Dung beetle communities in Madagascar

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Academic dissertation

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o'clock noon.

Vain olennainen on tärkeää.
— Tuntematon

CONTENTS

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I   Montreuil, O. and Viljanen, H. 2007. Contribution à l'étude des Canthonini de Madagascar (7ᵉ note) : Mises au point taxonomiques et nomenclaturales dans le genre *Nanos* Westwood,1947 (Coleoptera, Scarabaeidae). — *Revue Française d'Entomologie*, 29, 1–10.

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CONTRIBUTIONS

Contribution table:

	I	II	III	IV	V
Original idea	HV, OM	HV	IH	IH, HV	HV
Study design		HV	IH, HV	PR, IH	HV
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ABSTRACT

The traditional aim of community ecology has been to understand the origin and maintenance of species richness in local communities. Why certain species occur in one place but not in another, how ecologically apparently similar species use resources, what is the role of the regional species pool in affecting species composition in local communities, and so forth. Madagascar offers great opportunities to conduct such studies, since it is a very large island that has been isolated for tens of million of years. Madagascar has remarkable faunal and floral diversity and species–level endemism reaches 100% in many groups of species. Madagascar is also exceptional for endemism at high taxonomic levels and for the skewed representation of many taxa in comparison with continental faunas. For example, native ungulates that are dominant large herbivorous mammals on the African continent are completely lacking in Madagascar. The largest native Malagasy herbivores, and the main dung producers for Malagasy dung beetles, are the endemic primates, lemurs. Cattle was introduced to Madagascar about 1,000 yrs ago and is today abundant and widespread.

I have studied Malagasy dung beetle communities and the distributional patterns of species at several spatial scales and compared the results with comparable communities in other tropical areas. There are substantial differences in dung beetle communities in Madagascar and elsewhere in the tropics in terms of the life histories of the species, species' ecological traits, local and regional species diversities, and the sizes of species' geographical ranges. These differences are attributed to Madagascar's ancient isolation, large size, heterogeneous environment, skewed representation of the mammalian fauna, and recent though currently great human impact.

Summary

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1 Introduction — Why travel 10 000 km to study dung beetles in Madagascar?

Natural history and early ecology were preoccupied with the identification and listing of species found locally, regionally, and globally. Surveys of species revealed many patterns in the occurrence of species that continue to fascinate ecologists even today. For instance, several empirical and theoretical papers have been published on latitudinal gradients of species diversity, in other words why communities in the tropics typically have many more species than comparable areas at higher latitudes (Pianka 1988, Rohde 1992, Willig *et al.* 2003). Another example is the species abundance distribution in local communities: why are communities typically dominated by a few abundant species while the rest comprise a long tale of rare species (May 1975, Whittaker 1975, McGill *et al.* 2009). For a long time, the aim of community ecology has been to understand the origin and maintenance of species richness in local communities (Clements 1916, Gleason 1926, MacArthur 1970, Wilmé *et al.* 2006, Ricklefs 2008), why species occur in one place but not in another (MacArthur 1965, 1972, Diamond and Gilpin 1982, Davis *et al.* 2002, Wilmé *et al.* 2006), how ecologically apparently similar species use resources (MacArthur *et al.* 1967, Diamond 1975, Wirta *et al.* 2008), and so forth.

The structure of local communities is influenced by various ecological factors such as competition for limited resources and habitat selection and dispersal capacity of the species. However, the structure of particular communities is also influenced by various historical events and by anything that has influenced and influences the regional species pool to which the particular local community is connected, including evolutionary processes at longer time scales (Davis and Scholtz 2001, Davis *et al.* 2002, Ricklefs 1989, Ricklefs and Schluter 1993). Thus studying only local processes may not give a satisfactory understanding of community structure (Ricklefs 2008).

Currently, community ecology employs mathematical models and experiments to study the processes influencing the organization of communities (Finn and Giller 2000, 2002, Chave *et al.* 2002, Ruokolainen *et al.* 2009). This does not however mean that the more conventional approaches, based on observational studies, would be completely out of date. Especially in the case of complex multispecies communities there continues to be a need to document what actually are the structures of real communities. Observational studies often employ statistical models and comparisons with "null hypotheses" to address particular questions about communities (Vences *et al.* 2009).

Dung Beetles (Scarabaeoidea). Dung beetles have fascinated humans for thousands of years. In ancient Egypt 3,000 B.P. ball rolling dung

beetles, the sacred scarabs (*Scarabaeus sacer* and *Kheper aegyptiorum*), symbolised parts of the Egyptian polytheistic theory of the universe (Weiss 1927, Cambefort 1994). A beetle was seen to represent a god, Ra or Kheprera, and the ball the sun moving across the sky. The human soul was supposed to emerge from the mummy just as the scarab beetle was supposed to emerge (from the pupa underground) and to fly up towards the sun and heaven; thus the insect became a symbol of regeneration and of immortality. The daily appearance and reappearance of the sun represented the return of the soul to life. Today, dung beetles have a less romantic status among the general public, although dung beetles provide several vital ecosystem services to humans. For example, dung beetles are important in tropical forest regeneration (Box 1).

In fact, "dung beetles" constitute a morphologically and ecologically diverse group of species that use several kind of decomposing material — vertebrate dung, carrion, rotting mushrooms, rotting fruits, bird droppings, dead millipedes, snail excrement, and so forth — as food resources for adults and larvae (Halffter and Matthews 1966, Hanski and Cambefort 1991a). The true dung beetles (Scarabaeoidea) consist of some 7,000 described species of primarily tropical Scarabaeidae (c. 5,000 species) and primarily temperate Aphodiidae (c. 2,000 species) and Geotrupidae (c. 150 species). Although dung beetles, by which I refer to Scarabaeidae below if not otherwise stated, may date back to the late Mesozoic and were well differentiated during the Cenozoic, dung beetle biogeography and the occurrence of dung beetles in different ecosystems mostly reflect evolution since the Miocene to Pleistocene (Cambefort 1991). Patterns in the geographical occurrence of dung beetles are related to the ecology, biogeography and evolution of major mammalian taxa (Davis *et al.* 2002), while local community structure

is primarily dependent on the regional composition of large herbivorous mammals (**V**, see also a section of *Hunting* in Box 1). Davis and Scholtz (2001) suggested two principal ecological factors influencing the present tribal, generic, and species richness patterns of dung beetles at the global scale: climate and the range of different types of dung. Droppings vary physico–chemically according to the body size and the diet of the mammal. These differences influence dropping mass and fibre and moisture contents (Davis 1989, Edwards 1991). The diversity of dung types varies between biogeographical regions according to the evolutionary history of mammals, being greatest in Afrotropical, Oriental, and Palearctic regions (4 types) and lowest in Australasia and Madagascar (2; Davis and Scholtz 2001). At present, human impact in the form of deforestation, extermination of large native mammals, introduction of domesticated mammals, and changing practices of animal husbandry play a role in structuring dung beetle communities in many parts of the world (Box 1).

At the local scale, resources for dung beetles (especially dung and carrion) are ephemeral small patches with dissimilar densities and spatial configuration in different ecosystems. For dung beetles individual droppings and carcasses are concentrations of high–quality resource, for which competition is often severe (Hanski and Cambefort 1991b). For example, Krell *et al.* (2003) and Krell–Westerwalbesloh *et al.* (2004) found in their study conducted in Africa that competitively superior dung beetles (rollers, see below) occur only in habitats and are active only in times that are energetically most suitable for them (open areas at the warmest time of the day), while the activity period of the inferior groups were restricted to less favourable times of the day and less favourable habitats. Horgan and Fuentes (2005) found in their experimental studies on Central–American tunnelling

Box 1. Dung beetles and humans — swingin' together

How dung beetles affect humans — Servants with minimum wage?

Soil. Apart from keeping the surface of the Earth clean of dung and carcasses dung beetles provide several other vital ecosystem services to humans. While feeding in, tearing up and burying a dung pile, dung beetles contribute to decomposition processes and nutrient cycling. Dung beetles dig tunnels in the ground and mix dung with the soil, and they enhance nutrient availability for plants by mixing nitrogen into the soil and at the same time aerating and oxygenating the soil (Bornemissza and Williams 1970, Mittal 1993). For example, Bornemissza and Williams (1970) observed substantial increases in plant yield when dung beetles were present compared to experiments without dung beetle activity, and they concluded that dung beetle activity is of great benefit to plant life. Actually, a dung pile is of little nutritional value to the plants in the absence of dung beetles. In addition, dung beetle activity enhances bacterial growth including those responsible of nitrogen mineralization by improving aerobic conditions in dung and by elevating C and N levels in the upper soil layers (Yokoyama and Kai 1993, Yokoyama *et al.* 1991a,b).

A good example of the importance of dung beetles comes from Australia. Before 1788 there were no cattle in Australia. The native dung beetles have not evolved the ability to process large wet cow dung pads but instead use the dry pellets of marsupials. In addition, most of the native species inhabit forests rather than open cattle pastures (Matthews 1974). Soon after the introduction of cattle two major problems arose. First, dung pads started to accumulate and even cover the ground and thereby ruining the pastures for cattle. Second, the numbers of flies breeding in cattle dung pads started to increase. Especially two pest species, the buffalo fly (*Haemotobia irritans*) and the bush fly (*Musca vetustissima*) became problematically abundant. In the years 1969–84 a team of CSIRO introduced 52 species of dung beetles to Australia from various parts of the world, mostly Europe and Africa (Tyndale–Biscoe 1996, 2001). By the year 1989 23 introduced species became well established (Ridsdill–Smith *et al.* 1989). At present, the benefits of the presence of dung beetles are noticeable. Dung beetle activity has not only slowed down the reproduction of flies (see also section on *Parasite suppression*), but also released the nutrients from the dung pads and returned them to the ground. Water penetrates more easily into the soil thus reducing run–off and increasing root penetration and soil aeration. Undeniably the introduction of dung beetles has increased pasture productivity in Australia (Borbemissza 1960), and similar results have been reported for other parts of the world as well (Edwards and Aschenborn 1978, Brussaard and Hijdra 1986, Rougon and Rougon 1983).

Parasite suppression. In addition to keeping the ground clean and taking part in the decomposition processes, dung beetles influence the abundance of many pathogens and pest flies. Bergstöm *et al.* (1976) have noted that dung beetles exert important control over the egg and larval populations of flies and parasitic nematodes (Ostertagia and *Trichostrongyl axei* worms) that are present in fresh dung of mammals. Numbers of trichostrongylid eggs decreased 24 to 90% in dung pads inhabited by dung beetles. In more natural habitats Bergström (1983) found that *Aphodius* beetles act as biological control agents of elk

lungworm, *Dictyocaulus hadweni*. In Australia several studies have been conducted on the benefits of dung beetle activity to livestock industry by reduction of gastrointestinal worms (Bryan 1973), reduction in fly numbers (Doupe 1986, Doupe *et al.* 1988, Tyndale–Biscoe and Hughes 1969, Ridsdill–Smith and Matthiesen 1988), and by increasing the live–weight and health of cattle in general (Tyndale–Biscoe 1996, 2001).

Seed dispersal and pollination. In tropical forests, several if not most tree species are adapted to animal (primate) dispersal of seeds (Howe and Smallwood 1982, Janson 1983). However, on the ground the seeds dispersed by primates are vulnerable to rodents, insects and fungi. In tropical areas, dung beetles are found to act as important secondary seed dispersers while moving and burying seeds in primate feces during their feeding and nesting activities (Shepherd and Chapman 1998, Andresen 1999, 2002, Feer 1999, Estrada and Coates–Estrada 1991). Shepherd and Chapman (1998), Andresen (1999, 2002) and Feer (1999) all found higher proportions of surviving seeds and seedling establishment when seeds were covered by feces and buried by dung beetles compared with clean seeds not attractive to dung beetles but attractive to rodents, other insects and fungi. In addition, dung beetles' body size distribution clearly affected the proportion of buried seeds, depending also the size and density of seeds. The authors concluded that by moving and burying seeds, dung beetles decrease seed aggregation, seed predation by rodents, and provide nutrition (nitrogen) for seeds and are therefore essential for forest regeneration.

Dung beetles act as pollinators of some orchids, though the only well–documented case study comes from Malaysia, where Sakai and Inoue (1999) found that dung beetles pollinated *Orchidanta* species (Lowiaceae). Dung beetles were attracted to the dung–like odour of the orchids, though the flower did not reward the pollinating beetle by nectar or by other nutrition.

How humans affect dung beetles — Good old times vs. the brave modern world

Agriculture. Human impact on the landscape through agriculture and domesticating mammals has been significant in Europe for thousands of years (Birks 1986 and references therein). Cattle dung is, and probably has been so for a long time, an important resource for the dung beetle fauna in Europe as cattle were domesticated in Europe ca 8,000 BP (Garner 1944, Hanski 1986). This is less so in North America, as the native Americans did not have domesticated animals expect the dog. The different histories of agriculture and patterns of deforestation are clearly seen in these two regions in terms of the numbers of dung beetle species inhabiting pasture ecosystems (high in Europe) and forests, where the beetles use the pellets of small mammals or wild ungulate dung (high in North America). Evidently the increase of large herbivorous mammals has increased the amount of resources for dung beetles and thereby enhanced dung beetle abundance and species richness in Europe. At present, on the other hand, the land use and agricultural practises are changing rapidly. The great intensification and modernisation of agriculture since the 20th century has changed the spatial pattern of dung availability, and drastic decrease in dung beetle diversity has occurred in Europe both locally and regionally (Lumaret 1990, Barbero *et al.* 1999, Roslin 1999, Lobo *et al.* 2001). In Finland, Roslin (1999) found that the spatial connectivity of farms correlated

significantly with dung beetle species richness, and the pasture specialist species were only found in the areas that were still located close by to other farms. Several dung beetle species that are pasture specialists and have limited dispersal capacity due to their small size have declined considerably following changes in agricultural practises, and some species have even gone extinct in Finland (Roslin 1999, Roslin and Heliövaara 2007, and references therein).

The impact of domesticated mammals on dung beetles is less studied in subtropical and tropical areas. For example in Africa and Asia, where native large herbivorous mammals still exist, the effect of cattle may be compensating for decreasing native ungulates. However, animal hunting in tropical forest areas has an indirect effect on dung beetle abundance, biomass, species richness, and species composition (see section on *Hunting*). These effects are not neutralised by the increase in cattle pastures as forest inhabiting species are not either able to inhabit open (dry and hot) areas or do not use ungulate dung as food resource (see section on *Habitat destruction and deforestation*). However, in Madagascar a few endemic and originally dry forest inhabiting dung beetle species have been able to expand their habitat use from forest to open areas, and their resource use from primate feces and carcasses to cattle dung, within the last 1,500 years (**IV**). Following the shift in resource use, these species have been able to expand their geographical ranges.

Habitat destruction and deforestation. There is a growing body of research on the effects of habitat destruction, namely deforestation and fragmentation, on tropical forest inhabiting dung beetles (Halffter and Arellano 2002, Andresen 2003, Feer and Hingrant 2004, Horgan 2007, Gardner *et al.* 2008, Vulinec *et al.* 2008). In their quantitative literature review and meta–analysis based on several tens of original research articles on global dung beetle responses to tropical forest modification and fragmentation, Nichols *et al.* (2007) concluded that tropical forest dung beetles respond strongly and negatively to increasing modification of forests and declining forest fragment size. Heavily modified habitats with little or no tree cover and fragmented forest areas had species–poor dung beetle communities with high rates of species turnover, dramatically altered abundance distributions and smaller overall body size in comparison with communities in intact forests. However, secondary and selectively logged forests had similar dung beetle communities than the intact forests.

In Madagascar, extensive deforestation may already have caused the extinction (or near extinction) of tens of endemic species. Madagascar has lost about half of its original forest cover since 1953, and today perhaps only 10% of the original forest cover remains. Hanski *et al.* (2007) compared species in the tribe Helictoleurina recorded from Madagascar before 1953 (museum samples in the Muséum National d'Histoire Naturelle, Paris) and today (Madagascar–wide sampling program, see Box 2). Large–scale sampling in 2002–06 yielded 29 of the 51 previously known species with locality data. The most significant factor explaining apparent extinctions was forest loss within the historical range of the focal species. The authors concluded that deforestation has already caused the extinction or effective extinction of large numbers of locally endemic insect species in Madagascar.

Alien species. No studies have been conducted on introduced dung beetle species affecting the native species, with the exception of *Digitonthophagus gazella* (Onthophagini, Scarabaeidae), an Afro–Eurasian species that is one of the most frequently introduced dung beetle species

worldwide. The species has become successfully established in Australia, North America, and Madagascar (Hanski and Camberfort 1991a, **IV**). In Madagascar, the effect of introduced *D. gazella* or introduced Aphodiidae species on native dung beetles (Scarabaeidea, Aphodiidae) seem to be non–existent or very limited (**IV**). However, Howden and Scholtz (1986) reported changes in the abundances of native species ten years after the introduction of *D. gazella* to Texas in 1972. The previously dominant *Onthophagus pennsylvanicus* (Onthophagini), as well as probably a few other species, appeared to have declined due to competition with *D. gazella*. In Australia, the 50 purposely imported species seem not to have had a large impact on the native species, as the former feed on cattle dung in pastures while the latter inhabit mainly forests (Matthews 1974). However, the previously introduced *Euoniticellus intermedius* (Oniticellini, Scarabaeidae) declined following the establishment of *D. gazella* (Doube *et al.* 1991).

Hunting. Large–bodied mammals and other game animals are declining in many parts of the world. From the dung beetle point of view the most important resource producers in the tropics, such as frugivorous primates and ungulates, are declining in Amazonian (Peres 2000, Peres and Palacios 2007), African (Fa *et al.* 2006), and Southeast Asia forests (Corlett 2007). At the same time, the relative or absolute abundances of small–bodied primates and ungulates are increasing (Peres and Dolman 2000, Jerozolimski and Peres 2003). The removal of large–bodied mammals and the proportional increase of small–bodied mammals in the regional species pool affect the dung beetle community in several ways, lowering the total amount of resources (by lowering total mammal biomass), by conversion of mammalian dung profile (by selective hunting), and by reducing the average dung pad size (Nichols *et al.* 2009). The reduced availability and density of high quality resources and increased spatial variance lowers the probability of encounter of the resources by dung beetles. The decrease in soft moist feces and increase in drier pelleted feces may lead to the extinction of dung beetles specializing on feces of hunted mammals, whereas generalists and species preferring the feces of non–hunted mammals can either stay the same, increase or decrease in abundance (Nichols *et al.* 2009). Reduction in the average dung pad size may drive large–bodied dung beetles to extinction. The key point here is that large bodied and specialist species suffer from hunting of large–bodied mammals.

However, only a few studies have been conducted on effect of mammal abundance and diversity on dung beetle community structure (Estrada *et al.* 1998, Estrada *et al.* 1999, Andresen and Laurance 2007, **V**). Some indirect evidence exists on the links between mammal and dung beetle species richness (Nichols *et al.* 2009). The relationship between the abundance, species composition and diversity of mammals and dung beetle diversity appears to explain the lack of large–bodied dung beetles and low species richness in local communities in Madagascar, where there are no native ungulates and the largest native herbivorous mammals are medium–sized primates, lemurs (**V**).

(see below) species (Dichotomiini, Coprini, Phaenini) that a large species (*Dichotomius*) out–competed smaller species, being able to pre–emptying resources and nesting sites and causing a reduction in population densities and species richness of the smaller species.

Dung beetles have evolved several ways to overcome competition by quickly removing and hiding a piece of dung (or other resource) from the potential competitors – including other beetles and flies – to a less crowded nesting place. These characteristics are likely to be primary factors in the evolution of the diverse morphology, behaviour and ecology of dung beetles (Philips *et al.* 2004). Dung beetles have been traditionally divided into three functional groups according to their mode of resource relocation: the rollers (teleocoprids), the tunnelers (paracoprids), and the dwellers (endocoprids) (Halffter and Matthews 1966, Hanski and Cambefort 1991a). The rollers, like the holy scarab, make balls of dung, which they roll away from the food source — and from the reach of other beetles and other dung or carrion inhabiting arthropods — before digging the ball in the soil and laying egg(s) into it. The tunnelers (including Geotrupidae) dig burrows and construct nest chambers right below the food source and push dung down into the tunnel. The dwellers (including Aphodiidae) construct their simple nests into the food source itself (typically a large dung pat of large herbivores) or lay eggs without nest construction. The larvae pupate either in the dropping or just below the dropping on the surface of the ground.

At present, the above classification is purely functional with limited phylogenetic significance due to polyphyletic origin of similar behavioural patterns (Phillips *et al.* 2004). For example, "true rolling" (ball pushed backwards by hind legs) is found within the monophyletic Scarabaeini (in part), Gymnopleurini, and Sisyphini, and in the polyphyletic Canthonini (in part, Phillips

et al. 2004). Several exceptions occur among the above rolling tribes. For instance, there are Scarabaeini species that hold dung or detritus between the hind legs and walk forward with the four remaining legs, while some species just push pieces of resource into their burrows (Sholtz 1989, Tribe 1976). Other Scarabaeini and American Canthonini have been observed to drag or carry dung held with their hind legs and moving backwards (Scarabaeini) or forwards (Canthonini; Halffter and Halffter 1989). Some Australian Canthonini hold food objects against their head with front legs, while walking backwards (Monteith and Storey 1981). Actually, rolling of pellets and other pieces of food has been observed among several other rolling and even tunnelling tribes (Phillips *et al.* 2004 and references therein; pers. obs). In summary, dung beetles are quite plastic in their ways of resource relocation and their morphology does not predispose them to a particular type of behaviour.

Dung beetles (excluding Aphodiidae) are considered as subsocial insects since all species show some level of bisexual cooperation in parental care (Halffter and Edmonds 1982). Dung beetles construct a nest for their young and provide food and parental care for the offspring (Halffter and Edmonds 1982, Hanski and Cambefort 1991a). Dung beetles invest little energy and time for precopulatory sexual behaviour but much for postcopulatory reproductive behaviour, nest construction and brood care. The basic pattern among rollers is that female and male meet at the food source, mate, reconstruct a ball, roll it away from the source, dig it in the ground, and construct a nest, after which the male departs. Mating may also take place underground. In tunnelers the pattern is largely the same, but the nest is constructed in a tunnel below the food source and pieces of food are dragged in the tunnel. The life–time number of offspring is remarkably small in many dung beetles, even down to three to four in some rolling taxa.

Low fecundity is evident in the reduction of the ovarioles just to a single one (Halffter and Matthews, 1966). Low life–time fecundity is associated with great longevity up to two years in some rolling taxa (**II**, Sato and Imamori 1986a, 1987, Edwars and Aschenborn 1988, 1989).

Madagascar. Madagascar has arguably the most unique large tropical biota due to its large size (587 000 km²) and ancient isolation (160 and 80 MY since the separation from the African continent and India, respectively; De Wit 2003). At present, Madagascar is separated by the 400 km wide Mozambique Channel from the African continent.

Due to the large size of the island and the mountain chain running for 1,300 km from south to north, the vegetation and climate vary greatly along the latitude and especially along the longitude. Remnants of the historically much more widespread tropical wet forests are located mainly on the eastern slopes of the main mountain chain (Fig. 1). Central Madagascar contains a mosaic of montane forest and savannah type vegetation, whereas west is covered by deciduous forest and southwest by shrub and sclerophyllous vegetation. The four vegetation zones are relatively uniform when it comes to mean precipitation, mean temperature, seasonality and topography, and the borders between zones are sharp lacking any long environmental gradients (Vences *et al.* 2009).

Madagascar is an island of remarkable faunal and floral diversity, where species–level endemism reaches 100% in many groups. Madagascar is exceptional for endemism at high taxonomic levels and for skewed representation of many taxa in comparison with continental faunas (Myers *et al.* 2000). For example, nearly half of the existing chameleon species in the world occur only in Madagascar. The insectivorous mammals include the endemic tenrecs and otter–shrews

Figure 1. The eastern wet forest belt in Madagascar. Black areas represent the mid– and high–elevation (700 to 2000 m asl) dense wet forests, while the lighter grey areas along the east coast represent a mosaic of degraded low elevation rain forest and (mostly) deforested areas that were previously forested. The scattered light grey on the western side of the island represents the dry forest areas embedded in open savannah type vegetation.

(Tenrecidae). Cats and dogs are absent, and the native carnivores are endemic civets. Ungulates that are dominant in the African continent are also completely lacking, excluding three extinct pygmy hippopotami (*Hippopotamus*). The largest native Malagasy herbivores, and the main dung producers for Malagasy dung beetles, are the endemic primates, lemurs (Lemuriformes). The ancestors of lemurs reached Madagascar 62 to 65 MY ago, had the main diversification approximately 30 MY ago, and the radiation of the extant genera occurred some 10 MY ago in the Miocene (Yoder *et al.* 1996, Yoder and Yang 2004), during the period when the modern dung beetle taxa are thought to have radiated (Cambefort 1991).

The extant >100 lemur species show extraordinary diversity of lifestyles, morphologies, and behaviours, but there are no large species (>7 kg). Before the arrival of humans about 2,000 years ago, there were at least 17 species of large–bodied lemurs, including *Archaeoindris* (160 kg) and *Babakotia* (20 kg), three species of hippopotami, the elephant bird (500 kg) and other related species, and giant tortoises, which all became exterminated in the next 1,000 to 1,500 years (the last hippopotamus was seen in the 1900s; Burney *et al.* 2004 and references therein). In the absence of natural enemies, the density of the megafauna was probably high, and they may have provided an important fraction of dung beetles' resource base. The domestic mammals were introduced while the native megafauna became exterminated; cattle was introduced about 1,000 yrs ago (Burney *et al.* 2004). At present, cattle are abundant and widespread, occurring mostly in central highlands and the deforested areas of the west but there are also feral cattle called "Baria" that occur in low densities in many wet forest areas. Nevertheless, the domestic mammals play a minor role, and probably a smaller role than humans themselves, as dung producers especially in eastern wet forests.

Unlike many other island biotas, the fauna of Madagascar has not (yet) suffered a major intrusion of species, accidentally or intentionally introduced by man. Apart from domesticated species, only seven non–endemic mammals occur in Madagascar: black rat (*Rattus rattus*), brown rat (*R. norvegicus*), house mouse (*Mus musculus*), two shrews (Soricidae), small Indian civet (*Viverricula indica*), and bush pig (*Potampchoerus larvatus*) (Garbutt 1999).

Malagasy dung beetles. In Madagascar, the dung beetle fauna consists mainly of the old Gondwanian tribe Canthonini and the endemic subtribe Helictopleurina (Oniticellini). The two genera of Helictopleurina, *Helictopleurus*

and monotypic *Heterosyphus*, have altogether 66 described species and subspecies, while Canthonini consists of 7 endemic genera and 191 described species (though taxonomy will change following ongoing taxonomic and molecular phylogenetic studies; O. Montreuil and H. Wirta, personal communications). The ancestors of the endemic taxa have reached the island overseas (Wirta *et al.* 2008 and in prep.). Helictopleurina is monophyletic and has radiated in parallel with lemurs, the largest herbivorous mammals in Madagascar, starting around 30 MY ago (Wirta *et al.* 2008). Helictopleurina are tunnelers and many species are entirely specialised on lemur feces (Wirta *et al.* 2008; **III**). Four species representing phylogenetically separate lineages and previously inhabiting the western dry forest areas have been able to switch to the new and abundant resource of cattle dung in the last 1,500 years (Wirta *et al.* 2008, Hanski *et al.* 2008, **IV**). Canthonini has colonised Madagascar at least three times, one clade (genera *Epilissus* and *Arachnodes*) earlier and two clades (*Epactoides* and *Nanos* plus *Apotolamprus*) later than Helictopleurina (Wirta *et al.* in prep.). Canthonini are rollers, mostly generalists, feeding on both lemur feces and carrion, but there are also several dung specialist species in the older lineages (Wirta and Monteruil 2008, Wirta *et al.* in prep., **III**). Although more specious than Helictopleurina, only four Canthonini (*Epilissus*) use cattle dung in open areas (Hanski *et al.* 2009, Wirta *et al.* in prep., **IV**). On the contrary to cattle dung–using Helictopleurina, these species are closely related.

In addition to Helictopleurina and Canthonini, there are records of three species of Scarabaeini (rollers), six species of Onthophagini (tunnelers; Paulian and Lebis 1960), and 30 species of Aphodiini and Didactyliini (dwellers; Aphodiidae, Bordat *et al.* 1990) in Madagascar, representing both endemic and introduced species.

Aims of this thesis. Table 1 summarises Madagascar and its dung beetle fauna as a model system to study community ecology in terms of community structure and species distributional patterns at several spatial scales. The Malagasy dung beetle fauna is largely made up of the two ecologically dissimilar and specious groups, which have originated and radiated on the island within the last tens of millions of years, in a situation, where the largest native herbivorous mammals are endemic primates. From the perspective of dung beetles, this is a major limitation, as many groups of dung beetles have evolved to use the dung of the largest herbivorous mammals, and especially that of ungulates (Artiodactyla, Perissodactyla, and Proboscidea), in mainland Africa (Cambefort 1991). The Malagasy dung beetles have evolved and currently occur in a situation with an unusually limited range of resources for dung beetles.

In this thesis, I study the taxonomy, population biology, community ecology and distributional ecology of endemic and introduced dung beetles in Madagascar. I address such questions as how the apparently ecologically similar and closely related species share their resources in local communities, and whether the limited range of resources, and especially the lack of large herbivorous

Table 1. Madagascar and dung beetles as a model system to study evolutionary diversification and community ecology of strongly competing species.

	Trait	Benefits as a model system
Madagascar	Large island	Heterogeneous environment
	Isolated for tens of million years	A nearly closed system for tens of MY
	North-South oriented mountain chain	Four uniform vegetation belts with sharp boundaries
	High endemicity at high taxonomic levels	Species (taxa) originated and speciated on the island
	High species richness	Much material, parallel evolution and species groups
	Skewed representation of taxa compared to continents	Simple communities, empty niches, new life styles
	Human arrived around 1,500 YA	Human/alien species impact on natural systems recent
	French colony 1896-1960	Museum records on many taxa
	The hottest biodiversity hotspot in the world	Need for studies
Dung beetles	Resources patchy and ephemeral	Highly competitive communities
	Easy to trap	Possible to sample large areas in short time
	(with) baited pitfall traps	Habitat requirements, diel activity, seasonality and resource use relatively easy to detect
	Moderate species number	Identification of large samples feasible
Malagasy dung beetles	Several specious radiations that differ in their ecology	Species (taxa) originated and speciated on the island, much material for evolutionary and ecological studies
	Canthonini among the least developed rollers	Light in the evolution of the nesting and breeding behaviour of rolling dung beetles
	Few introduced species restricted to cattle dung inhabiting open areas	No impact on natural communities (IV)

mammals and their dung, affects species richness locally or regionally (**III, V**). I study the role of the new but presently abundant resource of cattle dung as a potential resource for endemic species (**IV**). At the same time, I document the distributional ranges of the introduced species and their potential effect on native species (**IV**). I compare the community structure and distributional ranges of species inhabiting wet forests with those in open areas (**IV**). I have studied in greater detail the taxonomy, ecology and life histories of a monophyletic clade within the genus *Nanos* (Canthonini), which are representatives of probably the most primitive taxa among the roller dung beetles (**I, II**). Finally, I compare my results on Malagasy species and communities with the results of comparable studies conducted outside Madagascar (**II, III, IV, V**).

2 Madagascar dung beetle project— How to collect data fast and furiously?

The University of Helsinki has provided funding for a new research station in the Ranomafana National Park in eastern Madagascar. Professor Ilkka Hanski initiated a research project on Malagasy dung beetles in Ranomafana in 2002. From this year onwards, the project has expanded to cover the entire island of Madagascar (Box 2). The aims of the entire project have been (1) to reconstruct a molecular phylogeny of Malagasy Canthonini and Helictopleurina, (2) to obtain a record of the geographical ranges of the species across Madagascar, and (3) to investigate the ecology of particular species and local communities. My thesis work has contributed to this third aim of the Malagasy dung beetle project.

Material for molecular phylogenies and data on species habitat requirements, ecology, and distributional ranges have been collected by researchers and students in the Metapopulation Research Group, University of Helsinki, and by both Malagasy and foreign collaborators and students in several national park across Madagascar (Madagascar–wide sampling program). More intensive sampling of several local communities has been conducted in the course of the present thesis project and by others. Finally, information has been obtained from the extensive collections in the Muséum National d'Histoire Naturelle, Paris (Box 2).

In the next section I describe in more detail the material and methods used in this thesis work, which partly overlaps with the methods described above and in Box 2.

3 Material and Methods — Hole in thousand

Revision of the genus *Nanos*. To sort out the taxonomy of the genus *Nanos,* all material including genera *Apotolamprus*, *Arachnodes* (in part), *Cambefortantus*, *Nanos*, and *Sphaerocanthon* in the Muséum National d'Histoire Naturelle in Paris was examined (see also Box 2). Preliminary examination had indicated that these genera contained a large fraction of misidentified specimens and poorly defined species. The traits that were supposed to be diagnostic for the genera according to the original descriptions were examined carefully in the type specimens. Material collected by previous investigators was examined and the identifications were checked to obtain true distributional records for the species.

Mating and breeding behaviour of *Nanos viettei* and its relatives. Distributional data for the species were obtained from the results of the Madagascar–wide sampling and the collections in the Muséum National d'Histoire Naturelle, Paris. Molecular phylogeny for the species has been published by Wirta (2009). Data on species' resource use, diel activity,

Box 2. Madagascar dung beetle project — Still going strong!

Madagascar–Wide Sampling Program. In the years 2002 until 2007, 60 local communities in the eastern wet forests and western dry forest regions have been sampled, as well as 73 cattle pastures in central highlands and six clusters of pastures in the eastern side of the wet forest belt (Fig. 1). Cattle dung pastures were sampled by sorting beetles from dung pads by hand. Forest localities have been trapped during the rainy season (November to March) when dung beetles are most active. Trapping has been conducted with 40 carrion–baited (fish or chicken intestine) pitfall traps (plastic cups, 1.5 dl) over which a plastic cover or a large leaf was placed to prevent rain water entering the trap. Traps were filled up to one third of their volume with water containing soap to decrease water tension. A bait of approximately 3 cm³ was wrapped in gauze and the bundle was hanged from a stick above the trap. Traps were left in the forest for two days and nights, and samples were preserved in 90% ethanol for identification and counting.

Intensive sampling of 10 local wet forest communities. Local communities (from North to South) in Marojejy National Park, Anjanaharibe Sud NP, Makira, Masoala NP, Nosy Mangabe NP, Andasibe NP, Ambila–Lemaintso, Ranomafana NP, Manombo NP and Andohahelo NP have been trapped more intensively with traps baited with carrion and human or primate feces. In five communities trapping has been conducted at different altitudes. In three communities traps were set hanging from branches at 2 m above the ground level. Diel activity and seasonality have been studied in the Ranomafana NP.

Collections in the Muséum National d'Histoire Naturelle and identification of species. Most (95%) of the Malagasy dung beetle specimens that have been collected in the course of entomological studies are located in the Muséum National d'Histoire Naturelle (Paris). Canthonini and Helictopleurina that have been collected during the Madagascar–wide sampling program (above) were identified by Helena Wirta, Olivier Montreuil, and by myself based on comparisons with type specimens and series in the museum. New species have been described and several revisions on taxa have been completed by Montreuil (2003a,b, 2004, 2005a,b,c,d, 2006, 2007, 2008ab), Wirta and Montreuil (2008), and **I**. The type specimens are located in the Muséum National d'Histoire Naturelle, Paris. Aphodiidae were identified and new species described by Jason F. Mate from the British Museum of Natural History, London (Mate 2007) and by Patrice Bordat from the Muséum National d'Histoire Naturelle, Paris. The type specimens of the newly described species are located in the British Museum of Natural History, London, the Muséum National d'Histoire Naturelle, Paris, and the University of Antananarivo, Madagascar.

and elevational ranges were obtained by intensively sampling local communities in the Ranomafana NP (below) and in the Masoala NP. Seasonality of the focal species, *N. viettei*, was assessed by year–round trappings in the Ranomafana NP (below). Individuals were dissected under a microscope to characterize their maturity and the breeding status of females. Mating and breeding behaviour, including possible interspecific mating of selected closely related species, were studied in the laboratory in the Ranomafana NP during the rainy season (November to February), which is also the breeding season. Individuals of related species were collected for the experiments in the Masoala NP, Makira, the Andasibe NP, and Ambila–Lemaintso. Mobility and longevity of *N. viettei* were studied with the mark–release–recapture method during three years in the Ranomafana NP.

Studies on the ecology of individual species in the Ranomafana NP in 2003–2006. The Ranomafana NP is located in southeastern Madagascar. It covers 43,500 ha of relatively undisturbed rainforest ranging from 400 to 1,400 m asl. The climate is tropical (Moat and Smith 2007). The area is inhabited by 12 species of lemurs with diverse diets, body sizes and social population structures habits (Garbutt 1999, Tan 1999).

Beetles were trapped with baited pitfall traps (Box 2). Several different bait types (fish, chicken intestine, human feces, feces of seven lemur species (Table 2), cattle dung, pig dung, rotten fruit and dead millipedes) were used to study resource use (diet) in the Talatakely forest area (930 m asl) during the rainy season when beetles are most active. Diel activity was studied in the Talatakely and Vatoharana (1,000 m asl) areas in 2003, 2004 and 2006. In 2003 and 2004, traps were checked at 00, 04, 06, 10, 14, 17, 19, and 21 hours (total trapping effort 12 days, 30 traps), while in 2006 the traps were emptied at 05 and 17 hours (total trapping effort 14 days, 40 traps). Tree–traps were set 2 m and 15 m above the ground level to trap beetles living in the canopy. Seasonality, spatial distribution, and elevational ranges of the species were studied by conducting trappings year round in 22 different location in the Ranomafana NP ranging from 726 to 1,200 m asl.

The pooled material from the Ranomafana NP consists of 36 species (including 3 endemic Aphodiidae), 16,466 individuals (including 7,397 Aphodiidae), and 4,806 trap–nights. Comparable data from the community in the Masoala NP includes 31 species, 2403 individuals and 1,601 trap–nights.

Species using cattle dung in open habitats. Distributional data were obtained from the

Table 2. The seven lemur species that are the main dung producers in the Ranomafana NP (summarised from Garbutt 1999 and Tan 1999).

Species	Diet	Body weight (g)	Group size	Home range (ha)	Diel activity
Microcebus rufus	omnivory	40-45	1 -	1	nocturnal
Eulemur rufus	frugivory	2000-2750	8-10	100	diurnal
E. rubriventer	frugivory	1600-2400	2-6	19-40	diurnal
Hapalemur aureus	bamboo	1500-1650	2-6	26	diurnal
H. griseus	bamboo	750-900	3-6	15	diurnal
Prolemur simus	bamboo	2200-2500	4-7	62	diurnal
Propithecus edwardsi	vegetarian	5000-6500	3-9	100-250	diurnal

Madagascar–wide sampling of cattle dung in open areas. In addition, in the Ranomafana NP cattle dung–baited pitfalls were set inside the forest for comparison. Additional data come from the literature (Bordat *et al.* 1990). Kruskal's non–metric multidimensional scaling was used to characterise species composition across Madagascar with cattle density, altitude, latitude, and longitude as explanatory variables.

Species richness of mammals and dung beetles in tropical forests. Dung beetle species richness and body–size data were collated for 12 well–studied local communities of dung beetles in wet forests in Neotropics, Afrotropics and the Oriental region. The Malagasy communities in this comparison are the well–studied local communities in the Ranomafana NP and the Masoala NP. Data on the regional mammal faunas were obtained from the IUCN (2008) web site, and the weights of the mammals from the web site of the University of Michigan Museum of Zoology. I used regression analyses to study the effects of sampling effort, elevation and species richness of mammals on dung beetle species richness and on the number of large–bodied (> 15 mm) dung beetle species. For each region, beta diversity was calculated as the similarity in the species composition in local communities, and this was regressed against the distance between the communities.

4 Results and Discussion – Peculiar dung beetle communities in Madagascar

Species richness, new species to science, and need for further revisions. By the year 2008 tens of thousands of individuals belonging to 152 and 12 species of Scarabaeidae and Aphodiidae, respectively, have been sampled in the Madagascar dung beetle project,

including 38 and 2 species new to science. The species number is 61 and 40% of the currently recognized species of Scarabaeidae and Aphodiidae in Madagascar, respectively, and indicates how thorough the sampling has been. While identifying specimens, collecting information from museum collections, and reconstructing distributional maps for the species, it soon became evident that major revisions of most taxa were needed.

I have included in this thesis a revision of the genus *Nanos* (**I**), which exemplifies well the kind of revisions that are needed. In the revision, the genera *Nanos* and *Sphaerocanthon* are synonymised as the character originally distinguishing the genera was found to be size–dependent. New combinations and synonymies are established, and five species, originally considered *Nanos* due to their small size, are transferred to *Apotolamprus* and *Cambefortantus*. In addition, two new species sampled during the Madagascar–wide sampling program, *Nanos hanskii* and *N. manomboensis*, are described. A year before, Montreuil (2006) transferred three small *Arachnodes* species to *Nanos*. At present, it seems that *Apotolamprus* is a monophyletic clade within paraphyletic *Nanos* (Wirta *et al.* in prep.).

Several revisions of Malagasy dung beetles have been completed (Box 2), but much remains to be done. The taxonomy of Canthonini has been especially confused, but even in the better known Helictopleurina the status of several species is questionable (O. Montreuil, pers. comm.).

Peculiar life history of *Nanos viettei* (Canthonini). The life history of *Nanos viettei* differs in many respects from the known life histories among Scarabaeidae dung beetles (**II**). *Nanos viettei* reproduces during the rainy season in January and February, but produces only one or two offspring. The extremely low fecundity is accompanied by a great longevity.

The larval and pupal periods are short and immature adults are inactive in underground for six months. The maturing adults emerge in September to November and start a feeding phase that lasts for a few months, until they are ready to start breeding. Thus beetles do not start to reproduce until they are one year old, which is atypical among dung beetles and in Canthonini in particular, which typically live for a few months only (Favila 1993, Cambefort and Hanski 1991). In the mark–release–recapture studies the lifespan of the species was found to be at least up to two years, since individuals marked and released in the pervious rainy season were trapped again 12 months later. Exceptionally low fecundity during the breeding season must be accompanied with long lifespan, otherwise the species could not have viable populations.

Exceptionally long lifespan has been reported for several Malagasy mammals as an evolutionary outcome of reduced juvenile survival due to environmental variability and unpredictability (Richard *et al.* 2002). However, among dung beetles the long maturation period and lifespan are likely to be due to resource limitation during the colder and dried months, when several mammalian species are either inactive or their population sizes are low.

Another atypical feature for a dung beetle revealed by the mark–release–recapture studies was the very limited mobility of *Nanos viettei*; dung beetles are generally considered to be very mobile and strong fliers (but see Roslin 1999). The recaptured individuals marked in the previous year were found within only some tens of meters of the original release site (though some beetles may have moved beyond the limits of the study area during the year). In the same experiment, two individuals of another Canthonini, *Epilissus delphinensis*, were also trapped 12 months after their release, suggesting that long lifespan and low mobility may characterize Malagasy

Canthonini in general. These species belong to different evolutionary clades that have reached Madagascar at different times, 24–15 Mya (*Nanos*) and 64–44 Mya (*Epilissus*) (Wirta *et al.* in prep.).

Mating and breeding behaviour of *N. viettei* differs from the behaviours described for the rolling species of dung beetles as summarised by Halffter and Edmonds (1982). *Nanos viettei* does not exhibit sexual cooperation in nest construction and copulation seems to be forced by a male. Both sexes mate with multiple partners. Copulation is followed by a male guarding the female by hanging on her back, a behaviour that has never been observed for any other dung beetle before, though such guarding behaviour is common in many other insects (Rowe 1994, Vitta and Lorenzo 2009). In addition, in *N. viettei* the female is the active sex in nest construction.

Ecologically similar species of *Nanos*. Regardless of the extremely low fecundity, *Nanos viettei* and the related species of *Nanos* are generally the most abundant dung beetle species in local communities across Madagascar (**II, III**). The sizes of the geographical ranges of the species vary from very small in the microendemic species to several hundreds of kilometres in the eastern wet forest belt in Madagascar (**II, III**). The most striking feature in the distributional ecology of the species in the monophyletic *viettei*–group, including *Nanos viettei* and its close relatives, is that, as a rule, the species do not co–occur in the same communities (**II, III**). If two or more species are present in the same region, they show striking differences in their elevational distributions (**II, III**).

I conducted experiments on interspecific matings with species belonging to the *viettei*–group. These experiments revealed that heterospecific matings are very common, though generally the frequency of conspecific

matings was higher (**II**).Heterospecific matings also lasted for shorter time on average than conspecific matings, and were more often interrupted soon after the start of the copulation than conspecific matings. In general, species with very slight or completely lacking sexual dimorphism like the species in the *viettei*–group (Fig. 2) use chemical signalling for sex discrimination (Ortiz–Domínguez *et al.* 2005). This was observed in the present experiment, as males inspected a potential mate by stroking it with his antennae, and in case of a female, rushed to mate. Chemical signalling could also explain some of the differences found in the frequency of heteropecific matings and the duration of mating between different species. The frequency of heterospecific matings and the duration of these matings were lower and shorter between species co–occurring in the same region with different elevational distributions, suggesting selection for mate recognition in such essentially parapatric situations (**II**).

Similar community structure and patterns of resource partitioning in two local communities in the eastern wet forest region. The two best–studied wet forest communities of dung beetles in Madagascar, in the Ranomafana NP in southeast and in the Masoala NP in northeast, have strikingly similar species richness, 33 and 31 species, respectively. The species compositions in the communities are similar in terms of taxonomy (number of species in each genus) and resource use (high proportion of generalists, and similar ratios of generalists/specialists in Helictopleurina and Canthonini). The abundance distributions too are similar, with a few extremely abundant species and a tail of rare species, and so are the body size distributions (Fig. 3, **III**). However, only four of the 60 species in the pooled sample are found in both communities (**III, V**), under-
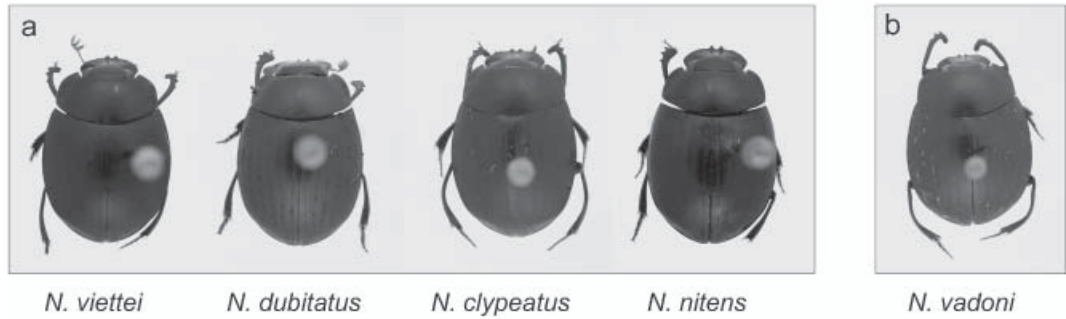
scoring the small geographical ranges in most species. The only clear difference between the two communities is the lack of small–bodied dung specialist Helictopleurina (Fig. 3) and Aphodiidae in the sample from the Masoala NP.

Based on the intensive 24–hr trappings conducted in the Ranomafana NP, the Malagasy Scarabaeidae community is clearly divided into diurnal and nocturnal sets of species that almost completely agree with taxonomy: Helictopleurina are diurnal and Canthonini are nocturnal. The few exceptions include *Epactoides frontalis* (Canthonini), which was most common from 06 to 10 am, and *Epilissus delphinensis* (Canthonini), which was active throughout the day and night. There are no strictly crepuscular species, only *Pseudarachnodes hanskii* (lemur dung specialist) was more abundant during dusk (7.7 individuals / hour) than night (2.3). In contrast to Scarabaeidae, there is clear differentiation of diel activity among the three endemic Aphodiidae (below).
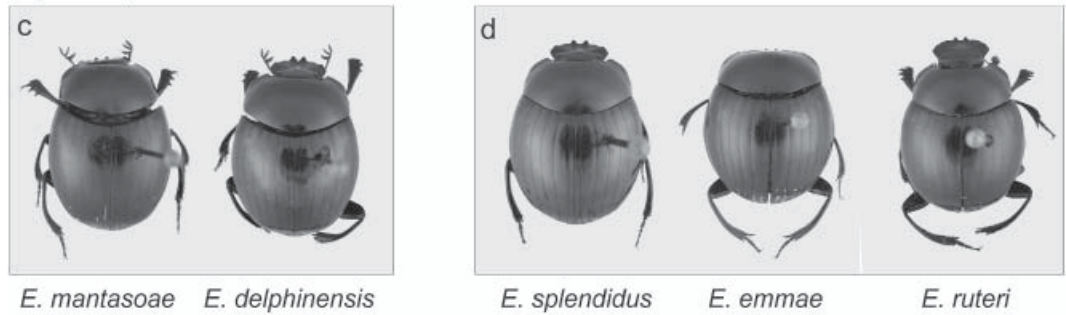
Diel activity of dung beetles has been associated with taxon, diet, color, body size, and functional group (Vulinec 2002, Krell–Westerwalbesloh *et al.* 2004, Feer and Pincebourde 2005), though the associations are often weak. In Malagasy dung beetles, diel activity is associated simultaneously with taxon, diet, and functional group (rollers versus tunnelers; Hanski and Cambefort 1991). Species' diel activity is most strongly related to resource use, as the more coprophagous Helictopleurina as well as the small Aphodiidae, and at least one of the two dung specialist Canthonini (*Pseudarachnodes hanskii*), are active during the day or at dawn and dusk, as are the largest lemur species, the most significant dung producers. Availability of fresh feces of diurnal mammals is not so important for Canthonini because of their broad diet.

The restricted diel activity of the two Aphodiidae at dawn and especially at dusk
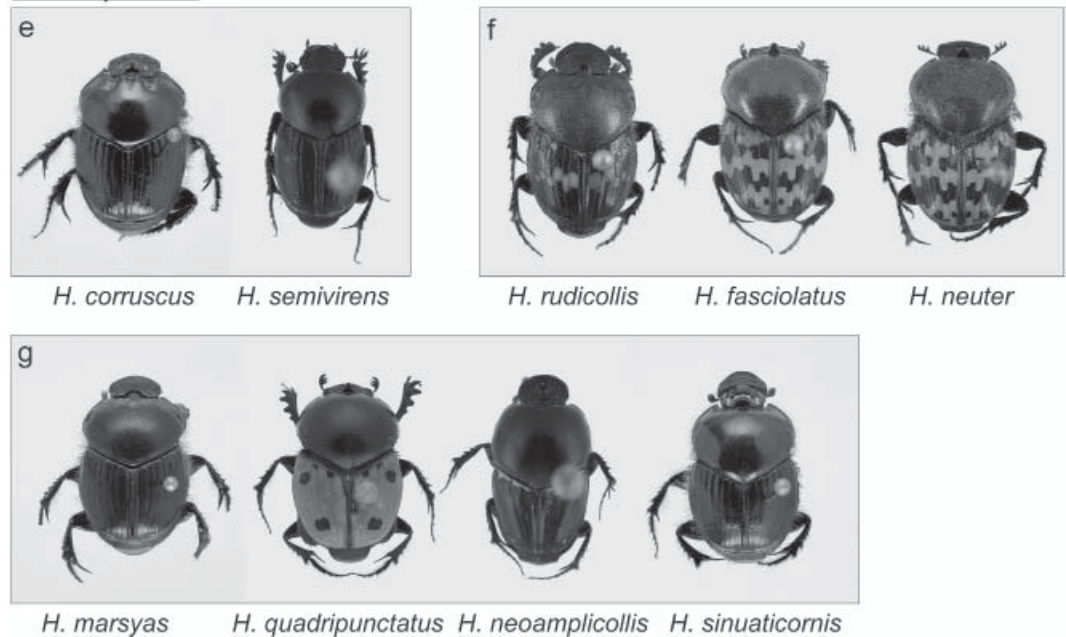
Nanos

N. viettei   N. dubitatus   N. clypeatus   N. nitens   N. vadoni

Epilissus

E. mantasoae   E. delphinensis   E. splendidus   E. emmae   E. ruteri

Helictopleurus

H. corruscus   H. semivirens   H. rudicollis   H. fasciolatus   H. neuter

H. marsyas   H. quadripunctatus   H. neoamplicollis   H. sinuaticornis

Figure 2. Malagasy dung beetles. Four of the six *Nanos* species in the *viettei*–group (a) and a representative of a closely related clade (b) (**I, II**); large bodied *Epilissus* species that occur in different elevation in the Ranomafana NP (c) and in the Masoala NP (d) (**III**); forest–inhabiting dung specialist (e) and generalist (f) *Helictopleurus* species, and four cattle dung specialist *Helictopleurus* that occur in open areas in Madagascar (g) (**III, IV**).

23

hours is probably related to their small body size, coprophagous feeding habits, and low ranking in competition against Canthonini and Helictopleurina. *Aphodius* sg. *Neoemadiellus humerosanquineum*, which is active at the same time as Helictopleurina, has a wider diet including both dung and carrion, although the species clearly prefers the feces of the largest lemur as do several Helictopleurina species. Though Aphodiidae are especially prevalent in temperate regions, they are also firmly established in the tropics (Cambefort 1991). Nonetheless, possibly because of competition with coprophagous Scarabaeidae, Aphodiidae have not been able to diversify in the tropics to the extent they have done in the temperate zone of the northern hemisphere. This is consistent with only three endemic Aphodiidae species in the Ranomafana NP and none at all in the Masoala NP. However, the lack of Aphodiidae in the sample from the Masoala NP may be due to a lack of appropriate bait type for Aphodiidae at higher elevation trappings in the Masoala NP. Two endemic species, *Aphodius (N) unctus* and *A. (N) perinetensis,* have been sampled above 600 m asl from the Marojejy NP in northeast Madagascar with human feces–baited traps. These species are likely to occur also in the Masoala NP (Bordat 1990, Mate 2006).

Several closely related species pairs exhibit clear elevational differences both in the

Figure 3. Schematic representation of the body sizes of Helictopleurina (A and B) and Canthonini (C and D) in the Ranomafana NP (A and C) and in the Masoala NP (B and D).

Ranomafana NP and in the Masoala NP. In the Ranomafana NP, where the trappings were conducted from 730 to 1,200 m als, two small bodied and two large bodied pairs of *Epilissus* (Canthonini) have overlapping distributions from 850 to 1,000 meters, with one of the species in these pairs occurring exclusively below and the other one exclusively above these altitudes. Similarly, two very similar *Apotolamprus* species (Canthonini) do not occur in the same elevations, but one occurs below and the other one above 800 m asl. In the Masoala NP, where trappings were conducted from sea level to 1,100 m als, three large bodied *Epilissus* have the following elevational ranges: the first one is found from the sea level to 900 m asl, the second one from 250 to 600 m asl, and the third species occurs solely above 900 m. There is thus clear differentiation in terms of elevational occurrence, though the first two species overlap. A similar pattern was found among the three most abundant *Nanos* species (Canthonini) in this community. One species occurs from the sea level to 900 m asl, the second one from 400 to 900 m, and the third one exclusively above 900 m asl.

Comparing the results for the elevations that were studied in the two communities, similar patterns are evident. First, among *Epilissus* the elevations where turnover in the species composition occurs are from 850 to 1,000 m and at 900 m asl in the Ranomafana NP and in the Masoala NP, respectively. The elevational range of one of the three large bodied *Epilissus* species in the Masoala NP does not reach the elevational range studied in the Ranomafana NP. However, there is a third species of large bodied *Epilissus* in the Ranomafana NP, *E. emmae obscuripennis*, which has been caught from 726 m asl in Mangevo, which is located in the southern tip of the Ranomafana NP. Second, the elevations for species turnover in *Apotolamprus* species in the Ranomafana NP and *Nanos* species in the Masoala NP are very similar at 800 m and 900

m asl, respectively. Recall that *Apotolamprus* is a monophyletic clade within paraphyletic *Nanos* (Wirta *et al.* in prep.). A randomisation test of the apparent elevational divergence of closely related species (**III**) suggested that the observed patterns are not due to chance but more likely due to an evolutionary divergence of ecological very similar and potentially competing species along an environmental gradient. On the other hand, not all closely related pairs of species or groups of species show such differentiation in their elevational occurrences. Several pairs of species are different in their diel activity, diet, or body size (**III**). In the Ranoamafana NP, the four most abundant *Helictopleurus* species do not show differentiation in their elevational occurrences but do show clear differences in body size and resource use: one small and one large species are generalists and one small and one large species are specialised to use primate dung (**III**).

Local endemics and high regional species turnover. As mentioned previously, among the *Nanos* species, the geographical ranges vary from local endemicity (species have been recorded from a single locality only) to ranges that extend several hundreds of kilometres along the eastern wet forest belt or the western dry forest area. As many as 27% of the *Nanos* species are known from a single locality only, and 39 and 54% of the species have documented ranges less than 50 and 250 km, respectively (**II**). Similar narrow geographical ranges are apparent also among other endemic forest–inhabiting species in Madagascar (Wirta *et al.* 2008, **IV, V**). To put it the other way round, in Madagascar forest communities that are located a few hundred kilometres apart do not share very many species (**III, V**). In the case of dung beetles, only four species out of the pooled number of 60 species occur both in the Ranomafana NP and in the Masoala NP with a distance of 600 km. Thus the often low local species

richness in Madagascar is compatible with very high total species richness because of the high species turnover (beta diversity) between regional communities. A similar pattern is evident among other Malagasy taxa, including lemurs (Wilmé 2006).

Dung beetle communities in forests and in open habitats. Altogether 28 dung beetle species are known to use cattle dung in Madagascar. Three species (one Helictopleurina and two endemic Aphodiidae) inhabit wet forests, but they are not cattle dung specialists. Most species using cattle dung are however specialists that occur in open habitats. These species include all introduced Onthophagini (Scarabaeidae) and Aphodiidae, but also some endemic Canthonini, Helictoplaurina and Scarabaeini (Scarabaeidae) and a few endemic Aphodiidae (most of the endemic Aphodiidae inhabit the eastern wet forests). Most of the endemic species using cattle dung occur also in the western dry forests, where they have been sampled with carrion–baited traps though in much smaller numbers than in open habitats. Four Helictopleurina species can be considered to be true cattle dung specialists, since they are not only much more abundant in open areas than in dry forests, which is most likely their original habitat, but they are very abundant across all of Madagascar. Such large ranges in the cattle dung specialising species represent a striking contrast to the narrow ranges of the closely related species living in wet forests (Wirta *et al.* 2008, **IV**). Interestingly, the four cattle dung using *Helictopleurus* species are not closely related to each other (Wirta *et al.* 2008).

In summary, there are around 250 and 30 dung beetle species inhabiting forests and open habitats in Madagascar, respectively. Forests are inhabited only by endemic species, whereas cattle dung communities in open habitats are dominated by the introduced species (Wirta *et al.* 2008, **IV**). A handful of endemic species have been able to switch their

habitat and resource from dry forests, carrion and lemur feces to open areas and ungulate dung within the last 1,500 years, since the introduction of cattle to Madagascar (Burney 2004, Wirta *et al.* 2008, **IV**). For the past 1,000 years, the area of open habitats has been expanding, whereas the area of forests has been shrinking and becoming fragmented due to human impact. The range and availability of dung beetle resources in forests are limited, most likely leading to severe resource competition, whereas the new resource of cattle dung is very abundant and is not often used so intensively by dung beetles that competition would be severe.

It is striking that only a handful of species use cattle dung in Madagascar, whereas hundreds of species use the same resource in comparable habitats in mainland Africa (**IV**). 1,500 years is a short time for species to be accidentally introduced to Madagascar across the 400 km wide Mozambique Channel, and apparently also short for many endemic species to adapt to use the new resource and new environmental conditions. The endemic species that have managed to shift to cattle dung in open areas have probably been at least to some extent "pre–adapted", by having use a wise range of resources in semi–open dry forests. The high species richness in wet forests reflects the very long evolutionary history over several tens of millions of years. Total diversity is elevated by small ranges of most species. At least in some taxa, such as *Nanos*, speciation has occurred in allopatry and closely related species are now in secondary contact. But the species may be ecologically too similar to coexist or they may still hybridize preventing species from expanding their ranges. All these processes contribute to the high total species richness in forests.

Malagasy dung beetle communities compared with communities elsewhere in the tropics. The local dung beetles communities in wet forests in Madagascar differ in many ways from those in other comparable tropical areas. First, species richness of the best studied communities in the Ranomafana NP and the Masoala NP is only 36 and 31 species, respectively, which is much less than in comparable communities in Neotropics, Afrotropics and in the Oriental region, where communities usually have more than 50 species and up to 90 species co–occurring locally (**III, V**). Second, Malagasy species are small in general, and small bodied species dominate local communities both in terms of numbers of individuals and total biomass, whereas medium–sized and especially large species are abundant in the other tropical areas (**V**). Third, a higher proportion of the Malagasy species are diet generalists (up to 70%) than in the other tropical communities (around 30%) (**III**). Fourth, patterns of diel activity in Madagascar are different from that elsewhere. In previous studies on diel activity patterns in tropical forest dung beetles, species have been divided into nocturnal, diurnal and crepuscular guilds of species (Andresen 2002, Feer and Pincebourde 2005), though many species have even more restricted periods of activity (Hanski 1983). Typically, and in contrast to the situation in Madagascar, there is variation in diel activity among genera in the same tribe as well as among species within genera. For instance, in the large genus *Onthophagus*, which are closely related to Helictopleurina (Wirta *et al.* 2008), there are both strictly nocturnal and strictly diurnal species in e.g. Sarawak in South–East Asia (Hanski 1983). In Madagascar, however, the vast majority of species in the tribe Canthonini are nocturnal while species in Helictopleurina are diurnal. Finally, species turnover between regional communities is higher in Madagascar than in the other tropical areas (**V**). In general, the similarity of the species composition of communities is directly related to the distance between the communities. However, the Malagasy data points lie clearly below a

common regression line for all tropical data, indicated clearly lower similarity in the species composition for a given distance separating the communities (**V**).

Low species richness in local communities, numerical dominance by small bodied species, and broad diet of most species can be explained by a smaller range of resources in Madagascar than elsewhere. Particularly the lack of large herbivorous mammals (ungulates) is significant for dung beetles (the largest extant lemurs weigh 7 kg). Furthermore, the pooled density and biomass of the most important dung producers is low. For instance, the five common diurnal lemur species in the well–studied Vatoharana primary forest area in the Ranomafana NP have the total density and biomass of 34 individuals and 107 kg per km², respectively (Johnson *et al.* 2003).

Large dung beetle species are known to prefer or may be entirely dependent on the large dung pads of large herbivorous mammals (Peck and Howden 1984), which could explain the lack of (extant) large–bodied dung beetles in Madagascar. In fact, the number of large–bodied (> 10 kg) mammals and the number of ungulates (Artiodactyla and Perissodactyla) explain well species richness of dung beetles and the numbers of large–bodied species in particular in tropical dung beetle communities (**V**). Apparently the small–bodied lemur species and the other small–bodied mammals in Madagascar cannot support equally specious local communities of dung beetles than the diverse mammalian assemblages of Neotropics, Afrotropics and the Oriental region.

5 Conclusions

In conclusion, there are substantial differences in dung beetle communities in Madagascar and in other tropical forest regions in terms of the life histories of the species (chapter **II**), local and regional species diversity (**III, IV, V**), and the sizes of species' geographical ranges (**III, IV**) . These differences are attributed to Madagascar's ancient isolation, large size, heterogeneous environment, skewed representation of the mammalian fauna, and recent though currently great human impact.

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