. The transition period from wet to dry seasons occurs over a matter of days. In the dry season, rainfall events are very rare and the climate is hot and dry during the day with cold nights and a temperature range from 16°C to 23°C (Hall 1971, Chapman and Chapman 2001, Macdonald 2007, Matthesius et al. 2011).

The Ngel Nyaki forest is of a submontane Afrotropical forest type and is highly diverse, with a unique floristic make up of over 146 vascular plant species, four of which are IUCN Red Data Listed species (Chapman and Chapman 2001). Many of the plant species are endemic to Afrotropical areas and the area is recorded as an important bird area (Bird Life International 2001). Mammals in the area include several primates, such as the chimpanzee *Pan troglodytes ellioti*, putty nose monkeys *Cercopithecus aethiops*, tanzania monkeys *Chlorocebus tantalus*, and baboons *Papio anubis*, as well as many species of cephalophine ungulates (duikers) and civet cats *Civettictis civetta* (Chapman and Chapman 2001, Chapman et al. 2004, Beck and Chapman 2008).

From 2000 to 2005, Nigeria lost 410,000 ha/year of their forests – the 7th highest net annual loss of forest area in the world (Birdlife 2001) – mainly due to an increasing human population and a lack of resources channeled into conservation efforts (Olson et al. 2001). Currently, the predominant land-use on the Mambilla plateau is livestock grazing and small-scale farming, which has detrimentally impacted the grassland matrix surrounding Ngel Nyaki forest reserve. Cattle, the main livestock animals in the area, cause soil compaction and erosion, and facilitate the invasion of tussock grass *Sporobolus ludetia* (Van Uytvanck and Hoffmann 2009). Every year the pasture areas are burnt during the dry season to promote grass growth for grazing, resulting in a gradual reduction in the forest size as fires often encroach on the forest boundaries. Cattle often graze into the forest edges, reducing ground vegetation and creating open edges that fires can easily ignite.

The Nigerian Montane Forest Project (NMFP) was founded to protect Ngel Nyaki forest reserve from poaching, further land clearing, fire encroachment and cattle grazing. To protect the forest, fenced exclusion zones up to 200 m from the forest edge were set up in the adjacent pastoral matrix. Trial exclusion zones were set up in four different areas along the forest edge and firebreaks were built alongside the fence during the dry season. These fenced exclusion zones protect the forest edge from the combined effects of fire and cattle grazing, resulting in altered matrix structure as these areas

regenerate and thus facilitates the re-establishment of extirpated species (Barnes 2011). These fenced exclusion zones are now used for a variety of scientific studies observing how vegetation structure recovers and how invertebrate communities change with the exclusion of fire and cattle grazing. In this study, the four fenced exclusion zones set up by the NMFP were between 3-5 years old. These areas provide an opportunity to test the various ecological effects of excluding anthropogenic threats from the forest edge (Figure 1.1).



Figure 1.1 Photos of two of the sites, one with forest protection (right photo) and one without (left photo).

Thesis structure

Because this thesis is written as a series of three stand-alone papers, there is inevitably some repetition of information in the Introductions of the respective chapters. In Chapter 2 I explore the influence of anthropogenic threats and seasonal variation on dung-associated community structure, using dung beetles as a particular focus. Additionally, I investigate whether non-random species loss is occurring due to the influence of these factors, and discuss the implications for the functioning of the ecosystem. In Chapter 3 I explore how changes in the attractiveness of the dung resource, caused by abiotic factors, are altered over short and long timescales and how these changes alter a community's structure. I also investigate how competitive effects are partitioned out for different sizes and numbers of dung beetles to assess how this affects the amount of dung buried. In Chapter 4 I focus on competition networks, and whether or not these can be constructed by simply observing which species co-occur. I also investigate how seasonal variation and mitigating anthropogenic threats alters the structure of both types (competition and co-occurrence) of dung-associated interaction

networks. In my final chapter, I synthesise the results from the previous three chapters and extend the conclusions from this research to other systems, providing suggestions for future directions in this field.

Chapter 2 The effects of forest reserve protection on the structure and functioning of dung-associated communities

Abstract

Communities are influenced by many factors, with anthropogenic impacts being one of the strongest. In particular, farming practices such as livestock grazing are common threats to the surrounding ecosystem. These effects are often exacerbated by variation across seasons that can significantly influence community structure and may have filtering effects on the response traits, such as body size, of species. This can result in non-random species loss, which in turn can have further flow-on effects that alter ecosystem processes, resulting in ecosystem-level responses to these drivers. The dung-associated community in an Afromontane forest in Nigeria was chosen as a focal study system because it contains species guilds that are commonly used as biological indicators of ecosystem health. Taking season into account, I tested how protection of forest from livestock grazing and fire threats affected the structure of the dung-associated community and how these factors affected the ecosystem functions of dung removal and secondary seed dispersal performed by this community. I also quantified the relative importance of the main guilds within the dung-associated community and their contributions to the functioning of this system, measured as dung removal. Additionally, I measured how dung beetle (Coleoptera: Scarabaeinae) abundance and size responded to forest protection and seasonal variation and how these influenced dung removal and secondary seed dispersal. Community structure was influenced by forest protection, and dung beetles were the most functionally important guild within the dung-associated community. The size and abundance of dung beetles increased in the wet season and in protected areas of the forest, which significantly increased the amount of dung removed and the number of seeds secondarily dispersed. Thus, the exclusion of anthropogenic threats from habitat adjacent to forest reserves influences the structure of the community, the size of dung beetles, and significantly increases ecosystem functioning. This study highlights the importance of protecting forest habitat to prevent further non-random species loss that could precipitate a decline in ecosystem processes.

Introduction

Communities are influenced by many factors, with anthropogenic impacts recently becoming the strongest threat to natural ecosystems - possibly resulting in the sixth major extinction event in biological history (Dirzo and Raven 2003, Barnosky et al. 2011). Of the many anthropogenic drivers of biodiversity loss, land-use change has the largest impact on terrestrial ecosystems and is particularly severe in tropical forests, where over 40% of potential forest area has been destroyed (Sala et al. 2000, Wright 2005, Lewis 2009).

Anthropogenic effects can also affect the ability of species to cope with seasonal changes (Lewis 2009, Morris 2010), which strongly influence both vertebrate and invertebrate communities (Abrahamczyk et al. 2011). Effects of changing seasons can influence community structure and are especially large in areas with pronounced wet and dry seasons, such as dry tropical forests (Murphy and Lugo 1986, Bullock et al. 1995). For example, a recent study found that butterfly communities in a tropical forest were strongly influenced by changes from wet to dry seasons, with higher species richness and more unique species present in the dry season (Abrahamczyk et al. 2011). Similarly, ant community composition is strongly affected by changes across seasons (Neves et al. 2010). Habitat loss and fragmentation may reduce the habitat available for species, which can negatively impact their ability to persist as it can reduce the resources they need to survive and therefore impair a species' ability to cope with seasonal changes (Bullock et al. 1995, Lewis 2009, Morris 2010).

Threats such as habitat fragmentation can have a strong filtering influence on community structure, because different responses across species can result in non-random species loss (Ewers and Didham 2008). In particular, traits of a species dictate how it will cope when subjected to an environmental stressor (Pakeman 2011). For example, a study by Larsen et al. (2005) showed that large-bodied bee and dung beetle species are most prone to extinction in response to habitat loss. Larsen et al. (2005) also found that losing a high proportion of large-bodied bee and dung beetle species resulted in a greater-than-expected loss in ecosystem function than if species were lost at random. The same effect was also noted in a study by Barnes (2011), which found that species loss in dung beetle communities due to habitat degradation resulted in decreased ecosystem function. Thus the traits that determine species responses to anthropogenic threats can simultaneously determine the effect that those species have on ecosystem

functioning, with the largest species possibly being both the most extinction-prone and the most functionally important (Lavorel and Garnier 2002, Larsen et al. 2005). Therefore, variability in species loss can occur because their response to anthropogenic threats is mediated by their physical or behavioural traits (Lavorel and Garnier 2002). Furthermore, the extent to which species loss affects ecosystem processes depends on the ability of remaining species to compensate for those that are lost (Yachi and Loreau 1999, Suding et al. 2006).

To investigate the effects of anthropogenic threats and seasonal variation on community composition and the ecosystem services of dung removal and seed dispersal, I conducted a study at Ngel Nyaki Afromontane forest reserve in Nigeria. Afromontane forests are a unique ecosystem that has pronounced wet and dry seasons (Matthesius et al. 2011). Land-use change in these forests is occurring at an alarming rate, and is exerting a strong influence on communities in adjacent forest reserves (Olson et al. 2001). My study, replicated across both the wet and dry seasons, was conducted in areas of the forest where anthropogenic threats were excluded from the adjacent matrix through the use of fences and firebreaks (hereafter ‘forest protection’). Forest protection made the matrix more similar to the forest as tall grasses and shrubs and tree species were gradually colonising these areas, thereby mitigating some of the impacts of anthropogenic threats (see Chapter 1) (Nichols et al. 2007). This study focused on the dung-associated community, as they are a key indicator species guild for ecosystem health and stability in the face of anthropogenic impacts (Davis et al. 2001). The influence of forest protection and changing seasons on dung beetle (Coleoptera: Scarabaeinae) size and abundances, along with their effects on ecosystem functioning, were also determined to assess whether non-random species loss occurred. The effects of different sized dung beetles on ecosystem functioning was partitioned out to test whether losing larger species resulted in a more rapid decrease in ecosystem functioning. I also analysed the relative ecosystem functioning of the most numerous guilds separately, so that the most functionally-important guild within the dung community could be identified.

Methods

Sampling design and bait selection

All field experiments were carried out at eight sites, with four in protected areas of the forest and four in unprotected areas of the forest (which was subject to the predominant land-use of cattle grazing). Sampling points within sites were spaced at least 50 m apart to retain trap independence (Larsen and Forsyth 2005), and were at least 100 m from the edge of the fence to ensure that samples within the fenced exclusion zones were independent of those outside the fenced exclusion zones. To assess the importance of seasonal variation, experiments were conducted during both the wet and dry seasons. Experiments in the wet season were run from the start of October until mid November when the rain stopped, and experiments in the dry season were run from late November until mid December. Trials for each experiment within a site were set within 15 minutes of each other, beginning at 9:30 am, and samples were collected after 24 hours.

All experiments required the use of dung baits, which were modeled on the dung of tanzania monkeys (*Chlorocebus tantalus*), a common species predominantly found around the edge of the Ngel Nyaki forest (Grassham 2012). Tanzania monkeys are omnivorous and are an important source of dung in this system. The average mass of one tanzania dung is 20 g (Grassham 2012) so I weighed every dung bait to 20 g (± 0.05 g) for all experiments. To keep diet and dung age constant, pig (a species historically found within Ngel Nyaki forest reserve (Chapman and Chapman 2001)) dung was used, as they are also omnivores and could be kept in captivity and fed a constant diet. Additionally, omnivore dung was used as it is the most attractive dung type for dung beetles (Hanski and Cambefort 1991, Whipple and Hoback 2012). To ensure freshness, dung was collected daily and was homogenised before use. After each test, dung was collected in a clean plastic bag and on return to the laboratory any invertebrates found in the dung were removed and preserved in 70% ethanol for future identification in the laboratory in New Zealand. Insects were identified to family level and other invertebrates identified to order level (using CSIRO 1996). All debris was then brushed off and the dung was then placed in a paper bag in a drying oven for 24 hours and thereafter weighed repeatedly until a constant and accurate reading was achieved. For all experiments, apart for the exclusion experiment, dry dung weights were compared to

a dried sub-sample of dung taken from the same batch to account for any natural inconsistencies in the dung over time.

Pitfall traps (Figure 2.1) were constructed using 500 ml plastic cups (11 cm deep and 8 cm diameter; hereafter ‘plastic cups’) that were buried flush with the soil surface. A wooden trap cover was used to protect the contents from falling debris and was held c. 20 cm off the ground by four wooden supporting stakes. Traps were baited with a 20 g ball of dung that was suspended from a trap cover at the same height as ground level. Bait was wrapped in muslin to allow the scent to permeate the surrounding area but prevent invertebrates from accessing the dung. The pitfall traps were set for 24 hours, after which the contents were collected and preserved for identification in New Zealand.

For experiments in which dung beetles were caught alive (‘Exclusion experiment to determine the major invertebrate guilds’ and ‘effect of beetle size on ecosystem processes’, see below) funnels with a 3 cm hole at the bottom were placed in the plastic cup (‘pitfall trap with a funnel’). Strips of flagging tape were taped to the inside of the funnel so they hung downwards inside the cup, preventing dung beetles from flying out.



Figure 2.1 Dung-baited pitfall trap.

Sampling of the dung-associated community

Dung-baited pitfall trapping (Figure 2.1) was conducted to determine the composition of dung-associated invertebrates in this system. This experiment was

repeated in all eight sites in both the wet and dry seasons and two replicates per site were used to control for the effects of different microclimates present within a site. Pitfall traps were all placed at 40 m inside the forest edge so that any effects of forest protection would be detected, but not so close that grassland invertebrate species were sampled. The traps were half filled with water and contained a drop of detergent to break the surface tension and the order in which traps were set was fully randomised. After the 24 hour period, all collected invertebrates were removed and preserved for future identification. A total of 32 samples were obtained, with 16 samples per season, eight of these in protected sites and eight in unprotected sites, giving a total of four replicates per season for the effect of forest protection compared with unprotected sites (four replicates).

Exclusion experiment to determine the major invertebrate guilds

Exclusion experiments were used to assess the relative importance of dung beetles for carrying out ecosystem processes (measured as dung removal) compared with the remaining dung-associated community. Four sampling points, each placed at 40 m inside the forest edge, were assigned within each site, as four different treatments were used. The order that each site was set up and the order each treatment was set up within a site were randomised. Treatments were applied in all eight sites to account for the possible impacts of forest protection and changes across seasons. A total of 42 trials per treatment were run, with six in the protected areas and 12 in the unprotected forested areas during the wet season. In the dry season there were 13 replicates in protected areas and 11 replicates in unprotected forested areas.

Four exclusion treatments were used: (1) a control accessible to the entire community, (2) a cage where I added a predetermined number of dung beetles, (3) a cage where anything larger than 3 mm in diameter was excluded and (4) a second control, which was a cage placed directly on the ground where everything was excluded. To obtain dung beetles for treatment two, live pitfall traps with funnels were used. After a 24 hour period any dung beetles found in the cup were counted, identified to genus, and then placed in a cage situated within 10 cm of the pitfall trap with dung bait placed in the middle. By using actual locally-collected dung beetle assemblages and then placing the experimental trial within close proximity of each associated live trap, this allowed for the most accurate experimental quantification of community processes

carried out by the local species pool at a particular microsite. The other three treatments were set up at the same time and after 24 hours all remaining dung was collected in labeled plastic bags and then processed, dried and weighed. The ‘all-exclusion’ treatment (4) was used to control for seasonal effects, as in the wet season the dung was often partially washed away. To take this into account, the dry weight remaining from each treatment was compared to the dry weight of the all-exclusion treatment, where there was no access to the dung, making it possible to accurately determine if any dung was removed by invertebrate action rather than just being washed away by rain.

Forest protection and effect of changing seasons on species assemblages and their ecological role

I tested the effect of forest protection, while accounting for variation across seasons, on the composition of the dung-associated community and the ecosystem processes they perform (dung removal and secondary seed dispersal). This experiment was carried out over differing distances from the forest edge so that the majority of species were sampled, as the dung-associated community shows significant rates of turnover within distances of mere meters from the forest edge (Barnes 2011). The distances used for each trial were on a doubling scale from 5 to 160 m from the forest edge (i.e., 5, 10, 20, 40, 80, and 160 m). The experiment was repeated at each distance within each site in both the wet and dry season; a total of 96 trials were carried out with four replicates of each distance per season for the effect of forest protection, compared with the four unprotected replicates.

Before setting up the tests, a known number of seeds of three different species and sizes were homogenised into each dung ball. The seed species and numbers used in each dung bait were *Aframomum angustifolium* (20 seeds), *Leea guineensis* (14 seeds) and *Leptaulus zenkeri* (5 seeds), all of which are found in tantalus dung (Grassham 2012). The seeds were assigned to size classes of small, medium and large, respectively. The mean length and width (\pm SEM) of small seeds was 4.7 mm (\pm 0.10) x 2.7 mm (\pm 0.08), medium seeds were 4.7 mm (\pm 0.08) x 3.8 mm (\pm 0.07), and large seeds were 14.8 mm (\pm 0.39) x 9.7 mm (\pm 0.42). A total of 30 replicates were used for each seed size and they were all measured using digital calipers.

Plastic cups were buried flush with the soil surface and refilled with the soil that was dug out for the cups and was then compacted to replicate the surrounding soil as

closely as possible. By using cups, dung beetles that buried dung for reproductive efforts were easily found. As tunneling dung beetles, which are the dominant group of dung beetles at Ngel Nyaki forest reserve (Barnes 2011), bury their dung directly beneath the dung pat (Hanski and Cambefort 1991), I assumed that the majority of dung beetles that utilised the resource were found. The roller clade of dung beetles, which generally move the dung horizontally away from the source, comprised 0.8% of the total community at this study site in a study by Barnes (2011) and were found predominantly in the grassland. The order in which each trial was set up at each distance was randomised within a site.

After 24 hours, I recorded any invertebrates and seeds found on the soil surface within the cup diameter, after which I sieved the soil by removing 1 cm at a time from the cup until reaching the bottom of the cup, recording any invertebrates, seeds and dung found at each level. The cup was then removed and the soil replaced in the hole. Meanwhile, the dung was removed from the plastic cups and placed in a labeled plastic bag so that all invertebrates and seeds inside the dung could be counted and identified at the laboratory. The dung was then dried and weighed to calculate the proportion of dung removed by dung beetles.

Effect of dung beetle size on dung removal and secondary seed dispersal

To determine how much dung individuals of different sizes removed, I carried out tests in which the size of dung beetles present was experimentally fixed. This was done using wooden boxes (30 x 30 x 30 cm) filled with soil to a depth of 20 cm with a 20 g piece of dung placed directly on the soil surface. The top of the box was covered using a sheet of Perspex, allowing natural light levels into the arena. A single dung beetle was randomly selected from a species pool generally containing at least two species for the medium and large size classes, and for the small size class a beetle was randomly selected from a species pool containing at least three species. The single beetle was placed inside the box with the dung bait and left undisturbed for 24 hours, after which the soil inside was sieved in 1 cm increments until the beetle was found and its depth recorded. Dung beetles were never used in an experiment more than once. The dung was dried and weighed to determine the proportion of dung removed by the dung beetle.

Dung beetles were caught using live pitfall traps with a funnel and were kept in the laboratory for up to 24 hours in a dark container half filled with moistened soil to ensure they did not dry out. The beetles that were not used within 24 hours were released in an area of the forest where no data collection was carried out and each dung beetle was only used once. The size classes used were 2.5-4.5 mm in pronotum width (small), 6-8 mm (medium), and 9.5-12.5 mm (large). The small size class was made up of several species of *Onthophagus* (see Table 2.1) the medium size class contained *Onthophagus* sp.1 and *Proagoderus multicornis*, and the large size class contained *Diastellopalpus nigerrimus* and *Catharsius* sp. n. Trials in which the dung beetle did not remove dung were excluded from the analysis. In total, 34 trials were run, with at least 10 trials for each size class (trial order randomised).

Table 2.1 List of *Onthophagus* species included in the small size class (pronotum width 2.5-4.5 mm).

Species	Pronotum width (mm)
<i>Onthophagus alternans</i>	3.204
<i>Onthophagus</i> sp.2	3.615
<i>Onthophagus</i> sp.3	2.757
<i>Onthophagus</i> sp.4	2.715
<i>Onthophagus</i> sp.5	2.529
<i>Onthophagus</i> sp.6	2.468
<i>Onthophagus</i> sp.7	3.048
<i>Onthophagus</i> sp.8	3.885
<i>Onthophagus</i> sp.11	2.958
<i>Onthophagus</i> sp.13	2.905
<i>Onthophagus</i> sp.15	4.478

Statistical analysis

Community dissimilarity

To examine how the structure of the dung-associated invertebrate community was influenced by forest protection and the effect of changing season, the dissimilarity of species composition between sampling points was calculated using a log-base 10 Modified-Gower distance metric (Anderson et al. 2011) with the ‘vegan’ package in R (Oksanen et al. 2012). All analyses were performed using R (R Development Core Team 2012). The Modified-Gower dissimilarity metric considers an order of magnitude change in abundance equal to a change in composition and therefore accounts both for changes in the relative abundance of invertebrate families in the community and the compositional changes in the community (Anderson et al. 2006). The dissimilarity in community composition caused by forest protection and changing season was visualised using a non-parametric multidimensional scaling (NMDS) ordination. Subsequently, a permutational distance multivariate ANOVA, with ‘site’ used as a blocking factor to account for hierarchical nature of the sampling design, was used to test whether forest protection and season influenced community compositional dissimilarity.

Testing the effects on ecosystem processes

Here the aim was to determine whether dung beetles were the most important invertebrate guild influencing ecosystem processes. I performed a generalised linear mixed model (GLMM), using the ‘nlme’ package (Pinheiro et al. 2012), to compare whether the proportion of dung removed differed when only dung beetles were present, compared with the entire dung-associated community, specifying ‘site’ and ‘season’ as random effects. This method was also used to compare the proportion of dung removed with the influence of forest protection compared with sites that had no forest protection, specifying ‘site’ and ‘distance’ (from the forest edge) as random effects. For models in which the proportion of dung removed was the response tested, I followed methods set out in Warton and Hui (2010) and logit transformed the data. This transformation accounted for the presence of zeros and ones and normalised the variance which allowed the data to be tested using a linear model (Warton and Hui 2010). A GLMM with a Binomial error distribution and logit link function, using the ‘lme4’ package (Bates et al. 2011), was used to test the proportion of seeds removed by the different dung beetle size classes and the numbers of dung beetles present, with ‘site’ and ‘distance’ specified as random effects. A Gaussian model was used when testing the

proportion of dung removed as the data was normally distributed whereas a Binomial error distribution was used when testing the proportion of seeds removed as this was calculated from counted data and thus violated the assumptions of normality (Crawley 2007). The effects of forest protection and changing season on the mean size of dung beetles present were also tested using a GLMM model with a Binomial error distribution conducted in the ‘nlme’ package, with ‘site’ and ‘distance’ specified as random effects.

To test the influences of forest protection and season on secondary seed dispersal and the number of dung beetles present, a GLMM model was run with a Poisson error distribution conducted in the ‘lme4’ package, with the total number of seeds removed and the total number of dung beetles present both tested as responses. Overdispersion was accounted for by using a Poisson log-normal distribution whereby an observation level factor was included as a random effect (Elston et al. 2001, Bolker et al. 2009). Models were fitted using maximum likelihood estimation and all possible combinations of predictors and interactions were compared using AICc (Akaike Information Criterion corrected for small sample size) and Akaike weight (W_m) to rank and subsequently select the best-fit model to the data (Burnham and Anderson 2001). Models within two AICc units of the top-ranked model were considered equal and of these the simplest model was used. To separate out the effects of the different exclusion treatments and of different sized dung beetles on the proportion of dung removed, Tukey HSD tests with Bonferroni corrections were run using the ‘multcomp’ package (Hothorn et al. 2008).

Results

Sampling of the dung-associated community

A total of 74 insect families in 11 orders (Appendix Table 1.1) were recorded for the dung-associated community from the pitfall traps, of which 11% of the total number of individuals collected were dung beetles. Four genera of dung beetles were found: *Onthophagus* (N = 1617), *Diastellopalpus* (58), *Proagoderus* (47), and *Catharsius* (3). In the wet season, a total of 44 families (N = 3194) were trapped in the protected areas and 45 families (N = 2909) were trapped in the unprotected forested areas. In the dry season, a total of 57 families (N = 2114) were trapped in the protected areas, with 58 families (N = 1534) found in the unprotected areas.

Overall community richness was highest in the dry season, as on average 58 families were recorded compared to an average of 45 families recorded in the wet season. Nevertheless, both forest protection and season significantly affected the overall community structure (Figure 2.2, Table 2.2). Some families were recorded more often in the wet season. For example, calliphoridae (Diptera) abundance was 92 in the wet season, while only 66 individuals were recorded in the dry season. However, other families displayed the opposite compositional change. For example, while 157 gryllidae (Orthoptera) were found in the wet season, 238 were recorded in the dry season.



Figure 2.2 Non-metric multidimensional scaling ordination plot comparing overall community dissimilarity in fenced exclusion zones across wet and dry seasons using the Modified-Gower dissimilarity metric. Triangles: wet season. Squares: dry season. Open: unfenced sites. Closed: fenced sites.

Table 2.2 Results table for permutational multivariate distance ANOVA conducted on Modified-Gower community dissimilarity. Factors denote presence/absence of anthropogenic threat exclusion (fenced treatment) and wet/dry season.

Factor	Df	SS	MS	pseudo-F	R ²	P-value
Treatment	1	1.325	1.325	2.778	0.023	<0.001

Season	1	2.732	2.732	5.726	0.048	<0.001
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Exclusion experiments reveal the most functionally important invertebrate guilds

Exclusion treatments (cage type) significantly influenced the proportion of dung removed ($F_{3,164} = 18.68$, $p < 0.001$). There was no significant difference in the proportion of dung removed when the entire dung-associated community had access to the dung bait compared with either treatment two (predetermined number of dung beetles) or three (everything > 3 mm excluded). However, when these treatments were compared with the all-exclusion treatment (treatment four), they all significantly affected the proportion of dung removed (Table 2.3, Figure 2.3). Interestingly, the size of the dung beetles present did not affect the proportion of dung removed as when large beetles were excluded there was no significant difference between that treatment (treatment three) when compared to treatment two where large dung beetles were included ($z = -0.94$, $p = 0.783$). When restricted to small beetles (< 3 mm diameter) the proportion of dung removed was 59.4 %, compared to 60.6% for the predetermined number of dung beetles treatment (Figure 2.3), which included species that ranged from 2.5 to 12 mm in thorax width.

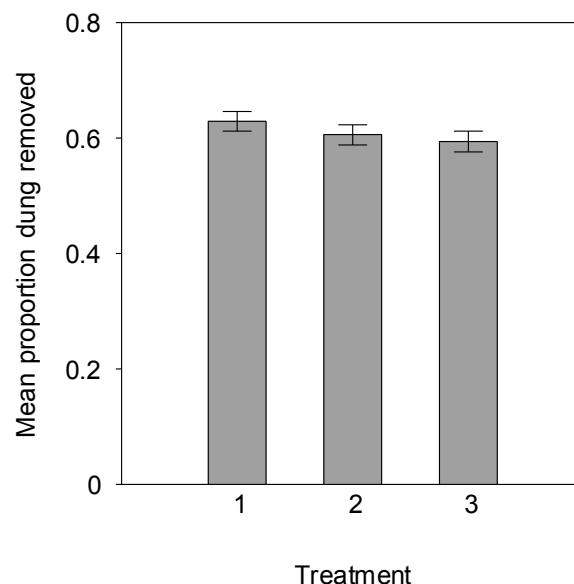


Figure 2.3 Mean (± 1 SE) proportion of dung removed in differential exclusion treatments. 1: control accessible by the entire community. 2: predetermined number of dung beetles. 3: anything > 3 mm in diameter excluded. The treatments were all scaled by the all exclusion control (treatment four) to account for rainfall washing away dung.

Table 2.3 Tukey tests on combinations of different exclusion treatments: 1, control accessible by the entire community; 2, predetermined number of dung beetles; 3, anything > 3 mm in diameter excluded; 4, control with everything excluded.

Treatment	Estimate	Std. Error	z value	p-value
1 - 4	0.4374	0.06183	7.074	< 0.001
2 - 4	0.36612	0.06113	5.989	< 0.001
3 - 4	0.30885	0.06249	4.943	< 0.001
1 - 2	0.07127	0.06038	1.18	0.639
3 - 1	-0.12854	0.05992	-2.145	0.139
3 - 2	-0.05727	0.06085	-0.941	0.783

Forest protection and effect of changing seasons on species assemblages and their ecological role

Dung beetles were recorded more often in the wet season with a total abundance of 1229 in the wet season and only 388 individuals recorded in the dry season. This affected the proportion of dung removed, with a significantly greater proportion removed during the wet season ($F_{1,45} = 91.53$, $p < 0.001$) (Figure 2.4). In contrast there was no significant main effect of forest protection on the proportion of dung removed ($F_{1,45} = 4.11$, $p = 0.089$), though it did interact negatively with the effect of changing seasons ($F_{1,45} = 26.45$, $p < 0.001$), producing a pronounced effect of forest protection in the wet season but not in the dry season (Figure 2.4). Additionally, the number of dung beetles present, both in the dung bait and found buried beneath it, positively influenced the proportion of dung removed ($F_{1,45} = 10.06$, $p = 0.003$).

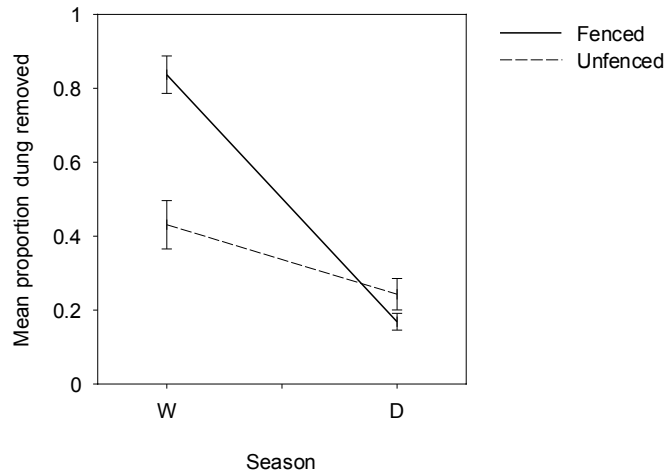


Figure 2.4 Mean (± 1 SE) proportion of dung removed for ecosystem functioning experiment in fenced and unfenced sites during the wet season (W) and the dry season (D).

As a further measure of ecosystem processes, secondary seed dispersal was measured. Seed dispersal was significantly influenced by variation across seasons ($z = 7.16$, $p < 0.001$) and by the size of the dung beetles present in the dung and buried beneath it ($z = 2.71$, $p = 0.007$) (Figures 2.5 and 2.6). Changes across seasons significantly affected the proportion of seeds taken for small (*L. zenkeri*) ($z = 8.28$, $p = 0.001$), medium (*L. guineensis*) ($z = 4.88$, $p < 0.001$) and large (*A. angustifolium*) ($z = 3.54$, $p < 0.001$) seeds, while forest protection only affected the removal of medium-sized seeds ($z = -2.81$, $p = 0.005$) (Figure 2.5). The mean body size of dung beetles present had a significant effect on the proportion of seeds removed for small ($z = 3.22$, $p = 0.001$) and large ($z = 3.56$, $p < 0.001$) seeds. For medium sized seeds, there was an interaction between mean dung beetle body size and forest protection ($z = 2.20$, $p = 0.028$), such that more seeds were removed in protected areas of the forest when larger dung beetles were present (Figures 2.5 and 2.6). Additionally, the removal of large seeds changed over the course of seasons and interacted with the size of the dung beetles present ($z = -3.16$, $p = 0.002$) and resulted in higher numbers of large seeds removed in the wet season when larger dung beetles were present (Figures 2.5 and 2.6).

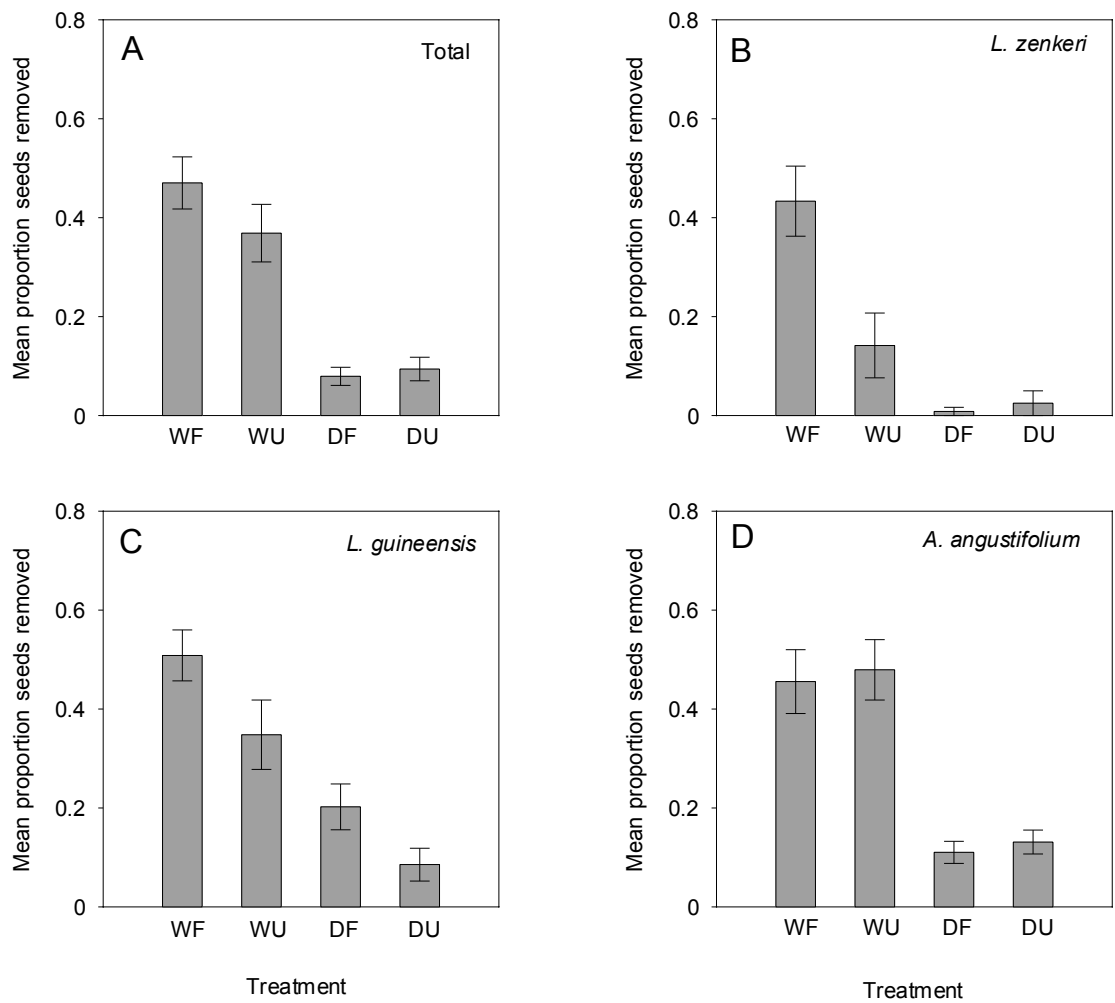


Figure 2.5 Mean (± 1 SE) proportion of seeds removed for A: the total number of seeds removed and B-D: for the three seed species. WF: fenced exclusion zones in the wet season. WU: unfenced sites in the wet season. DF: fenced exclusion zones in the dry season. DU: unfenced sites in the dry season.

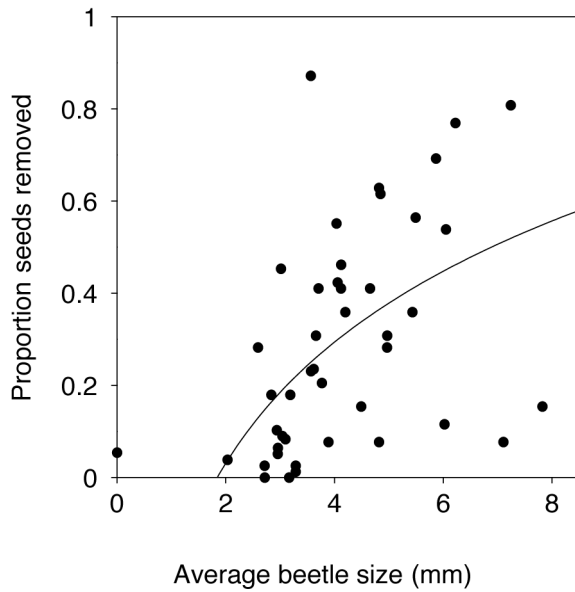


Figure 2.6 Proportion of seeds removed correlated with average size of dung beetles (measured by pronotum width (mm)) present at each distance and each site.

The number of dung beetles present at the dung was significantly influenced by forest protection ($z = -2.34$, $p = 0.019$) and varied across the seasons ($z = 8.72$, $p < 0.001$). The total number of dung beetles present was higher in areas that were protected from anthropogenic threats and in the wet season (Figure 2.7). Furthermore, the average body size of dung beetles present changed across seasons and with forest protection, with larger beetles being found in the wet season ($F_{1,47} = 24.85$, $p < 0.001$) and in protected sites (Figure 2.7, Table 2.4).

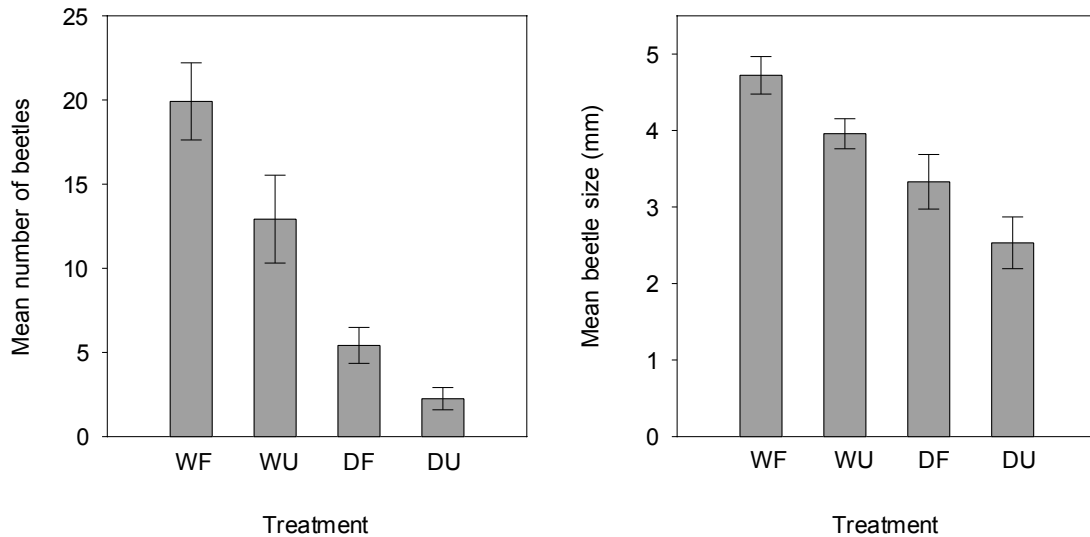


Figure 2.7 Mean (± 1 SE) number of dung beetles caught and mean (± 1 SE) beetle size (pronotum width) per season in both the fenced and unfenced areas. Treatment codes as in Figure 2.5.

Table 2.4 Mean number of beetles present per trap for each size class in fenced and unfenced sites in the wet and dry seasons. Beetles were sorted into size classes by pronotum width.

Factor	Small beetles (2.5-4.5 mm)	Medium beetles (6-8 mm)	Large beetles (9.5-12.5 mm)
Fenced wet season	101.75	18	2.75
Unfenced wet season	68.5	7.5	1.5
Fenced dry season	27.25	5	0.25
Unfenced dry season	13.5	0.5	0

Effect of dung beetle size on ecosystem processes

Dung beetle size had a significant positive effect on the proportion of dung removed ($F_{2,31} = 15.00$, $p < 0.001$). While I found that there was no significant difference between small and medium sized dung beetles in the amount of dung they removed, large dung beetles removed considerably more dung than either of the two smaller size classes (Figure 2.8, Table 2.5).

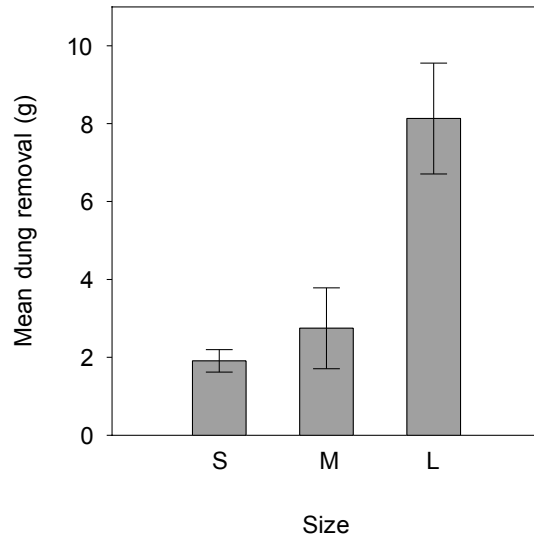


Figure 2.8 Mean (± 1 SE) per capita dung removal for trials with one dung beetle for each size class of small (S), medium (M), and large (L).

Table 2.5 Tukey tests on size combinations of dung beetles. Sizes are measured by pronotum width: Small 2.5-4 mm, Medium 6-8 mm, Large 9.5-12.5 mm.

Size combinations	Estimate	SE	z value	p-value
Medium - Large	-1.787	0.716	-2.495	0.033
Small - Large	-1.655	0.521	-3.178	0.004
Small - Medium	0.132	0.655	0.202	0.978

Discussion

These results show that the structure of dung-associated invertebrate communities in Afromontane systems were strongly affected by both the protection of the forest by excluding anthropogenic threats from forest reserves and by the pronounced wet and dry seasons. The dung-associated communities sampled in this study were made up of several invertebrate guilds, of which dung beetles were found to be the most important for ecosystem functioning. Average dung beetle size and abundance was higher in the protected areas and in the wet season, indicating non-random species loss in response to the effects of anthropogenic disturbances over changing seasons. Furthermore, these results suggest that ecosystem process rates (in this case dung removal and secondary seed dispersal) performed by this community

were highest during the wet season. Interestingly, the effect of forest protection was stronger in the rainy season and it resulted in greater rates of dung removal and secondary seed dispersal.

The experiment for testing the effect of dung beetle size on ecosystem processes demonstrated that larger dung beetles remove a greater proportion of dung than small dung beetles, supporting previous work by Larsen et al. (2005). However, when larger dung beetles were barred from the bait in the exclusion experiments, the proportion of dung removed by small dung beetles was very similar to that when larger dung beetles were also present. This was likely due to the high abundances of the small *Onthophagus* species and low relative abundances of the larger *D. nigerimus* and *P. multicornis*.

The number of dung beetles present was positively influenced by both forest protection and variation across seasons. Lower numbers of dung beetles present during the dry season was most likely due to low humidity levels that increased the risk of desiccation, which can be fatal for insects (Hanski and Cambefort 1991, Vernes et al. 2005). Larger dung beetles were found more often in areas that were protected from encroachment by grazing cattle and fire, but did not occur in either the protected or unprotected areas of the forest during the dry season. This suggests that non-random loss of species is occurring during the wet season and that an important response trait to ecosystem degradation in this system is body size. In turn, dung removal was directly related to the size of dung beetles present: the larger the dung beetle the larger the amount of dung they removed at a time, thus increasing the likelihood of seeds being removed along with it (Andresen 2003). Consequently, body size is also an effect trait for ecosystem functioning (Lavorel and Garnier 2002), as larger dung beetles secondarily disperse more and larger seeds and are capable of removing a higher proportion of dung (Andresen 2003). In general, these findings agree with the studies by Larsen et al. (2005) and Barnes (2011), which also found that body size of dung beetles is directly related to both extinction proneness (a response trait) and ecosystem functioning (an effect trait), with larger sized dung beetles being lost first. That these are also the most functionally important in this ecosystem makes it all the more important that conservation initiatives, such as forest protection, be pursued.

Dung beetles are important for secondary seed dispersal because they bury seeds along with the dung, and these are then protected from predation by ants and rodents (Shepherd and Chapman 1998, Andresen and Levey 2004). In this study, the majority of seeds that were removed from the dung were found buried beneath the dung, suggesting

that dung beetles are the most important invertebrate guild for secondary seed dispersal. While these results do not provide evidence for body size determining variation in dung removal rates by dung beetles at high densities, body size was important for secondary seed dispersal. As, larger dung beetles are capable of burying more seeds (Andresen and Levey 2004). Results from this study showed that season and the average body size of dung beetles present were the most important predictors of the numbers of seeds secondarily dispersed. Additionally, when seeds were partitioned by size, it was clear that large dung beetles increased the numbers of seeds removed, at least for *L. zenkeri* (large) and *A. angustifolium* (small). As more *L. zenkeri* and *A. angustifolium* seeds were dispersed in protected forest areas during the wet season, this could positively impact the plant communities in the protected areas of the forest (Andresen 2002, Lawson et al. 2012). This is because the burial of seeds by dung beetles increases their chances of germination as otherwise seeds are often predated by rodents (Estrada and Coates-Estrada 1991, Andresen 1999, 2001). This suggests that when these larger species of dung beetles are lost, the remaining community will not be able to compensate functionally for this loss in the unprotected areas of the forest. Furthermore, these results indicate that the majority of ecosystem functioning performed by this community occurs during the wet season. This may be due to higher humidity, a more even temperature range and higher leaf area providing a more favourable environment for invertebrates (Hanski and Cambefort 1991, Vernes et al. 2005, Neves et al. 2010).

During the wet season, forest protection positively increased both ecosystem functions of dung removal and secondary seed dispersal. However, the influence of forest protection was not apparent in the dry season, and if sampling had not been carried out across seasons, the positive affect of forest protection on ecosystem processes carried out by dung-associated communities would not have been detected. This highlights the importance of taking into account any variation across seasons in ecosystems when measuring the impacts of anthropogenic threats, as also suggested by both Abrahamczyk et al. (2011) and Neves et al. (2010).

In conclusion, ecosystem functioning of the dung-associated community was strongly, and positively, influenced by the protection of the forest from external anthropogenic threats and this influence became especially evident during the rainy season. Additionally, the body size of dung beetles was a strong determinant of dung removal rates and secondary seed dispersal but also appeared to determine the susceptibility of dung beetles to anthropogenic threats. These results clearly show that

relatively simple techniques to mitigate the effects of anthropogenic disturbances, such as the fencing of areas adjacent to the forest, is an effective conservation strategy that can prevent potential non-random species loss and the major loss of ecosystem function.

Chapter 3 Competition and community assembly on an ephemeral resource

Abstract

Abiotic and biotic drivers directly impact a community's structure and function within an ecosystem. The structure of communities can be highly variable over time, and the form or range of this variability can depend strongly on the temporal scale in question. Abiotic factors that alter resource quality over different temporal scales can mediate the intensity of competition within a community, with competition generally being higher when species within a community occur at high densities. Dung is a highly ephemeral resource, as it can be entirely exploited by associated invertebrates in a matter of hours and is also subject to rapid desiccation, therefore making this an ideal system for quantifying the abiotic and biotic determinants of community structure over time. I investigated how competition levels within a community vary over short timescales in an Afromontane forest in Nigeria, using a dung-associated community as the focal system. Over three days, I observed how dung desiccation influenced the communities attracted to this resource, and tested the influence of competition in this community by experimentally altering the size and numbers of dung beetles, which are the most functionally important taxonomic group in this system. Because environmental changes have dramatic effects on insect communities, experiments were also run in both the wet and dry seasons to better understand the relative influence of desiccation changes across seasons. Desiccation of the dung resource was significantly higher in the dry season, resulting in almost completely desiccated dung after three days. As a result, there were large compositional changes in the dung-associated invertebrate community over days and among seasons, with the highest overall invertebrate abundance found within the first day of dung deposition and during the wet season. As expected, dung removal increased significantly with increasing dung beetle size and densities. However, there was a reduction in per capita dung removal rates, with increasing dung beetle densities. This was most likely due to competition between individuals over the resource. As a consequence of these density-dependent processes, individual removal rates for beetles of a particular size-class were not additive and therefore could not be used to predict community-level removal rates based on individual level functional

efficiency. Thus, using body size is an ineffective predictor of community-level function if utilised without taking into account competitive interactions. Furthermore, the structure and functioning of dung-associated invertebrate communities are strongly influenced by both abiotic (dung desiccation) and biotic (size and density-dependent competition) factors over small and large temporal scales.

Introduction

Abiotic factors have large impacts on communities through the effects of factors such as, temperature, and rainfall (Begon et al. 1996). Changes in resources caused by abiotic factors over temporal scales are normally measured over the course of seasons or years (Maron et al. 2005), but can also take place over short timescales (Finn 2001). For example, changes in rainfall and temperature can occur over very short timescales (diel variation) and can drive strong community responses (Pauli et al. 2009). Likewise, other disturbance events, such as forest fires, can have a large impact on habitats and communities (Elia et al. 2012).

In addition to habitat changes, resources can change markedly over the space of hours and days, with concomitant impacts on the associated community (Finn 2001). These short-timescale changes can be caused by abiotic factors such as desiccation and temperature changes, or may be due to other constraints on a resource, such as flowers that have a limited life span (Finn 2001, Kitching et al. 2007). For example, pollinator communities associated with a floral resource that occurs over a limited period of time, show marked changes depending on what plant species are flowering at a given time (Kitching et al. 2007). Carrion is also an ephemeral resource, and the associated community is strongly affected by the different stages of decomposition as succession occurs (Hanski 1987, Ives 1991). Similarly, decomposition of dung resources over time directly affects the associated invertebrate assemblages (Hanski and Cambefort 1991, Begon et al. 1996, Krell-Westerwalbesloh et al. 2004). In these ephemeral systems, invertebrates aid decomposition of the carrion and dung communities and show successional changes (Finn 2001). In the dung system, flies (Diptera) and dung beetles are the first major insect guilds that arrive, as are carrion flies in the carrion system, and these invertebrates contribute to decomposition (Ives 1991, Finn 2001). At later stages in decomposition in both systems, predators colonise when diptera larvae and other prey species are present (Hanski and Cambefort 1991). These ephemeral resource systems can perform important ecosystem functions. For example, the dung-associated

invertebrate community performs a wide variety of ecosystem processes, ranging from nutrient cycling and control of pest species, through to secondary seed dispersal (Larsen et al. 2005, Andresen 2008, Nichols et al. 2008). The dung community comprises a diverse array of insects, such as dung beetles and coprophagous diptera that utilise the resource generally for feeding and breeding (Hanski and Cambefort 1991, Pinero and Avila 2004). Dung beetles are generally assumed to be the most important for removing the dung resource, and have been found to remove more of the resource when larger dung beetles are present and when dung beetles occur at high densities (Finn and Gittings 2003, Larsen and Forsyth 2005, Larsen et al. 2005). Other important insect guilds in the dung-associated community are ants and staphylinids that predate on other invertebrates found in and around the dung resource (Pinero and Avila 2004). Therefore, these ephemeral resources are strongly affected by both abiotic and biotic factors that can alter the functioning of the ecosystem.

Competition also strongly affects community structure on finite resources (MacArthur 1958, Pimm and Rosenzweig 1981). In tropical ecosystems with high dung beetle (Coleoptera: Scarabaeinae) densities, the colonisation and complete removal of the resource happens very quickly (Hanski and Cambefort 1991), whereas in temperate areas with low diversity and abundance of dung beetles, decomposition and removal of the resource can take months (Holter 1979). Competition has an important role in determining how many organisms can exploit the same resource, and is especially strong in resources that are ephemeral, as they have limited availability and thereby induce strong competitive interactions between species (Tilman 1982, Holt 1984, Begon et al. 1996, Finn 2001), and is important for structuring the community (Brose 2005, Kéfi et al. 2012). Additionally, the number of competing organisms regulates the number of organisms that can utilise the same resource and can promote coexistence of a diverse range of species (Tilman 1982, Davis 1996). For example, dung resources are highly ephemeral and can last from mere hours to several months, resulting in high competition levels within the associated community (Finn 2001). Competition is most intense in this system within the ‘tunneler’ functional group which competes most intensely for space (compared with ‘rollers’ that move dung away from the dung pat), as they bury the dung directly beneath the resource for breeding attempts, and therefore compete over space as well as over the dung itself (Hanski and Cambefort 1991, Slade et al. 2007). Therefore, in tropical forests, competition over the dung resource can be

assumed to be strong and have a limiting influence on dung-associated invertebrate community composition (Estrada et al. 1993).

This study explores how both short and long timescale changes altered the dung-associated community in tropical forests where competition is especially intense. It was conducted at Ngel Nyaki Afromontane forest reserve in Nigeria. Afromontane forests are a unique ecosystem that is naturally fragmented, and due to rapid growth in the human population in Nigeria, these forests are now being cleared at an increasing rate (Olson et al. 2001, Chapman et al. 2004). Afromontane forests are also highly seasonal, with pronounced wet and dry seasons (Chapman and Chapman 2001), and dung communities have been shown to show strong responses to seasonal changes (Vernes et al. 2005, Nyeko 2009). I used the dung-associated community as it is an ideal study system to investigate competitive effects among species, and is a good indicator of ecosystem health (Davis et al. 2001, Finn and Gittings 2003). Also, dung is a high quality resource and the quality is determined by the amount of moisture, fibrous material and nutrients available, which differs as the resource ages and changes in attractiveness (Hanski and Cambefort 1991, Kishi and Nishida 2006). In this system I investigated whether desiccation rate of the dung resource was different over the course of days and across changes in seasons and whether these changes resulted in community level fluctuations. I also tested whether the densities and sizes of the dung beetles present at the resource altered dung removal rates due to altered competition levels between dung beetles.

Methods

Assessing short and long term temporal changes in the dung-associated community

To assess whether forest community structure differs across seasons, sampling was replicated during the wet and dry seasons, and carried out in eight sites in different areas of the forest, and at two points within a site to account for spatial heterogeneity (see Chapter 1). Four of the sites used were in areas of the forest that were protected from anthropogenic threats as I used this same experiment to test these effects compared with no forest protection in Chapter 2. However, as I was not interested in these impacts for this experiment, this ‘treatment’ affect was added as a random effect in statistical models to account for variation between these sites compared with sites with no forest protection. To determine how changing dung moisture content over time

influenced the community structure, pitfall traps (for details see Chapter 2) were set for three days with the same dung and the contents emptied and the trap refilled with water mixed with detergent every 24 hours. All of the insects caught in these traps were preserved in 70% ethanol and brought back to New Zealand where insects were identified to family level (using CSIRO 1996). A total of 94 samples were obtained, with 48 collected in the wet season and 46 in the dry season (two traps did not contain insects during the dry season so were not counted).

Determining competition levels in the dung-associated community

To determine competition levels within the dung beetle community, I carried out experiments in which the size of the dung beetles and the numbers present were varied. Dung beetles were grouped into size classes based on their pronotum width. The size classes used were 2.5-4.5 mm (small), 6-8 mm (medium), and 9.5-12.5 mm (large). The small size class was made up of several species of *Onthophagus* (see Chapter 2, Table 2.1) the medium size class contained *Onthophagus* sp.1 and *Proagoderus multicornis*, and the large size class contained *Diastellopalpus nigerrimus* and *Catharsius* sp. n. The number of dung beetles was varied for each size class, with three density treatments of 1, 2 and 5 dung beetles for medium and large size classes and five density treatments of 1, 2, 5, 10 and 20 dung beetles for the small size class. The small size class had trials with greater numbers because during field-based experiments I often observed up to 30 small dung beetles present at the dung resource, whereas for the medium and large size classes the abundance observed was much lower (generally no greater than 7). This is because smaller dung beetles require less of the resource and therefore are often found at higher densities (Hanski and Cambefort 1991). Trials in which the dung beetle/s did not remove any dung were excluded from the analysis. In total, 120 trials were run, with at least 10 trials for each size class.

Tests were conducted in wooden boxes (30 x 30 x 30 cm) filled with soil to a depth of 20 cm, with a 20 g piece of dung placed directly on the soil surface. The top of the box was covered using a sheet of Perspex, allowing natural light levels into the arena. The dung beetles used for this experiment were always found directly beneath the dung resource, even though there was unutilised space to the sides, and were never observed at the bottom of the experimental containers used. Therefore, it appeared that dung beetle movements were not constrained by the size of the boxes used. Dung

beetle/s for each size class were randomly selected from a species pool generally containing at least two species for the medium and large size classes. For the small size class, a dung beetle was randomly selected from a species pool containing at least three species. The dung beetle/s were placed inside the box with the dung bait and left undisturbed for 24 hours, after which the soil inside was sieved in 1 cm increments until the dung beetle/s were found. Dung beetles were never used in an experiment more than once. The dung was dried and weighed and compared to a 20 g sample of dung from the same day, which had none removed, to accurately determine the proportion of dung removed by the beetle and control for slight differences in the dung moisture levels from day to day.

Experimental dung beetles were caught using pitfall traps with a funnel (see Chapter 2) that allowed live capture. The dung beetles used for this experiment were kept in the laboratory for up to 24 hours in a dark metal 2 L container half filled with moistened soil to ensure they did not dry out, and those that were not used within 24 hours were released in an area of the forest where no data collection was carried out. This experiment was carried out over two field seasons, in 2009 and 2010.

Evaluating changes in dung desiccation over time

Dung attractiveness is, among other things, related to water content (Hanski and Cambefort 1991), so I assessed dung desiccation rate during the wet and the dry seasons. This was done by marking six transects that ran on a doubling scale (0, 5, 10, 20, 40, and 80 m) from the forest edge to 80 m inside the forest edge to account for increasing humidity levels with increasing distance from the forest edge (Didham et al. 1998).. Transects were placed a minimum of 20 m apart along two separate areas of the forest edge. A 20 g ball of pig dung wrapped in muslin and tied to a wooden stake was placed at each distance along each transect. Pig dung was collected fresh every day and then homogenized to ensure an even composition, and the pigs were fed a consistent diet to remove any variation in nutritional quality. The dung was wrapped in muslin to prevent invertebrates from accessing the dung, thereby permitting the dung to dry as naturally as possible. The muslin used to wrap the dung was standardized and measured 20 x 20 cm (average weight: 0.72 g \pm 0.045 SEM). The dung ball was weighed in the field after 24 hours and 72 hours. This experiment was replicated in the wet season and

the dry season along the same transects and at the same distances so the effect of season on desiccation rates could be accurately determined.

Statistical analysis

Assessing short and long term temporal changes in the dung-associated community

All analyses were performed using R (R Development Core Team 2012). To examine how the dung-associated invertebrate community structure was influenced by the effect of day and changing season, the dissimilarity of species composition between sampling points was calculated using a log-base 10 Modified-Gower distance metric (Anderson et al. 2011) with the ‘vegan’ package in R (Oksanen et al. 2012). The Modified-Gower dissimilarity metric considers an order of magnitude change in abundance equal to a change in composition and accounts both for changes in the relative abundance of invertebrate families in the community, and the compositional changes in the community (Anderson et al. 2006). The dissimilarity in community composition through time was visualised using a non-parametric multidimensional scaling (NMDS) ordination. To test whether time since dung deposition affected community compositional dissimilarity, a permutational distance multivariate ANOVA was used, with ‘site’ used as a blocking factor to account for hierarchical nature of the sampling design.

To summarise how the dung-associated community changed by day and season, I calculated total insect abundance, dung beetle abundance, and the total number of families present per trap within each site and each season. The effects of the treatments of day and variation across seasons on total insect abundance, dung beetle abundance, and number of families were tested using generalized linear mixed models (GLMM’s) within the ‘lme4’ package (Bates et al. 2011), with a Poisson error distribution and specifying ‘site’ as the random effect. Overdispersion of the data was accounted for by using a Poisson log-normal distribution, whereby an observation level factor was included as a random effect (Elston et al. 2001, Bolker et al. 2009). All possible combinations of predictors and interactions were tested for all models run and models were fitted using maximum likelihood and were simplified using AICc (Akaike Information Criterion corrected for small sample size) and Akaike weight (W_m) to rank and subsequently select the best-fit model to the data. All models included ‘forest fencing treatment (see Chapter 2)’ as a random effect to account for the influence of

forest protection at four of the eight sites used. Post hoc Tukey HSD tests with Bonferroni corrections were then run using the ‘multcomp’ package (Hothorn et al. 2008).

Determining competition levels in the dung-associated community

To test the effects of the size and number of dung beetles on dung removal, I logit transformed the proportion of dung remaining to account for the presence of zeros and ones in the data and to normalise the variance so the data could be tested using a linear model (Warton and Hui 2010). A GLMM model was then run using the ‘nlme’ package (Pinheiro et al. 2012), with the field season as a random effect to account for any variation caused by running this experiment across two years. After model simplification, a post hoc Tukey HSD test with Bonferroni corrections was used to test the effects of combinations of different size classes of dung beetles on the proportion of dung removed (Hothorn et al. 2008).

Evaluating changes in dung desiccation over time

Dung desiccation rates were tested using a GLMM model run using the ‘nlme’ package with ‘transect’ and ‘distance’ from forest edge as random effects to account for microclimatic differences between transects and to account for the effects of distance from forest edge.

Results

Assessing short and long term temporal changes in the dung-associated community

The number of families caught in traps decreased with increasing dung age. Overall there was a total of 74 recorded families, 63 of which were recorded on day one, 54 on day two and 45 on day three (Table 3.1). There were several families that were affected by seasonality. Of the 74 families recorded, I caught 5 families in the wet season, 21 families in the dry season, and recorded 48 that occurred in both the wet and dry seasons. This indicates that the community composition during the dry season is quite different to that occurring during the wet season, with several Hymenoptera families that were recorded only during the dry season (Table 3.1). This resulted in significant community composition changes across days ($F_{1,90} = 17.43$, $p < 0.001$), seasons ($F_{1,90} = 5.52$, $p < 0.001$), and the daily changes were stronger in the dry season

(i.e. there was a significant interaction between these two factors $F_{1,90} = 1.93$, $p = 0.045$) (Figure 3.1).

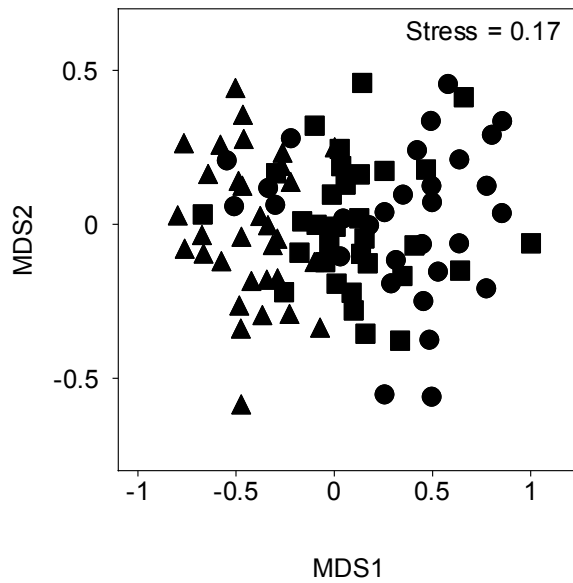


Figure 3.1 Non-metric multidimensional scaling ordination plot comparing overall invertebrate community composition over days 1-3, using the Modified-Gower dissimilarity metric. Each point represents a single pitfall trap sample with triangles, squares, and circles to denote day 1, day 2, and day 3 samples, respectively.

Table 3.1 List of families caught in the experiment for assessing short and long timescale effects with their abundance for each trapping day, diet preference (Goulet and Hubert 1993, CSIRO 1996), and their seasonality. Orders are listed according to total abundance with families grouped by order and, where applicable, by superfamily (in italics).

Order	Family	Day 1	Day 2	Day 3	Diet	Seasonality
Coleoptera	Anobidae	4	4	12	saprophage	both
	Chrysomelidae	3		1	phytophage	both
	Hydrophilidae	172	40	47	saprophage	both
	Latridiidae	4			mycophage	dry
	Nitidulidae	2			omnivorous	both
	Ptiliidae	7	4	1	mycophage	both
<i>Curculionidae</i>	Brentidae	1	1		xylophage	dry
	Curculionidae		2		xylophage	both
<i>Carabidae</i>	Broscini	6	3	2	predator	both
	Carabidae	1			predator	dry
<i>Scarabaeidae</i>	Aphodiinae	27	1	3	coprophage	both
	Melanthropine			1	coprophage	both
	Scarabaeinae	1204	182	213	coprophage	both
<i>Staphylinoidea</i>	Pselaphidae	17	19	6	predator	both
	Scaphidinae	1			predator	dry
	Scydmaenidae	1			predator	both
	Staphylinidae	1107	297	156	predator	both
<i>Tenebrionoidea</i>	Anthicidae	2			scavenger	dry
	Mycetophagidae	9	7	3	scavenger	dry

Diptera	Anthomyiidae	9	2		saprophage	both	
	Calliphoridae	144	11	3	coprophage	both	
	Cecidomyiidae	25	18	12	parasitoid	both	
	Curtonotidae	2			saprophage	dry	
	Dolichopodidae		3	1	pollinator	dry	
	Helomyzidae	1754	185	163	saprophage	both	
	Helosciomyzidae	1			omnivore	dry	
	Muscidae	97	10	14	saprophage	both	
	Phoridae	162	66	35	saprophage	both	
	Pipunculidae	1	1	1	parasitoid	both	
	Sarcophagidae	11	2	1	saprophage	both	
	Sepsidae	87	108	165	coprophage	both	
	Sphaeroceridae	70	18	9	coprophage	both	
	Syrphidae	38	6	10	pollinator	both	
	Therevidae	2	2		predator	both	
	Tipulidae	2	5	2	nectivore	wet	
	Hymenoptera	Apidae	13	1		pollinator	both
		Austroniidae	3	2		parasitoid	dry
		Braconidae	4	8	3	parasitoid	both
		Ceraphronidae		1		parasitoid	wet
Diapriinae			1	5	parasitoid	both	
Eucoilidae		5	2	3	parasitoid	both	
Eurytomidae		2			parasitoid	dry	
Formicidae		1555	681	464	omnivore	both	
Ichneumonidae		3	2	1	parasitoid	both	
Nyssonidae				1	predator	dry	
Pompilidae				1	predator	dry	
Pteromalidae				1	parasite	dry	

	Rhopalosomatidae	2			parasite	dry
	Scelionidae	1		2	parasitoid	both
Hemiptera	Cicadellidae	19	12	15	phytophage	dry
	Cydnidae	33	19	13	phytophage	both
	Hebridae	1	1	1	omnivore	both
	Idiostolidae	1	2	4	phytophage	dry
	Piesmatidae	1	2		phytophage	both
	Psyllidae		1	1	phytophage	both
	Reduviidae	3	5		predator	dry
	Rhopalidae	2	3	1	phytophage	both
Lepidoptera*	Brachodidae	1			puddling	wet
	Cossidae	1			puddling	dry
	Galacticidae	3	1	1	puddling	both
	Palaephatidae	5	1		puddling	both
	Satyridae	6	6	2	puddling	both
	Sphingidae	10	3		puddling	wet
Orthoptera	Gryllidae	115	112	132	omnivore	both
	Pyrgomorphidae		1		omnivore	wet
	Tetrigidae	2	2	5	omnivore	both
Blattodea	Blattidae	18	6	17	omnivore	both
	Rhinotermitidae		2		xylophage	dry
Dermaptera	Anisolabididae	2	2	5	predator	both
Plecoptera	Perlidae	3	4		omnivore	both
Embioptera**	Embioptera	3	1	2	phytophage	both
Neuroptera	Chrysopidae	1			predator	dry

* Puddling behaviour is specific to the Lepidoptera order when using the dung resource (Boggs and Dau 2004).

** The Embioptera order could not be identified further because I did not have access to the necessary insect keys.

Variation across seasons altered the total insect abundance (including dung beetles) ($z = 2.20$, $p = 0.028$) and dung beetle abundance ($z = 4.05$, $p < 0.001$), but not the number of families present ($z = 0.63$, $p = 0.526$), resulting in lower overall insect and dung beetle abundances in the dry season (Figure 3.2). The abundances of all insects, dung beetles, and insect families caught in a trap also changed over short timescales. When comparing the insect community on days two and three after dung deposition with the insect community present one day after deposition there was significantly lower insect abundance ($z = -4.86$, $p < 0.001$), fewer dung beetles ($z = 4.05$, $p < 0.001$) and fewer families present ($z = -7.17$, $p < 0.001$) (Figure 3.2). The difference in the overall abundance of insects and dung beetles between days two and three was not significant. However, the differences between all other combinations of the overall insect abundance, dung beetle abundance and the number of families present over days were significant (Figure 3.2).

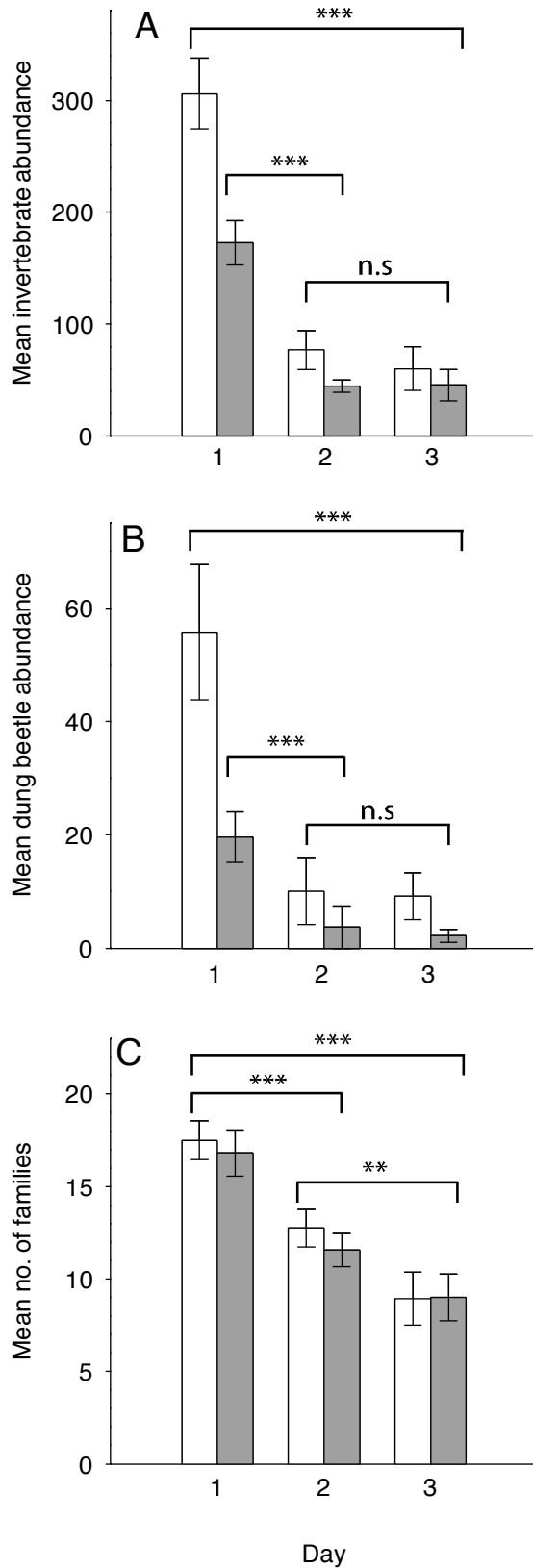


Figure 3.2 Mean (± 1 SE) abundance across the three sampling days for all invertebrates (A), dung beetles (B), and overall number of invertebrate families (C). Open and closed bars denote wet and dry season samples, respectively and ‘*’ denotes level of significance between combinations of size classes, ‘n.s.’ denotes non-significance.

Determining competition levels in the dung-associated community

The amount of dung removed was significantly affected by the size of dung beetles ($F_{2,106} = 35.08$, $p < 0.001$) and the number of beetles present ($F_{1,106} = 6.12$, $p = 0.015$), which meant that more dung was removed when larger dung beetles were present and when higher numbers of dung beetles were present. Also, there was a significant positive interaction between the size and number of beetles in each trial on the amount of dung removed ($F_{2,106} = 3.48$, $p = 0.034$), this resulted in larger beetles removing a greater proportion of dung when at higher densities (Figure 3.3). However, when per capita removal rate for each size of dung beetle was calculated, dung beetles from all three size classes removed less dung as densities of beetles in the trials increased (Figure 3.4). Also, there was a significant negative interaction between size and number of beetles on per capita removal ($F_{2,106} = 18.68$, $p < 0.001$), such that larger beetles removed more dung per capita at low densities (Figure 3.3). The same trend of reduced per capita dung removal at high densities was found for dung beetles in the small size class (Figure 3.4). Additionally, when all possible size combinations were tested, all but the combination of small and medium beetles were significantly different in their influence on the amount of dung that was removed (Table 3.2).

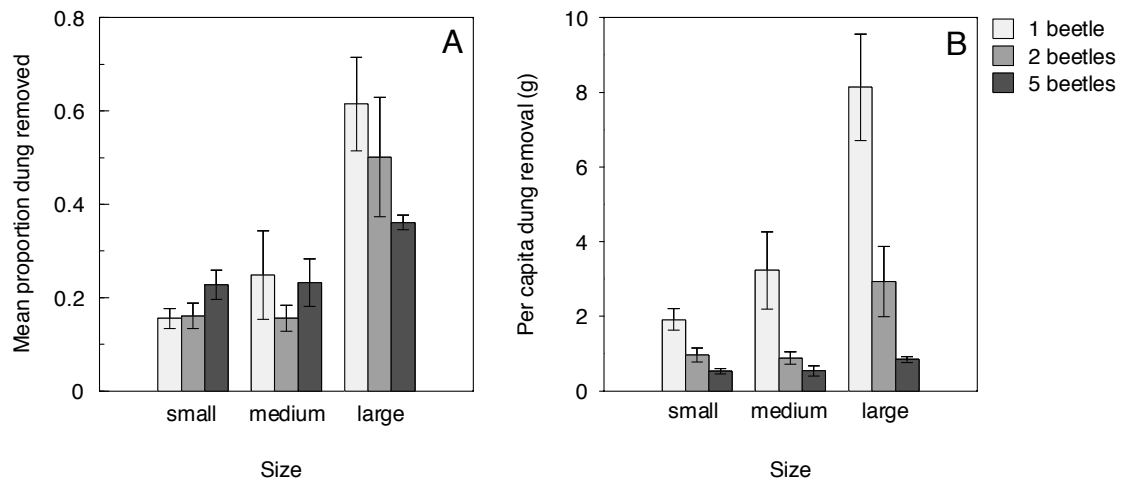


Figure 3.3 Mean (± 1 SE) proportion of dung removed (A) and mean (± 1 SE) per capita dung removal rates (B) for different dung beetle numbers (1-5) and sizes.

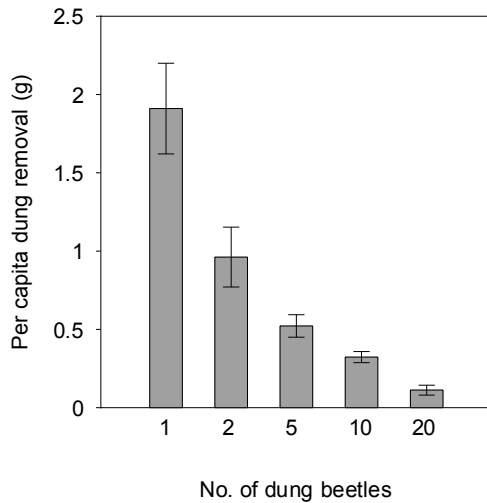


Figure 3.4 Mean (± 1 SE) of per capita dung removal for five dung beetle density treatments for dung beetles in the small size class.

Table 3.2 Tukey tests on combinations of size classes. S: small. M: medium. L: large.

Sizes	Estimate	Std. Error	t value	p-value
S - M	-0.070	0.510	-0.137	0.989
S - L	-2.979	0.436	-6.832	< 0.001
M - L	-2.909	0.614	-4.740	< 0.001

Evaluating changes in dung desiccation over time

Dung desiccation rates differed significantly depending on season ($F_{1,139} = 651.96$, $p < 0.001$) and day ($F_{1,139} = 17.30$, $p < 0.001$), with a significant interaction between both factors ($F_{1,139} = 32.58$, $p < 0.001$) that resulted in no desiccation occurring during the wet season over three days, but near complete desiccation during the dry season over three days (Figure 3.5). The completely dried dung bait weighed an average of 7.8 g (from a standardised wet weight of 20 g), equating to a decrease of 61% from the original weight. Three days after deposition during the dry season, the dung weighed on average 8.8 g, therefore any dung resource remaining after three days was already almost completely dried out.

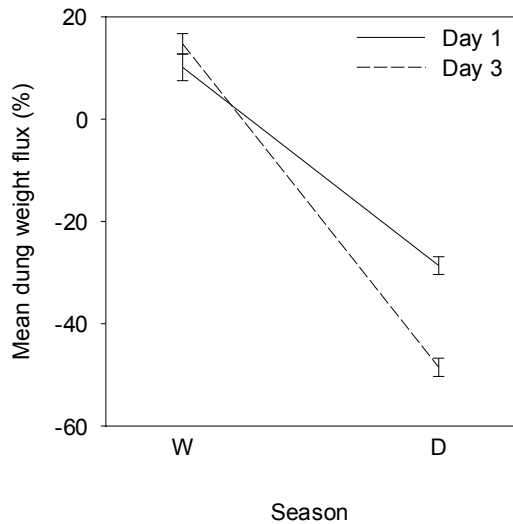


Figure 3.5 Mean (± 1 SE) percentage change in dung weight with the influence of season and day 1 and day 3.

Discussion

These findings show that there were marked changes in invertebrate abundance over seasons and over short timescales in the dung-associated community, as more insects were caught during the wet season and immediately after dung deposition. Additionally, both the size and number of dung beetles present affected the amount of dung removed, with larger dung beetles removing more of the resource, particularly at high densities. However, dung beetles removed less dung per capita at higher densities, regardless of size. Also, the quality of the dung changed over seasons, with minimal or no change in weight over time during the wet season, due to continuous rainfall, whereas during the dry season the dung dried out completely after three days. Therefore, as adult dung beetles feed on the water content of the dung (Finn and Gittings 2003), it is likely that the resource would not have been attractive to adult dung beetles shortly after deposition in the dry season, as was illustrated by the very low numbers of beetles caught several days after the dung resource was exposed.

Seasonality and changes in the dung resource over short timescales had a strong influence on the dung-associated community structure. There were more insects and dung beetles present in the wet season than in the dry season, which is most likely due to a lower range of temperatures coupled with high humidity during the wet season, which decreases the risk of an insect desiccating fatally (Hanski and Cambefort 1991, Andresen 1999, Vernes et al. 2005, Nyeko 2009). The dung-associated community also

changed strongly over short timescales, as abundances of the overall insect community, dung beetles, and insect families present were much higher on the first day after dung deposition (Finn 2001). Additionally, families that were present after a couple of days were generally a subset of the families present on day one after resource deposition. The only notable exception to this was three hymenopteran families that were only present on the third day of trapping. These families were parasitoids and predators that colonised the dung resource after the coprophagous insects, as the dung attractiveness changed (a trend also noted by Hanski and Cambefort 1991). Also, while there was no desiccation of the resource during the wet season, the community composition still showed strong changes over the course of days with the same effects of species diversity decreasing and total insect and dung beetle abundance decreasing. Possibly because the scent of the dung changed over time as the dung resource aged, thereby becoming less attractive to insects that utilised the resource. Therefore, the attractiveness of the dung resource changed over the course of just days and was not just affected by desiccation rates.

The amount of dung removed by dung beetles was higher when larger dung beetles were present and at higher dung beetle densities, which agrees with results from other studies (Finn and Gittings 2003, Larsen and Forsyth 2005, Larsen et al. 2005). However, per capita removal rates declined dramatically with increasing densities for all sizes of dung beetles. Thus, the amount of dung removal per beetle at higher densities was not additive. This is most likely due to increasing competition levels between individuals that resulted in reduced access to the resource (Finn and Gittings 2003, Vernes et al. 2005). Additionally, this reduction in per capita removal rates was particularly strong for large dung beetles. This could be due to a saturated community, as one large dung beetle was capable of removing the entire dung bait. If the resource used had been larger, the decrease in per capita rates may have not been as strong for the larger beetles. However, as I modeled the size and weight of the dung bait used in these experiments on the dung of tamar monkeys (see Chapter 2), which are ubiquitous throughout this system (Grassham 2012), these levels of competition may reflect actual competition rates in the natural ecosystem. Furthermore, the majority of dung beetle species caught in experiments were from the ‘tunneler’ functional group which bury the resource directly beneath the dung pat (Hanski and Cambefort 1991). Barnes (2011) only observed dung beetle species from the ‘roller’ functional group in the grasslands and at the edge of the forest, and only one species was always observed

as present within the dung resource and was never found beneath it. This ‘tunneling’ behaviour creates spatial competition beneath the dung resource, which increases with higher densities (Hanski and Cambefort 1991). Spatial constraints at high densities could interact with competition over the dung resource and ultimately result in reduced per capita removal rates at high dung beetle densities. Competition rates can influence the ecosystem function performed by a community, as the dung removal rates were not additive with increasing densities of dung beetles. Therefore, the ecosystem function performed by a single beetle could not be used to predict ecosystem function performed by an entire community, even when measured separately for different dung beetle sizes.

In conclusion, the dung-associated community was impacted by both seasonal variation and short timescale changes in the resource that was affected by changing dung attractiveness over time caused by abiotic factors. Competition was apparent in this system, with higher densities of dung beetles removing less dung per capita than lower densities of dung beetles. Therefore, competition at higher densities directly decreased ecosystem functioning carried out by this community and was most apparent when the resource was most attractive and insects were present at high abundances. Also, because the level of dung removal performed by individuals within a community was not additive with increasing densities of dung beetles, it therefore could not be used to predict the function performed by an entire community. Therefore, this study demonstrates the importance of taking into account not only abiotic factors, but also competition between individuals to accurately predict resulting ecosystem function.

Chapter 4 Body size scaling within a competition network

Abstract

Interaction networks are made up of a community of species that share a common resource and all interact together through trophic and non-trophic interactions. Both of these interaction types can alter the effect of the other and are important for structuring the community. Non-trophic interactions are generally measured by counting the number of co-occurrences of species at a shared resource, thereby inferring the existence of competition. However, this is not always an appropriate measure, as different species may use different parts of the resource. Consequently, when measuring actual competition in a community it may be more effective to visually observe which species interact and how often. The structure of trophic interactions between species in food webs can in part be predicted by the ratio of predator to prey body size, and this ratio may also be useful for predicting the outcome of non-trophic interactions. This study aimed to test whether co-occurrences can be used to infer the response of competitive interactions to anthropogenic activities, such as habitat loss. This was tested using the dung-associated community in an Afromontane forest in Nigeria, as this is a highly competitive system. Video analysis was used to determine which species competed and how often, and then trapping was carried out to sample the community. The structure of the community was compared between protected and unprotected areas of the forest. Sampling was carried out in both the wet and dry seasons to account for strong temporal variation. Food-web metrics were measured to gain an understanding of the interaction network structure. Connectance was higher in the co-occurrence network, and the number of compartments in a network was higher in the competition network. Nestedness of a network differed between protected and unprotected forest and varied with season in the competition network, however no effect of these factors was detected in the co-occurrence network. The body-size ratio between winners and losers of a competition was also a good predictor of an interaction outcome, especially when the ratio in body size was greater than four between competing individuals. Therefore, when determining network structure, measuring the actual rates of competition gives more accurate results than numbers of co-occurrences, and the body-

size ratio between competing species can be a useful tool to aid in predicting the outcome of competitive interactions or to estimate non-trophic effects in food webs.

Introduction

A community is made up of the species that share a habitat and its resources, and it is linked by the network of interactions between these species (Pimm et al. 1991). The interactions within a community can be classified as either trophic or non-trophic (Goudard and Loreau 2008). The trophic interactions within networks are feeding links (e.g., plant-herbivore or predator-prey) and non-trophic interactions are non-fatal interactions, such as mutualism and competition that can modify the influence and strength of a trophic interaction (Kéfi et al. 2012). Trophic interaction networks have been well studied, and this work has resulted in some general inferences about stability that can be inferred from network structure (Melian et al. 2009). For example, how nested a community's structure is has been shown to directly influence a network's stability (Bascompte et al. 2003, Allesina and Tang 2012). Nestedness occurs when the species that interact with specialists are a subset of species that interact with generalists (Atmar and Patterson 1993). A nested network has a non-random structure and is highly cohesive where generalist species interact with each other and form a core of interactions, to which specialist species are connected through their interactions (Atmar and Patterson 1993, Bascompte et al. 2003). In this sense, a generalist is a species that interacts with many other species and a specialist only interacts with one or two other species (de Ruiter et al. 2005), rather than, for example, a habitat generalist. Additionally, the density of links within a community also provides information about its stability (Dunne et al. 2002b). As, a highly connected network can make it more robust to disturbances (McCann 2000, Dunne et al. 2002b, Bluthgen 2010). Thus, measuring different aspects of network structure gives a comprehensive overview and allows predictions of a community's stability and how it may respond when subjected to a disturbance (Dunne et al. 2002b, Thebault and Fontaine 2010).

Non-trophic interactions are rarely studied, especially in conjunction with other interaction types (Melian et al. 2009, Olf et al. 2009, Thebault and Fontaine 2010, Fontaine et al. 2011). This is because the fundamental physiological requirement for food (which defines trophic interactions) has been seen as more important for structuring interaction networks (Paine 1980, Berlow et al. 2009). Recently, the importance of studying non-trophic interactions has been discussed in more detail, with

models focusing on the importance of taking into account non-fatal interactions that influence the structure of the community by changing the strength of trophic interactions (Arditi et al. 2005, Brose et al. 2005, Fontaine et al. 2011, Kéfi et al. 2012). Non-trophic interactions are important to quantify as they can drive species diversity and composition and alter the persistence of communities (Kéfi et al. 2012). Interactions are normally measured by counting the number of co-occurring species (Perner and Voigt 2007, Faisal et al. 2010, Gomez et al. 2011). Building an interaction network from the co-occurrence of species implies that all those species interact. However, this may not be an accurate depiction, as not all species that co-occur on a resource use it for the same purpose and therefore may not compete (Hanski and Cambefort 1991, Bastolla et al. 2005). Therefore, directly observing how species compete over the shared resource may enhance our understanding of how these networks are structured and of the functioning of the ecosystem.

Competitive and mutualistic interactions are two main types of non-trophic interactions. Mutualistic interactions are where both species involved gain from the interaction whereas competitive interactions generally have a negative effect on at least one of the constituents involved (Kéfi et al. 2012). Mutualistic interactions have been studied in several types of networks, such as ant-plant, pollination, and seed dispersal networks (Bascompte et al. 2003, Chamberlain and Holland 2009, Ings et al. 2009, Gomez et al. 2011). The main types of competitive interactions are exploitative and interference competition (MacIsaac and Gilbert 1991, Kéfi et al. 2012). Exploitative competition occurs among organisms that use a common resource that is limited and is more commonly studied than interference competition (Tilman 1982). Interference competition is competition over space or nutrients that are required for feeding and/or breeding (Schoener 1983, Grether et al. 2009). Also, interference competition generally occurs between basal species over access to a resource but can also occur between predators (Eichenberger et al. 2009). Therefore, incorporating these competitive interactions in interaction networks can give more information about a community as they determine how many species utilise the same resource and can coexist, which alters the composition and stability of communities (Kéfi et al. 2012).

Indirect interference competition generally occurs when one individual is much larger than the other (Grether et al. 2009). Thus, integrating species body size within interaction networks may enable better prediction of network structure and stability (Woodward et al. 2005, Melian et al. 2009). Additionally, the ratio between the body

size of predators and their prey can be used to predict food-web structure (Emmerson and Raffaelli 2004, Brose et al. 2006b). As trophic level increases, generally so does the body size of species within those trophic levels and these species generally consume species that have a smaller body size which, generally occur at lower trophic levels within a food web (Woodward et al. 2005, Otto et al. 2007). There are however exceptions to this general rule, for example parasitoids and hyperparasitoids are smaller than their prey species (Cohen et al. 1993, Brose et al. 2006a). Therefore the scaling of predator to prey body size ratios can influence network structure, and the distribution of interaction strengths can be predicted by body size distributions of predators and their prey (Emmerson and Raffaelli 2004). Brose et al. (2006a) found that increasing the body-size ratio between predators and their prey positively influenced the community stability. This was because of a corresponding reduction in interaction strength that promotes community stability (Pimm et al. 1991, Brose et al. 2006a). This same pattern of interaction link structure being predicted by the body-size ratio of predators and their prey may also apply to non-trophic interactions, but this remains to be tested.

The structure of an interaction network can be influenced by the environment as well, with anthropogenic impacts, spatial scale and temporal effects all influencing an interaction network's structure (Tylianakis et al. 2007, Olf et al. 2009). For example, Tylianakis et al. (2006) found changes in species diversity over time and with different habitats that were influenced by anthropogenic impacts, and this altered average body sizes of consumer and resource species and how they interacted (Laliberté and Tylianakis 2010).

Here I investigate how competition networks are structured and whether these can be constructed by simply determining which species co-occur, instead of visually observing competitive interactions among species and using these to construct a network. This study was carried out at Ngel Nyaki Afromontane forest reserve in Nigeria. Afromontane forests are a unique ecosystem with pronounced wet and dry seasons where anthropogenic impacts strongly influence communities in forest reserves (Olson et al. 2001, Matthesius et al. 2011) (see Chapter 1). In Ngel Nyaki forest reserve, several areas of the forest were protected via exclusion zones to stop livestock from grazing up to and inside the forest reserve and to stop fires that are lit every year to promote grass growth from encroaching inside the forest edges. Consequently, studying an interaction network in this system allowed me to test the effects of forest protection on community structure. Also, I was able to test how competitive interaction networks

were altered by environmental factors such as temperature and rainfall in a system that exhibits strong climatic changes across the course of seasons. I used the dung-associated invertebrate community as a model system, as they are a good indicator of forest health, have high levels of non-trophic interactions and utilise a well defined resource that is easily replicated in space and time (Davis et al. 2001, Finn 2001). In the dung-associated community interactions generally took the form of competition that acted either directly through a physical interaction between individuals or indirectly where one individual limited access of another to a resource (Grether et al. 2009, Kéfi et al. 2012). I tested commonly used network metrics that can be used to infer community stability for both types of interaction network: the co-occurrence network built from species co-occurrences and the competition network built from observed competitive interactions between species pairs (hereafter referred to as the ‘co-occurrence network’ and ‘competition network’). Additionally, whether the body-size ratio between competitors could be used to aid in predicting the outcome of an interaction was also tested to see if it followed similar rules to those outlined in Brose et al. (2006a) for trophic networks (i.e. that the body-size ratio of two interacting species could predict which of the species involved was a predator and which was the prey).

Methods

Interaction network based on observed rates of competition within the community

Competitive interference interactions between species were recorded to determine accurate levels of competition in the dung community. To observe these interactions, video cameras (Sony DCR-HC52E) were set up and left to record so that natural invertebrate behaviour could be documented. Videos were recorded for 30 minutes and were then cut down to 25 minutes, removing 4 minutes at the beginning of the video and 1 minute at the end so that invertebrates at the dung bait were not influenced by any disturbances created from setting up and retrieving the camera. Recording took place at midday and dusk to observe both the period of highest activity (midday) and to ensure any crepuscular species were recorded (dusk). A dawn time period was also initially included but after a couple of days of sampling at several different sites and finding no activity, recording at this time period was discontinued. The dung bait was set out at 9 am, prior to recording to allow time for the dung-associated community to colonise and then recording took place at 12:30 pm for the

midday session and 5:40 pm for the dusk session. Also, videos were recorded on the same day as the dung resource was placed at each site, as during the wet season the dung was often completely removed within 24 hours after dung deposition and the community was present at highest densities within the first 24 hours (see Chapter 2 and Chapter 3).

Sampling was carried out at eight sites, four in protected areas of the forest and four in unprotected areas of the forest (predominant land-use) (see Chapter 2). The order in which sites were sampled was randomly determined. To assess the importance of seasonal variation, this experiment was conducted during both the wet and dry seasons. Wet season sampling was done in October and dry season sampling was conducted at the end of November after the rains had ceased for 2 weeks.

The cameras used had infrared lights so that recording at night was possible. A CEM light meter (DT-1301) was used to detect at what exact time the light had completely faded and recording started 30 minutes prior to that. This method was used because the light levels decreased faster in the forest than in the grassland, at 30 minutes prior to the light levels completely fading ($\text{lux} = 0$), the light intensity inside the forest measured c. 40 lux. Cameras were attached to a stand overlooking a 20 g dung bait (see Chapter 2). The stand was constructed using a wooden stake with a cross-piece attached at a 90° angle at the top with a tripod strapped to it, thereby allowing the camera to point straight down with a field of view of ~ 20 cm around the dung bait (Figure 4.1). A total of 64 videos were recorded, 32 from each season and 16 from each time period (midday and dusk).



Figure 4.1 Video recording set up with dung bait on the ground directly below the camera.

Videos were analysed by counting the number of interference competitive interactions and identifying to family level the competitors involved. Competitive interactions were defined as an interaction between two individuals that resulted in one individual being displaced from the resource and leaving the field of view (loser) and one individual remaining on the resource (winner). This included direct and indirect forms of interference competition where a direct interaction was a physical competitive interaction between two individuals and an indirect interaction was where one individual limited access to the resource for other individuals. These invertebrate competitors were identified to family level by matching the morphological characteristics to a reference collection of all the invertebrate families that were collected from the same points within the forest at the same sites (from invertebrates collected for the co-occurrence network). Other invertebrates were very rarely observed, so non-insect invertebrates were not included as part of the species matrices. For example, there was one observed occurrence of a hunting spider that preyed on one diptera fly and one occurrence of a millipede interacting with a dung beetle. Additionally, the invertebrate families observed at dusk were the same as the families that occurred at midday with very few competitive interactions were observed, so the dusk time period was not utilised for further analysis. There was no method available for recording all activity simultaneously as invertebrates utilised both the inside and outside of the resource, so the families observed competing were the ones that occurred

on the upper surface of the dung. However, in experiments (see Chapter 2) where invertebrates that were found inside and buried beneath the dung resource were identified, the only families recorded were Formicidae, Scarabaeinae and Staphylinidae. Therefore, the majority of invertebrate diversity and interactions occur on the upper surface of the dung as I recorded 64 families in total that utilised the dung resource and only three of these were found to occur inside and beneath the resource.

Interaction network based on co-occurrences

The co-occurrence networks were constructed from the invertebrate community that was sampled using dung baited pitfall traps (see Chapter 2). The invertebrates within a trap were all assumed to co-occur and were used to build a network based on the co-occurring species in each trap. This experiment was carried out the day after a video was recorded at the same points in the forest and the same eight sites to ensure the community was as similar as possible to that observed. The traps were set over a 24 hour period, after which the collected invertebrates were preserved for later identification in New Zealand using general family keys (CSIRO 1996). Invertebrates were not identified beyond the family level, as it was not possible to accurately identify all insect orders caught to either the genus or species level from the insect keys available. A reference collection was made from this that included every family caught and was then used to identify invertebrates that were recorded interacting together (competition network). This experiment was replicated in both the wet and dry seasons and a total of 32 samples were collected.

Body mass as a predictor of the outcome of an interaction

Body mass was measured for all the different families caught in the trapping experiment used to build the co-occurrence network. It was calculated by weighing a sub sample of 20 individuals from each family caught. Insects were randomly picked from several samples for each family. As some of the rarer families were represented by singletons or fewer than 20 individuals, all of the individuals caught in traps were weighed for these families. For each family all the insects to be weighed were placed in a container, dried for 24 hours in a drying oven and then weighed at least twice, two hours apart, to ensure an accurate dry weight was calculated. All insects were weighed using a scale accurate to 4 d.p. of a gram and then weights were converted to

milligrams. An average weight was then calculated for each family and used in analyses for body size.

Statistical analysis

Interaction networks based on co-occurrences and observed rates of competition within the community

To compare the competition and co-occurrence networks, binary matrices were constructed where species were entered as rows and columns for the co-occurrence network and winners entered as rows with losers entered as columns for the competition network. Matrices for the competition and co-occurrence interaction networks were built separately for each trap within a site for the co-occurrence network (matrices constructed from all co-occurring species), and for each video within a site for the competition network (matrices constructed using all interacting species). This resulted in 32 unipartite matrices for each interaction network type. All networks were unipartite as there were only eight predation events, which were too few to group the networks by trophic level, so any predation events were not included in the analysis. Consequently, all interactions were between invertebrates that utilised the dung resource to feed on and/or for breeding. To explore how the competition and co-occurrence networks were structured, the network metrics: nestedness, connectance, and the number of compartments were calculated (Almeida-Neto et al. 2008, Tylianakis et al. 2010, Gomez et al. 2011). Nestedness was calculated in the ‘vegan’ package (Oksanen et al. 2012) for R (R Development Core Team 2012), using the nested NODF metric outlined by Almeida-Neto et al. (2008). The NODF measures overlap and decreasing fill of a matrix and calculates the totals independently for rows and columns and combined for the whole matrix, the metric is outlined in Almeida-Neto et al. (2008). Connectance measures the proportion of possible links weighted by the number of species, and compartmentalisation is measured by counting the number of compartments that are subsets within a network (Tylianakis et al. 2010). These metrics were used as they calculated different aspects of community structure and have been shown to have some influence on community stability (Thebault and Fontaine 2010, Tylianakis et al. 2010, Gomez et al. 2011). These metrics were calculated using the functions in the ‘bipartite’ package (Dormann et al. 2009).

To test if the network metrics above showed different patterns depending on how the interaction networks were sampled, I ran generalized linear models (GLMM) with the values for each metric as the response, network type (competitive or co-occurrence), protection (fenced or not) and season as predictors, with each matrix as a replicate (there were 64 replicates for each network metric, 32 for each network type). GLMM's were run using the 'nlme' package (Pinheiro et al. 2012) for R, with 'site' and traps nested within sampling points within sites as random effects (to control for the non-independence of samples from different dates). Models were run with all combinations of measured predictors and all possible interactions, and competing models were compared using AICc (Akaike Information Criterion corrected for small sample size) and Akaike weight (W_m) to rank and subsequently select the best-fit model to the data (Burnham and Anderson 2001). Models within two AICc units of the top-ranked model were considered to be equivalent in their fit and of these the simplest model was used. Separate paired t tests were run to test if the network metrics changed with the effect of season in both the protected and in the unprotected areas of the forest.

Body mass as a predictor of the outcome of an interaction

Additionally, to test if the outcome of an interaction could be predicted by the competitors' body mass, the mean body mass for invertebrates that won an interaction was compared with the loser's mean body mass for the same interaction using a paired t test. Body mass was transformed using log base 10 to allow for orders of magnitude difference as insects ranged in mass from 0.07 mg to 226.96 mg.

Results

Interaction networks based on co-occurrences and observed rates of competition within the community

A total of 64 families in 11 orders were recorded from pitfall traps that were set for 24 hours, and of these only 20 families were observed directly competing over the dung resource (Table 4.1, Figures 4.2 - 4.9). All families observed in videos were also present in pitfall traps. The majority of families that were not involved in competitive interactions over access to the dung resource occurred at low abundances (Table 4.1). From a total of 27 hours of video footage, only eight trophic interactions occurred, compared with a total of 1,292 non-trophic observed interactions (or 0.006% of

interactions were trophic). The trophic interactions that occurred were two instances of parasitism of diptera larvae found in the dung, one predation event by a carabid beetle on a calliphorid fly and five predation events by Formicidae (classified as ‘large’ in Figures 4.2 - 4.9) on various Diptera families.

Table 4.1 List of families with their total occurrence recorded in both networks, for the competition networks the total number that occurred were grouped by the number of times an insect either won or lost. Families are split by order and, where applicable, by superfamily (in italics) with orders listed according to total numbers of co-occurrences.

Order	Family	Co-occurrence	Competition		
			Won	Lost	
Coleoptera	Anobidae	4			
	Brentidae	1			
	Chrysomelidae	3			
	Hydrophilidae	172			
	Latridiidae	4			
	Nitidulidae	2			
	Ptiliidae	7			
	<i>Carabidae</i>	Broscini	6		
		Carabidae	1		
	<i>Scarabaeidae</i>	Aphodiinae	27		
Scarabaeinae		1204	88		
<i>Staphylinoidea</i>	Pselaphidae	17			
	Scaphidinae	1			
	Scydmaenidae	1			
	Staphylinidae	1107	73	3	
<i>Tenebrionoidea</i>	Anthicidae	2			
	Mycetophagidae	9			
	Tenebrionidae	1			
	Zopheridae	1			
Diptera	Anthomyiidae	9	110	125	
	Calliphoridae	144	241	868	
	Cecidomyiidae	25			
	Curtonotidae	2			
	Dolichopodidae*			1	
	Helomyzidae	1754		20	
	Helosciomyzidae	1			
	Muscidae	97	13	91	
	Phoridae	162	2	11	
	Pipunculidae	1			
	Sarcophagidae	11	4	11	
	Sepsidae	87	26	74	

	Sphaeroceridae	70	9	17
	Syrphidae	38		
	Therevidae	2		1
	Tipulidae	2		
Hymenoptera	Apidae	13	5	
	Austroniidae	3		
	Braconidae	4	27	
	Eucoilidae	5		
	Eurytomidae	2		
	Formicidae	1555	301	5
	Ichneumonidae	3	26	
	Rhopalosomatidae	2		
	Scelionidae	1		
Hemiptera	Cicadellidae	19		
	Cydnidae	33		
	Hebridae	1		
	Idiostolidae	1		
	Piesmatidae	1		
	Reduviidae	3		
	Rhopalidae	2		
Lepidoptera	Brachodidae	1		
	Cossidae	1		
	Galacticidae	3		
	Palaephatidae	5		
	Satyridae	6	290	9
	Sphingidae	10		
Orthoptera	Gryllidae	115	1	1
	Tetrigidae	2	3	1
Blattodea	Blattidae	18	2	
Dermaptera	Anisolabididae	2		
Plecoptera	Perlidae	3		
Embioptera**	Embioptera	3		
Neuroptera	Chrysopidae	1		

*The Dolichopodidae family was present in samples on subsequent days of trapping which were not included for analysis in this chapter.

**The Embioptera order could not be identified further because I did not have access to the necessary insect keys.

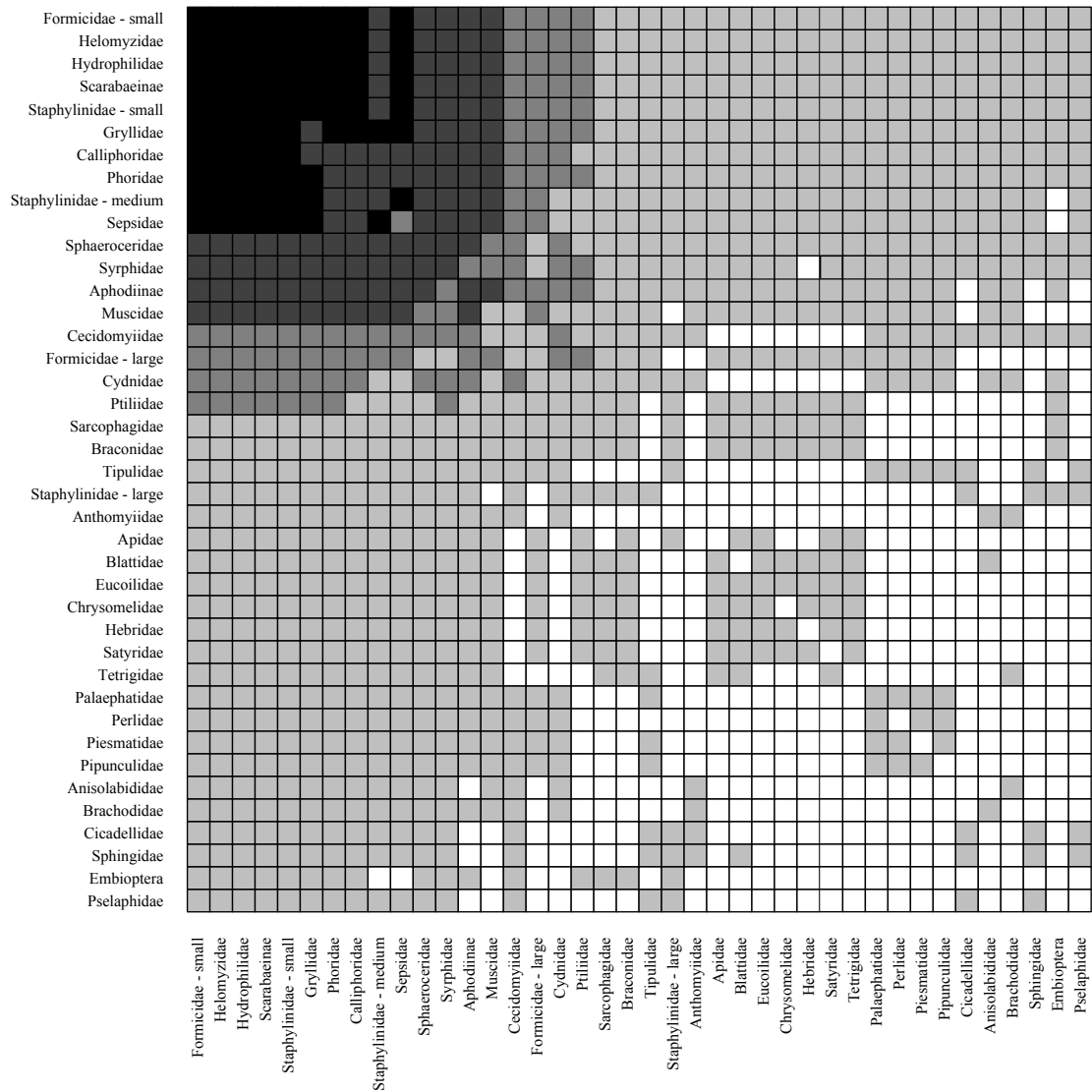


Figure 4.2 Co-occurrence interaction matrix depicting the community present in the protected forest sites during the wet season. Squares show interactions between families, the colour depicts how many times they co-occurred (from 0 to 8 where white = 0, light grey = 1-2, mid grey = 3-4, dark grey = 5-6, black = 7-8). The families Staphylinidae and Formicidae are split up into different sizes depending on their body length and for Formicidae whether they are winged.

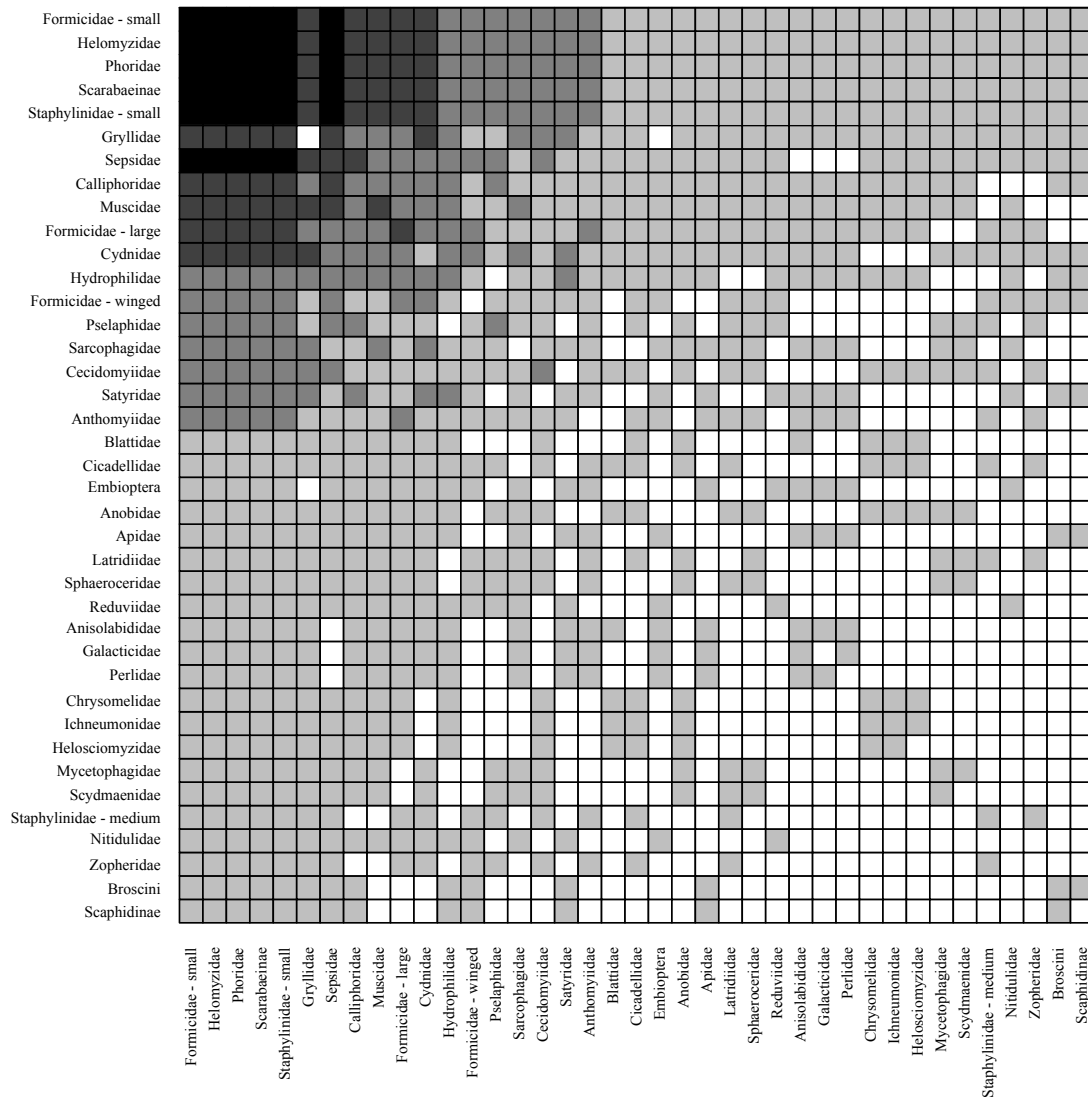


Figure 4.3 Co-occurrence interaction matrix depicting the community present in the protected forest sites during the dry season. Squares show interactions between families, the colour depicts how many times they co-occurred (from 0 to 8 where white = 0, light grey = 1-2, mid grey = 3-4, dark grey = 5-6, black = 7-8). The families Staphylinidae and Formicidae are split up into different sizes depending on their body length and for Formicidae whether they are winged.

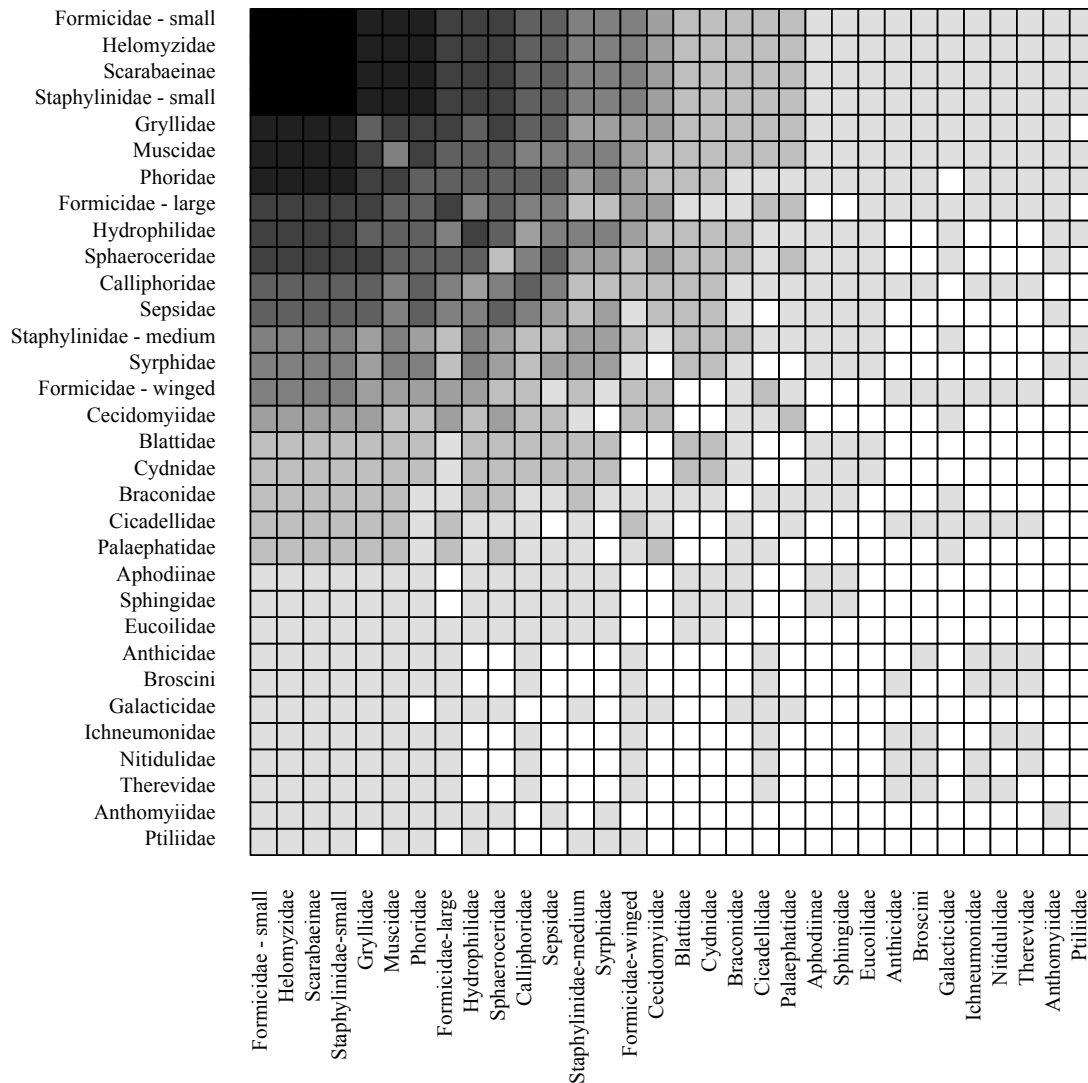


Figure 4.4 Co-occurrence interaction matrix depicting the community present in the unprotected forest sites during the wet season. Squares show interactions between families, colours as in Figure 4.2. The families Staphylinidae and Formicidae are split up into different sizes depending on their body length and for Formicidae whether they are winged.

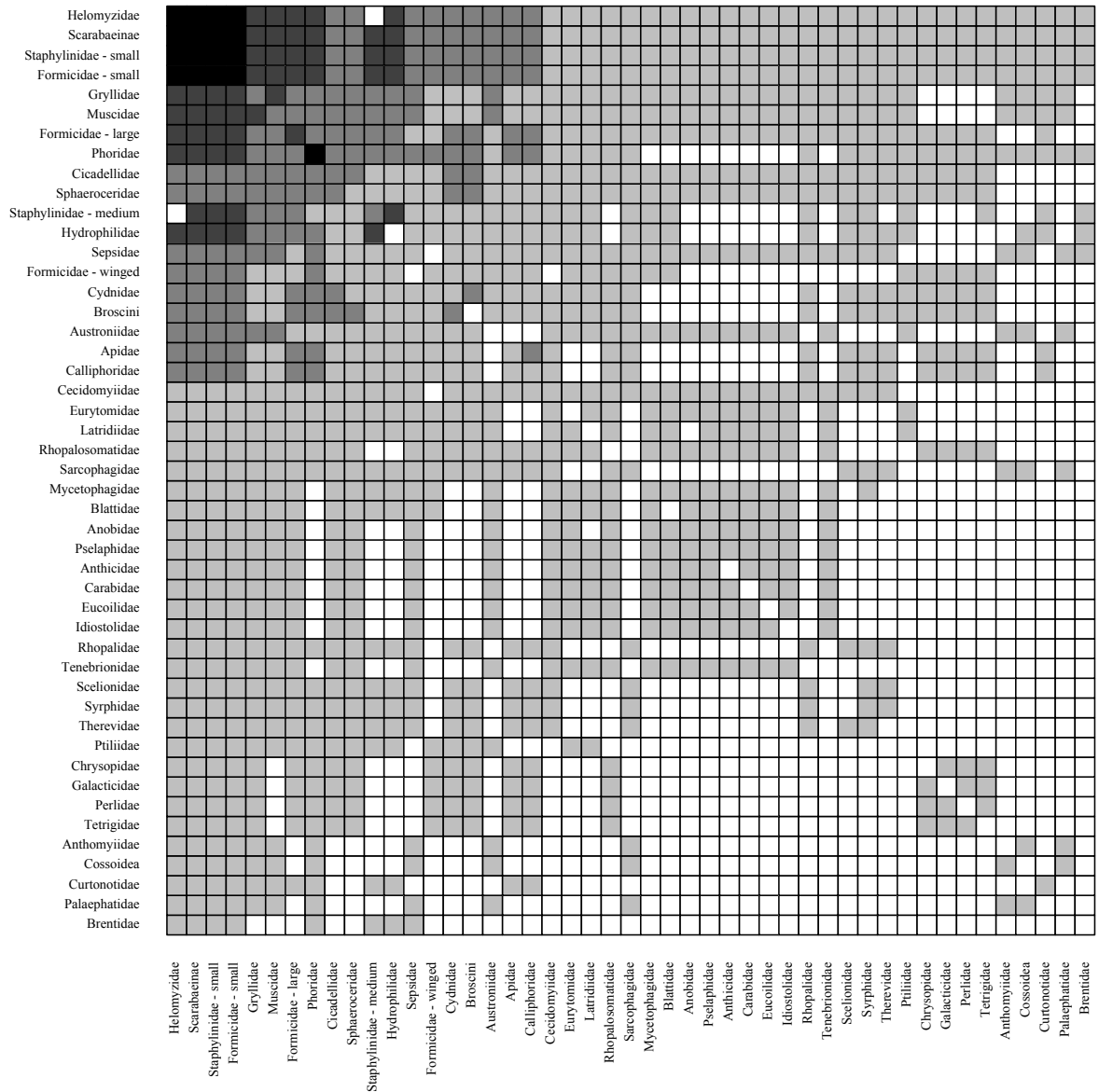


Figure 4.5 Co-occurrence interaction matrix depicting the community present in the unprotected forest sites during the dry season. Squares show interactions between families, colours as in Figure 4.2. The families Staphylinidae and Formicidae are split up into different sizes depending on their body length and for Formicidae whether they are winged.

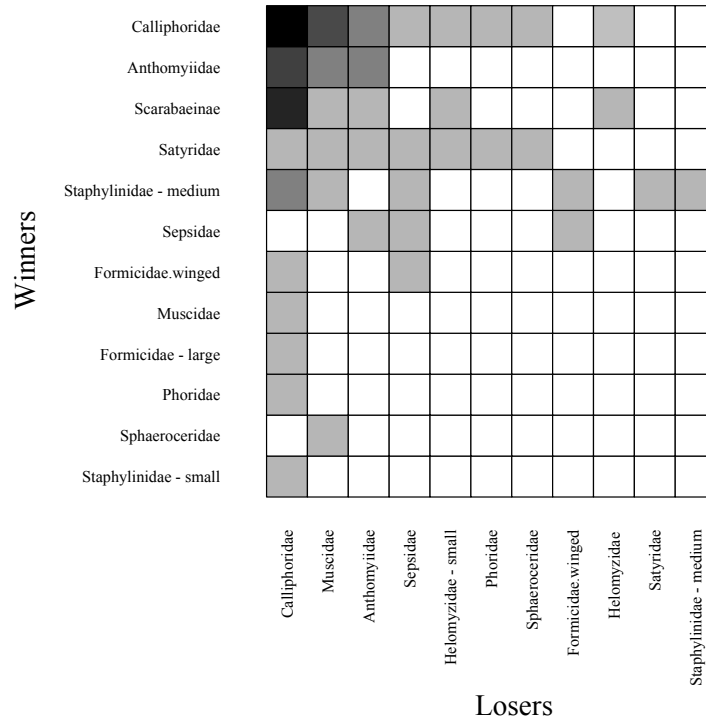


Figure 4.6 Competition interaction matrix depicting competitive interactions in the protected forest sites during the wet season. Squares show interactions between families, colours as in Figure 4.2. The families Staphylinidae and Formicidae are split up into different sizes depending on their body length and for Formicidae whether they are winged.

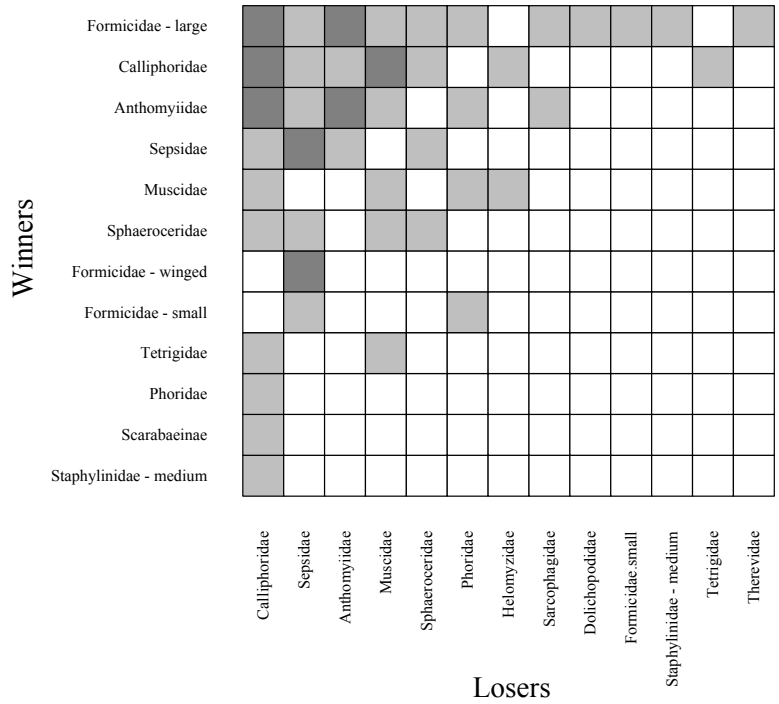


Figure 4.7 Competition interaction matrix depicting competitive interactions in the protected forest sites during the dry season. Squares show interactions between families, colours as in Figure 4.2. The families Staphylinidae and Formicidae are split up into different sizes depending on their body length and for Formicidae whether they are winged.

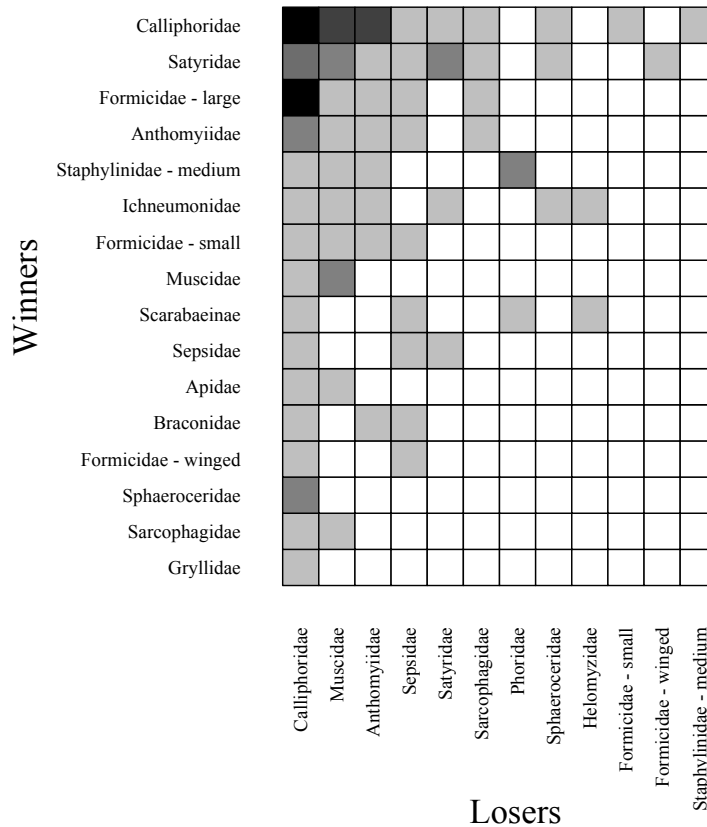


Figure 4.8 Competition interaction matrix depicting competitive interactions in the unprotected forest sites during the wet season. Squares show interactions between families, colours as in Figure 4.2. The families Staphylinidae and Formicidae are split up into different sizes depending on their body length and for Formicidae whether they are winged.

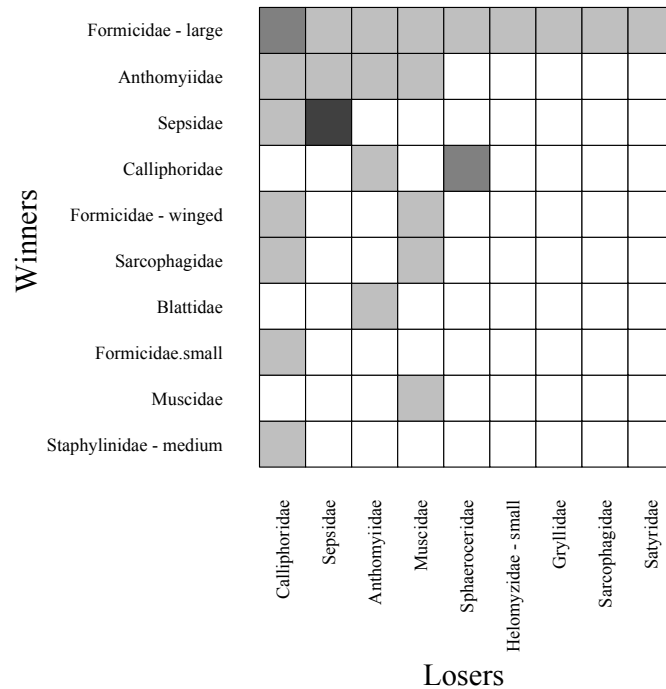


Figure 4.9 Competition interaction matrix depicting competitive interactions in the unprotected forest sites during the dry season. Squares show interactions between families, colours as in Figure 4.2. The families Staphylinidae and Formicidae are split up into different sizes depending on their body length and for Formicidae whether they are winged.

Connectance was significantly higher ($F_{1,47} = 125.74$, $p < 0.001$) in the co-occurrence network than in the competition network, though compartmentalisation was significantly higher ($F_{1,47} = 7.52$, $p = 0.009$) in the competition network, where there were often 2 or 3 compartments present (Table 4.2). However, nestedness of the networks was not significantly different ($F_{1,42} = 0.28$, $p = 0.598$) when the methods used to construct an interaction network were compared (Table 4.2, Figure 4.10).

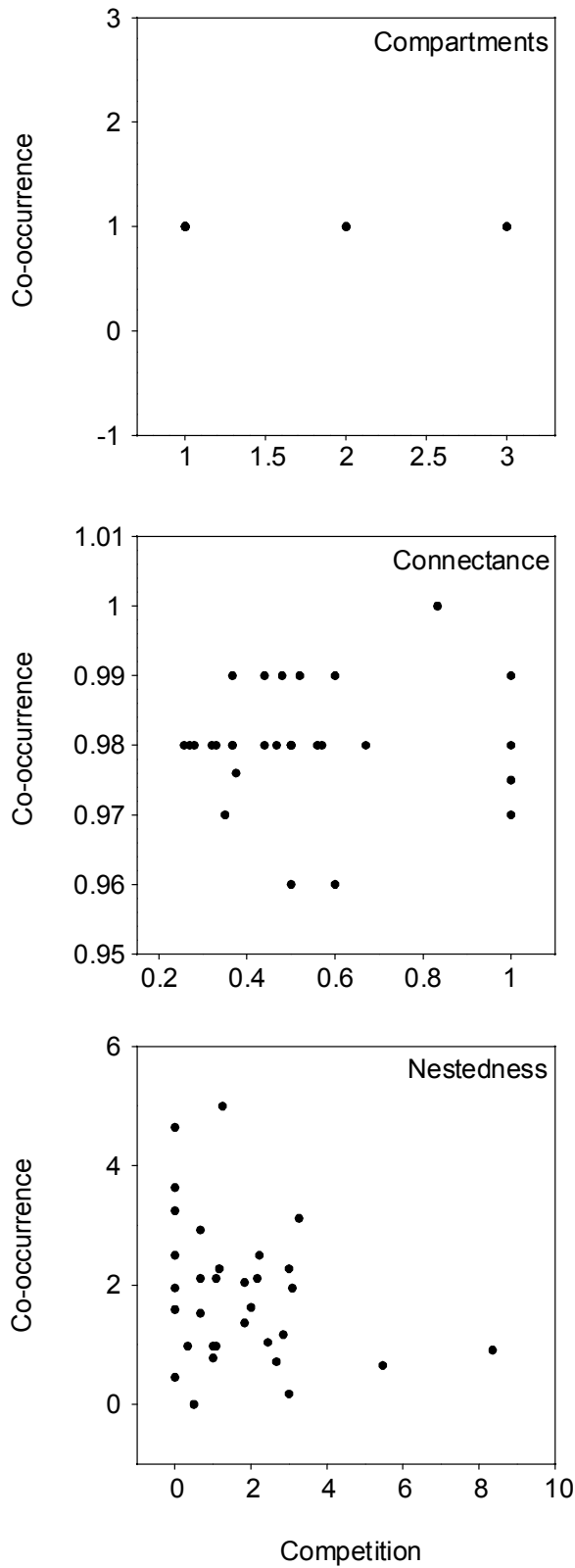


Figure 4.10 Relationship between the competition network and co-occurrence network for all network metrics.

Table 4.2 Mean values for each network metric for both the co-occurrence and competition interaction networks.

Network metrics	Co-occurrence	Competition
Compartmentalisation	1.000	1.313
Connectance	0.978	0.474
Nestedness	1.853	1.675

The effects of forest protection and changing season altered the distribution of nestedness calculated for the competition networks, but not for the networks constructed from co-occurrences. Nestedness of the competition networks was significantly influenced by season ($F_{1,42} = 4.16$, $p = 0.0478$), by an interaction between network type and season ($F_{1,14} = 9.65$, $p = 0.003$), and by a three way interaction between network type, season, and forest protection ($F_{1,42} = 8.53$, $p = 0.006$) (Figures 4.2 – 4.9, 4.11). Nestedness of the competition network was higher in the wet season, but when forest protection was taken into account the difference in nestedness between seasons became small under forest protection (Figure 4.11). Additionally, when this interaction was tested, there was no significant difference ($t = 0.49$, $df = 7$, $p = 0.640$) in a community's nestedness in protected areas of the forest across the effect of changing seasons. Though, when tested in the unprotected areas of the forest was significantly different across seasons (treatment x season interaction $t = 4.03$, $df = 7$, $p = 0.005$) (Figure 4.11).

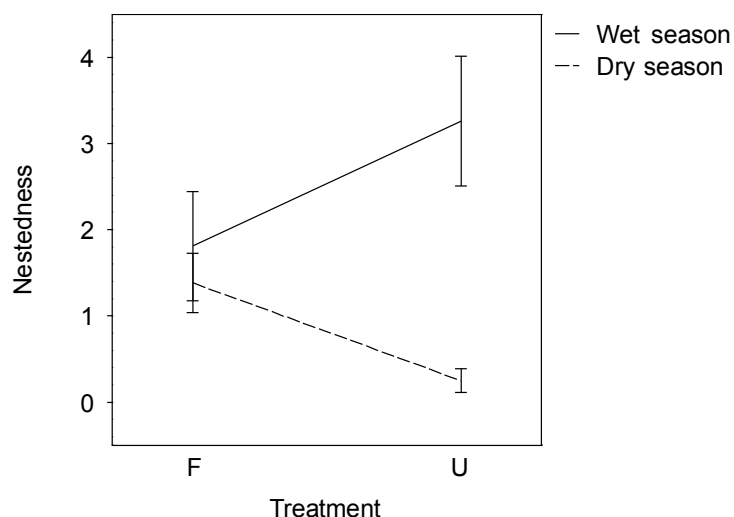


Figure 4.11 Mean (± 1 SE) of nestedness scores for the effects of treatment and season in the competition interaction network. F: fenced sites. U: unfenced sites.

Body mass as a predictor of the outcome of an interaction

Larger individuals were significantly more likely to win contests ($t = -9.165$, $df = 1288$, $p = 0.012$), with the average mass of winners being c. 20 mg, compared with 5 mg for losers. However, when the ratio of body size between the winner of a contest and the loser of a contest was calculated, the winner was not always larger, as in 45% of the interactions the loser's size was greater than the winner's size. Additionally, 62% of the time when the body size of the winner was smaller than the body size of the loser, the winner of the interaction was an ant. Furthermore, the disparity in the body mass when the winner was larger was much higher (mean = 36.4 times the loser's size) compared to the disparity in the body mass ratio when the loser of a competitive interaction was larger than the winner (mean = 3.5 times the winners size).

Discussion

In my observations of the dung-associated community, there were many more non-trophic interactions than trophic interactions. Additionally, the way in which a network was constructed (i.e. competition vs. co-occurrence) influenced the distribution of the network metrics across traps and forest protection treatments. When the co-occurrence network was compared with the competition network, the former had higher connectance, but a lower number of compartments. Furthermore, patterns of nestedness of the competition network fluctuated less in the protected areas of the forest, irrespective of whether the community was sampled in the wet season or the dry season. Interestingly, the outcome of a non-trophic interaction was influenced by the body size of competitors, as an invertebrate was more likely to win a competition if it was larger than the other competitor.

Both types of interaction networks displayed a nested structure, which was only influenced by the effect of changing season and forest protection in the competitive networks. In the competition networks, there were generally two or three families that interacted with all the other species observed to compete. These families would therefore be classified as highly 'generalist', and they formed the core of the observed nested structure. This was illustrated by the occurrence of large ants that became more 'generalist' in areas of the forest that were unprotected, especially during the dry season. Ants are a generalist species in many ecosystems (Begon et al. 1996, Moya-Laraño and Wise 2007) and may therefore alter network structure in these areas as well.

Additionally, the competitiveness of ants with other species was higher in unprotected areas of the forest. This finding may mean that, in these areas that are more disturbed by anthropogenic impacts, super generalist species have more of an impact because the community in these areas is more simplified, thereby making them less stable (McCann 2000).

The interaction networks were more structurally stable through time in the protected areas of the forest. Nestedness was the same in protected areas of the forest regardless of the sampling season, whereas in the unprotected areas of the forest nestedness fluctuated with higher values in the wet season and dramatically reduced values in the dry season. This could be because the community fluctuated more in the unprotected areas of the forest, whereas it was more stable in the protected areas of the forest. This has been found in mutualistic networks as nestedness of the community also increased following species loss (Thebault and Fontaine 2010, Aizen et al. 2012), which may be non-random with respect to the position of species in the network. Competitive networks may follow the same trend as mutualistic networks, because non-random species loss did occur in this ecosystem in areas of the forest that were not protected from anthropogenic impacts (see Chapter 2). These patterns were only found in networks that were built by observing competitive interactions, whereas in the co-occurrence networks there was no influence of forest protection or changing season on the distribution of the network metrics. Consequently, the competition networks were better able to detect a community response to the environmental factors of forest protection and seasonal variation.

The majority of species that were observed to co-occur but not compete occurred in low numbers and may have been adventive species that fell into traps as they were moving around the forest floor. This is illustrated by the observation that the insect orders Dermaptera, Embioptera, Hemiptera, Neuroptera, and Plecoptera were recorded in pitfall traps (the co-occurrence network) but were never observed competing over the dung resource. Therefore, when incorporating non-trophic interactions into an interaction network with several interaction types, measures of species co-occurrences may be more influenced by sampling technique than the observation of competitive interactions. For example, without first observing the actual competitive interactions, it would not have been possible to determine *a priori* whether pitfall traps would accurately sample the interacting community. This will limit the

extent to which data collected for other purposes can be used to estimate non-trophic interaction structure.

The competitive interactions observed were in the form of interference competition as interactions were either physical competitions between species or interference where one individual reduced access to the resource of another individual. Exploitation competition is inherent in the dung-associated community as all invertebrates attracted to the resource utilise it for feeding and/or breeding (Hanski and Cambefort 1991). The two major invertebrate guilds that reduce the availability of the resource for other invertebrates are dung beetles and dung flies and their larvae as they all feed on the dung itself (Hanski and Cambefort 1991). However, the only accurate method for quantifying exploitation by these invertebrate guilds would be to measure how much of the resource was consumed or removed by each individual. In Chapter three, the decrease in per capita removal rates by dung beetles at higher densities inferred that competition was occurring between individual dung beetles over access to the resource. However, this was not able to be quantified in the same experiment as observations of what species competed. If these interactions had been included in the network the number of links would have increased and the number of families present as well. Therefore, if these interactions had been included in the network, they may have increased the connectance as network connectance has been shown to scale with diversity (Dunne et al. 2002a). However as this would have only included two or three more families per individual network the number of species present would still have been much less than the number present in the co-occurrence networks. Therefore, it is unlikely that the structure of the competition network would have converged on the structure of the co-occurrence network.

The outcome of a competitive interaction between two individuals was positively influenced by body mass, as on average the larger of the two competitors won a contest. Therefore, the outcome of an interaction may be possible to predict by the body size of both individuals involved. However, in nearly half of all interactions recorded the loser was the larger individual. Nevertheless, the disparity in the body size when the loser was larger was less than the disparity in body mass when the winner of a contest was larger. When the winner of a contest was on average greater than four times larger than the loser it was more likely to win a competition. This outcome could be due to behavioural factors, as ants instigated more than half of contests in which the winner was smaller than the loser. Ants are naturally aggressive and they regularly attack

organisms larger than themselves and can even negatively affect other predators in the same ecosystem (Moya-Laraño and Wise 2007).

At higher size ratios between two competitors, direct interference was less likely to occur and indirect interference competition was more likely to take place (Grether et al. 2009). This finding of body-size ratio predicting the outcome of an interaction was similar to that observed between predators and their prey, as generally predators are larger than their prey species (Cohen et al. 1993, Brose et al. 2006a). This result that larger individuals are more likely to win an interaction also applies to competition between predators over a resource. As, in a study by Eichenberger et al. (2009) comparing competitive ability among different size predators, they showed that spider species that were large could outcompete smaller spider species when taking over their web. Therefore, the finding that larger species are more likely to win an interaction when competing with a smaller species could also be used to predict competitive interaction outcomes within a network.

In conclusion, observing which species compete within an interaction network gives a more detailed depiction of the response of community structure to perturbations than does a network incorporating only the co-occurrences of organisms. Also, measuring the body size of competing organisms allows predictions to be made about the outcome of these interactions, whether they are trophic or non-trophic. Therefore, constructing networks from observed interactions is a more accurate method for incorporating competitive interactions into networks.

Chapter 5: Discussion

Overview

Ecosystems are influenced by many factors, and of these factors anthropogenic disturbances are the largest driver of biodiversity loss (Sala et al. 2000). Among the anthropogenic threats that can negatively impact natural ecosystems are livestock grazing and farming, as land is often cleared to provide space for these activities (Cowling et al. 2003, Chapman et al. 2004). The exclusion of these anthropogenic threats from forest reserves can help to mitigate their negative impacts and aid in restoring communities within these forests (Cowling et al. 2003). However, the ability to detect any effect of such conservation efforts can depend on other factors such as strong variation across seasons that can mask or drive responses in community structural changes (Bullock et al. 1995, Vernes et al. 2005). Thus, sampling communities across time provides an understanding of how their structure varies under different environmental conditions and may aid in detecting the effects of anthropogenic threat mitigation on these communities. Ultimately, by developing a better understanding of how these processes determine community structure and the resulting function of these communities, this can provide a wider understanding of ecosystem-level responses to anthropogenic disturbances and the relative benefits of different management approaches.

In this study, the dung-associated community was affected by excluding livestock from the matrix adjacent to forest habitat as higher abundances of insects were trapped in these areas. Also, these impacts changed with the effect of variation across seasons, as an influence of forest protection was only apparent in the wet season. These strong community responses resulted in greater levels of dung removal and secondary seed dispersal, indicating that ecosystem functioning can be enhanced through the protection of forest reserves from external anthropogenic threats, which could ultimately result in altered plant communities in these areas (Wu et al. 2011).

Responses to protection of forest reserves can also be apparent at the species level. These trait-mediated species responses can result in the non-random loss (or gain) of species in response to environmental changes, and thus allow prediction of the functional consequences of global change (Lavorel and Garnier 2002, Slade et al. 2007). Body size was shown to be an important response trait, as it determined which

species could persist, and that larger beetles were less likely to persist in unfenced areas of the forest, which agrees with findings by Larsen et al. (2005). Therefore, large beetles were more affected by habitat degradation, and raises the question of which traits dictate the importance of a species for performing ecosystem functions. Body size of dung beetles was also an important effect trait, as it influenced the amount of dung removed and seeds secondarily dispersed. Therefore, this study gives an example of how anthropogenic threats can alter a community in a non-random manner and the resulting effects can be especially severe for the functioning of these ecosystems through a response-effect trait correlation (Lavorel and Garnier 2002, Larsen et al. 2005).

The ability to detect non-random loss of species may be confounded by species responses to environmental factors over short and long timescales (Ewers and Didham 2006). For example, species assemblages can change dramatically over short timescales, especially when a community is based around an ephemeral resource (2001). This finding (Chapter 3) was correlated with short-timescale changes in the dung resource as attractiveness altered over the course of days as the resource desiccated. This resulted in much lower abundances of dung-associated invertebrates as time since dung deposition increased, with predator and parasitoid species colonising later after initial colonisation of invertebrates that utilised the dung resource for feeding and/or breeding, which parallels findings in carrion communities (Ives 1991). These short-term changes (over just three days) in community assemblages were observed across seasons as rainfall stopped and humidity levels decreased, resulting in overall lower invertebrate abundance in the dry season. Therefore, the dung-associated community was strongly affected by small and large timescale changes that altered the resource and thereby altered the associated community.

The abundance of species at the dung resource altered individual-level interactions, as density-dependent levels of competition between dung beetles were observed to alter the rate at which they removed the dung resource. Findings from experiments run in Chapter 3 showed that body size determined the amount of dung removed, with large beetles removing more dung than smaller dung beetles, which agrees with findings by Larsen et al. (2005). Additionally, as numbers of dung beetles present increased the overall amount of dung removal increased. However, as density increased, the amount of dung removed per capita decreased, thereby suggesting that competition between individuals reduced the amount of dung they were able to remove.

This resulted in decreased per capita functional efficiency of dung removal as competitive levels among individuals increased. Therefore, the overall amount of dung removal performed by these communities was not additive as competition between individuals altered their per capita functional efficiency.

The outcome of interactions between species can be determined by body size (Brose et al. 2006a). This has been shown for predator-prey interactions and for competitive interactions (Brose et al. 2006a, Eichenberger et al. 2009, Grether et al. 2009). Experiments run in Chapter 4 clearly showed that competitive interactions in the dung-associated community were strongly structured by body size. Larger invertebrates were more likely to win an interaction when competing with a smaller invertebrate. Therefore, taking into account the body-size ratio of competing species can allow prediction of the structure and outcome of an interaction.

Species interactions within a community can also be altered by anthropogenic threats (Tylianakis et al. 2007) and variation across seasons. The exclusion of anthropogenic threats from matrix habitat adjacent to forest remnants and the effect of changing seasons were shown to alter the patterns of nestedness in the individual networks. In protected areas, the network showed a nested structure that did not fluctuate across changes in seasons. However, in the unprotected areas of the forest, the network nestedness was high initially during the wet season but then decreased dramatically in these areas in the dry season. Therefore, protection of forest reserves had a stabilising effect on the nested structure of these communities, whereby forest protection buffered strong fluctuations in the invertebrate community among seasons. In this study the highly nested structure of the network was most similar to mutualistic networks that also show high nestedness in their structure (Bascompte et al. 2003, Fontaine et al. 2011), and this nestedness has been found to be stabilising (Bascompte et al. 2003, Allesina and Tang 2012). Additionally, connectance has been high in the competition networks, with high density of links between species, which has also been shown to be stabilising (Dunne et al. 2002b). Therefore, the structure of the competitive interaction networks was most similar to mutualistic networks, and was stable when nestedness was higher. Furthermore, variation across seasons had no influence on the nested structure of the dung-associated community in areas that were protected from anthropogenic threats.

Many studies use co-occurrences of species to build an interaction network (Perner and Voigt 2007, Faisal et al. 2010, Gomez et al. 2011) and this technique can

also be used to build competitive interaction networks. However, experiments run in Chapter 4 showed that building networks from co-occurrences were unable to detect the impacts of anthropogenic threats because not all the species that co-occur at a resource interact directly. These results suggest that studies measuring community structure only by co-occurrence of species may not be able to detect community level changes caused by anthropogenic impacts. Overall, this study demonstrates the importance of forest protection for conserving the dung-associated community.

Scaling up from species level to community level structuring processes

Species level changes were found to scale up to alter community level changes, in that abiotic factors that altered the attractiveness of the dung resource changed what species were present over time. The abiotic impacts of temperature and rainfall on attractiveness of the dung resource acted over the course of several days and across changes in seasons, with consequences for the dung-associated community as they affected which species were present on any given day. The changes over short timescales (a few days) were due to drying of the dung resource, the rate of which was driven by the amount of rainfall and humidity levels across seasons. Rainfall and humidity levels were much lower during the dry season (Chapman and Chapman 2001, Matthesius et al. 2011), and these combined effects caused rapid desiccation of the dung resource during the dry season. Water content of the dung has a strong effect on the associated community. Adult dung beetles cannot feed on the resource when it is dried and hardened, and this also makes it a less suitable environment for breeding of other invertebrates (Hanski and Cambefort 1991). Consequently, during the dry season the overall abundances of invertebrates attracted to the dung resource decreased more rapidly (over the course of days). This led to associated changes in the families present with different predators and parasitoids colonising the resource as dung attractiveness changed over short timescales. Changes in invertebrate abundance over seasons also meant that interactions among invertebrate families were stronger in the wet season when invertebrates were more abundant. The effect of forest protection mediated these impacts and resulted in higher overall abundance of invertebrates in these areas regardless of season, which altered the community structure.

Forest protection also influenced the species present, as dung beetles responded based on body size with larger dung beetles being recorded less often in areas without forest protection. Body size not only determined dung beetle species responses, but was

also a strong determinant of the functional importance of species, as larger beetles were found to remove more seeds and dung than smaller beetles (Chapter 2 and 3). Thus, anthropogenic disturbances resulted in species level trait-mediated responses (Webb et al. 2010, Violle et al. 2012). Therefore, traits that dictate how a species responds to a disturbance could be used to predict how anthropogenic activities can alter a community as certain species become locally extinct.

Competition was shown to alter the amount of dung removal, as increasing densities of dung beetles led to a corresponding decrease in their per capita dung removal rates. To my knowledge, this per capita decrease in function caused by increasing competition between individuals has not been measured previously in the dung-associated community. The body-size ratio dictating what competitor won an interaction could be used to predict the outcome of an interaction between two competitors. The scaling rules outlined by Brose et al. (2006a) for food webs were similar to those observed in this unipartite network, where larger organisms were more likely to win contests, analogous to the larger organism in predator-prey feeding interactions being more likely to be the predator. Competitive interactions could then be amassed to form an interaction network, describing the entire community.

Lower fluctuations in the nestedness of the competition network were observed in the protected areas of the forest. Nestedness was significant and high in this network, indicating that the species that interacted with specialists were a subset of the species that interacted with generalists (Atmar and Patterson 1993). High nestedness often occurs in mutualistic networks (Thebault and Fontaine 2010), and can be both a stabilising or destabilising force depending on whether it is the generalist or specialist species that are most affected by a disturbance such as anthropogenic threats that impact ecosystems (Bascompte et al. 2003, Tylianakis et al. 2010). This illustrates how individual level competitive interactions may determine the community level response. I found that the species trait (body size) that determined the interaction network structure also determined dung removal and secondary seed dispersal at the community level, which provides a link between community structure and ecosystem level responses.

General conclusions

Ultimately, these individual level processes scaled up to alter community level structure that resulted in a reduction in the amount of dung removal and secondary seed

dispersal performed by the dung-associated community during the dry season. Additionally, mitigating anthropogenic threats to ecosystems through protection of reserves had an effect on the structure of associated communities, but was only apparent when quantified with the effect of changing seasons. To progress the field of interaction network ecology, further research should incorporate several types of interactions such as competitive, mutualistic and trophic in order to develop a comprehensive understanding of how communities respond to environmental changes, and importantly how these responses determine the functioning of ecosystems.

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Appendix

Table 1 List of families caught in the experiment for sampling the entire dung-associated community. Orders are listed according to total abundance with families grouped by order and, where applicable, by superfamily (in italics).

Order and superfamily	Family
Coleoptera	Anobidae
	Chrysomelidae
	Hydrophilidae
	Latridiidae
	Nitidulidae
	Ptiliidae
<i>Curculionidae</i>	Brentidae
	Curculionidae
<i>Carabidae</i>	Broscini
	Carabidae
<i>Scarabaeidae</i>	Aphodiinae
	Melanthropine
	Scarabaeinae
<i>Staphylinoidea</i>	Pselaphidae
	Scaphidinae
	Scydmaenidae
	Staphylinidae
<i>Tenebrionoidea</i>	Anthicidae
	Mycetophagidae
	Tenebrionidae
	Zopheridae
Diptera	Anthomyiidae
	Calliphoridae
	Cecidomyiidae
	Curtonotidae
	Dolichopodidae
	Helomyzidae
	Helosciomyzidae
	Muscidae
	Phoridae
	Pipunculidae
	Sarcophagidae
	Sepsidae
	Sphaeroceridae
	Syrphidae
	Therevidae
	Tipulidae
Hymenoptera	Apidae

	Austroniidae
	Braconidae
	Ceraphronidae
	Diapriinae
	Eucoilidae
	Eurytomidae
	Formicidae
	Ichneumonidae
	Nyssonidae
	Pompilidae
	Pteromalidae
	Rhopalosomatidae
	Scelionidae
Hemiptera	Cicadellidae
	Cydnidae
	Hebridae
	Idiostolidae
	Piesmatidae
	Psyllidae
	Reduviidae
	Rhopalidae
Lepidoptera	Brachodidae
	Galacticidae
	Cossidae
	Palaephatidae
	Satyridae
	Sphingidae
Orthoptera	Gryllidae
	Pyrgomorphidae
	Tetrigidae
Blattodea	Blattidae
	Rhinotermitidae
Dermaptera	Anisolabididae
Plecoptera	Perlidae
Embioptera	Embioptera
Neuroptera	Chrysopidae

*The Embioptera order could not be identified further because I did not have access to the necessary insect keys.